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Effects of Chlorocholine Chloride on Phytohormones and Photosynthetic Characteristics in Potato (*Solanum tuberosum* L.)

Huiqun Wang · Langtao Xiao

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Abstract Effects of chlorocholine chloride (CCC) on phytohormones and photosynthetic characteristics of Zhongshu 3, a potato (*Solanum tuberosum* L.) variety widely cultivated in south China, were studied by foliar CCC application on 24 and 28 days after emergence, that is, at the tuber initiation stage. It was found that on 42 days after emergence, that is, at the tuber bulking stage, spraying CCC increased indolacetic-3-acid (IAA) and zeatin (Z) contents but decreased abscisic acid (ABA) content in leaves. The content ratios of IAA/Z, IAA/ABA, Z/ABA, and (IAA + Z)/ABA in leaves treated with CCC were higher than those of the control. CCC plays a prominent regulating role in the photosynthesis of Zhongshu 3. The net photosynthetic rate (P_n), stomatal conductance (G_s), intercellular CO_2 concentration (C_i), and transpiration rate (T_r) of treated leaves were superior to those of controls at the tuber bulking stage. CCC markedly increased tuber yield and quality. The contents of sucrose and starch in tubers treated with CCC increased at the end of the vegetation period, whereas the contents of reducing sugars and solanine decreased. CCC at 2.0 g L^{-1} was found to be the most effective concentration. Collectively, the results of this research identify phytohomonal metabolism and photosynthetic physiology of potato leaves as processes affected early after application of CCC resulting in significantly improved increases in tuber yield and quality.

H. Wang · L. Xiao (✉)
Hunan Provincial Key Laboratory of Phytohormones and Growth Development, College of Bioscience and Biotechnology, Hunan Agricultural University, Changsha 410128, People's Republic of China
e-mail: langtaotxiao@163.com

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Introduction

Phytohormones are major regulators of biochemical and physiologic processes in plants (Cao and Shannon 1997; Nadjimov and others 1999; Mok and Mok 2001; Borzenkova and Borovkova 2003). Plant growth regulators (PGRs) are synthetic chemicals that exert a variety of regulating roles for plant growth and development (Sembdener and Parthier 1993; Pruski and others 2001). The use of PGRs provides an opportunity to understand the potential of plant growth and to increase plant resistance to stresses (Bandara and others 1998; Kirillova and others 2003; Wheeler 2006; Zhang and others 2006a, b). The major role of PGRs in the adaptation of plants to stresses is primarily caused by changes in phytohormone levels (Nadjimov and others 1999; Margo and others 2000; Sawana and others 2001; Blessington and others 2007). It is well known that the mechanisms of action of PGRs are based either on simulation of the phytohormonal effects if growth regulators are their synthetic analogs or on modification of phytohormonal status of plants by changing the rates of biosynthesis and transport of phytohormones and the mechanisms of their actions (Gafurov and Zefirov 2007).

Chlorocholine chloride (CCC, 2-chloroethyltrimethylammonium chloride) is an antigibberellin growth retardant, with its mechanism based on the restraint of gibberellin biosynthesis in plant tissues. Specifically, CCC restrains the conversion from geranylgeranyl pyrophosphate (GGPP) to ent-kaurene. It is well known that CCC induces changes in the growth rate of grasses and the morphogenesis of potato plants cultured in vitro. It has been

suggested that CCC modifies the phytohormonal balance of plants (Aphalo and others 1997; Zhao and others 2000; Luoranen and others 2002).

In recent years, CCC has been widely used in potato production in China to increase yield and quality. It was found that CCC decreases the growth of stems, leaves, and stolons but promotes tuberization in potato. CCC also promotes tuberization in potato plants growing under noninducing long-day conditions and completely reverses the inhibitory effect of high temperature on tuber production. CCC treatment also effectively increases tuber yield under different salinity levels (referenced in Sharma and others 1998).

Our rationale for doing this work was to investigate the physiologic basis of the response of the potato to the application of commercial plant growth regulators (PGRs), in this case, the gibberellin biosynthesis inhibitor chlorocholine chloride (CCC). Knowledge of the secondary effects of a PGR on plant metabolism and physiology is extremely useful when selecting a PGR to achieve a specific outcome. The negative side effects associated with the application of the highest concentration should be considered. In addition, we monitored the physiologic processes that were affected soon after application of CCC to see how a new crop adapted to the CCC treatment to ensure that the concentration or application time used were yielding the expected early responses that lead to the final desired outcome. Therefore, it is important to study the effects of foliar spraying of CCC on the phytohormonal status, photosynthetic characteristics of potato leaves, yield, and quality indices such as low reducing sugar levels (processing quality) (Cheng and others 2004; Navrátil and others 2007), high sucrose or starch content (processing quality) (Cooke 1999; Jansen and others 2001; Kowalski and others 2006), and low solanine content (human consumption quality) (Linnemann and others 2006) of potato tuber. To our knowledge, these effects have not been studied systemically.

The goals of this study were (1) to study the effects of CCC on the content of phytohormones indolacetic-3-acid (IAA), zeatin (Z), and abscisic acid (ABA) and their content ratio, (2) to compare the photosynthetic capacity and tuber quality indices, especially solanine, after treatment with different concentrations of CCC in potato plants, and (3) to provide a theoretical basis for CCC application in the high-yield and good-quality cultivation of potato.

Materials and Methods

Plant Material and Experimental Design

Plants of potato (*Solanum tuberosum* L.) cultivar Zhongshu 3 were used as experimental material. The field experiments and laboratory analysis were conducted at the experimental farm of Hunan Agricultural University and Hunan Provincial Key Laboratory of Phytohormones and Growth Development, respectively, from September 2005 to January 2006. Potato plants were grown in paddy field soil, with agrochemical characteristics shown in Table 1. Soil humidity was maintained at a level of 60% field moisture capacity.

Field experiments were designed as follows: Each experimental plot had an area of 9.6 m^2 (1.6 m wide and 6 m long). The plots were randomly arranged in the field. The seed tubers (about 50 g in weight) were sowed in rows (40 cm between rows and 40 cm between seeds). CCC foliar spray treatments (until considerable runoff occurred) were performed twice on day 24 and day 28 after emergence, that is, at the tuber initiation stage,with four different concentrations (0, 1.5, 2.0, and 2.5 g L^{-1}). Each treatment had three replications. All plots were cared for by conventional field management measures.

Collection of Experimental Samples

The third fully expanded upper canopy leaves were used for determination of phytohormones and photosynthetic parameters (P_n, G_s, C_i, and T_r) at 42 days after emergence, that is, at the tuber bulking stage. After the aboveground organs of the potato plants had been completely dead for 7 days, tubers (80–100 g in weight) were harvested and used for measurement of yield and quality indices of sucrose, starch, reducing sugars, and solanine.

Extraction, Purification, and Determination of Phytohormones

IAA, Z, and ABA were extracted and purified from leaves using the unified method described in Zhang and others (2006a, b). Before extraction, 5 g of leaves were frozen for 2–3 min with liquid nitrogen, freeze-dried, and stored at −80°C. In the ice bath under weak light, the sample was

Table 1 The main agrochemical properties of the soil tested

pH value	Organic material (g kg^{-1} DW)	Total N (g kg^{-1} DW)	Total P (g kg^{-1} DW)	Total K (g kg^{-1} DW)	Available elements (mg kg^{-1} DW)					
					N	P	K	S	Ca	Mg
6.57	41.3	1.95	2.59	3.11	19.9	34.1	22.8	67.9	37.3	42.2

DW dry weight

ground using precooled 80% methanol. After 10 h of extraction in a refrigerator, samples were centrifuged at 4,500 *g* for 15 min at 4°C. The residue was extracted again according to the above method. The combined supernatants were concentrated by a Jouan vacuum concentrator (RCT60). The residue was dissolved in a 0.1 M ammonium acetic acid solution (pH 9.0) and purified by a polyvinylpolypyrolidone (PVPP) column, a diethylaminoethyl cellulose (DEAE) Sephadex A-25 column, and a Sep-Pak C_{18} cartridge with 50% methanol elution. The hormones were adsorbed by cartridges and the remnants were removed. The hormones were eluated from the Sep-Pak C_{18} cartridge with 80% methanol and collected in vials. The 80% methanolic solution was concentrated by a RCT60 concentrator, and the residue was dissolved in 80% acetonitrile for quantification of endogenous hormones. Concentrations of phytohormones were measured by high-performance liquid chromatography (HPLC; Agilent 1100 Series, Agilent Technologies, Santa Clara, CA) (Mapelli and Rocchi 1983; Battal and others 2004; Ağăr and others 2006) with some modifications. Solutions of IAA, Z, and ABA (Sigma, St. Louis, MO) were used as standard solutions for the determination. The extracts in the vials were injected into an HPLC equipped with a YWG-C_{18} stainless-steel column (4.6 mm × 25 mm, 10 μm, Waters Corp., Milford, MA), with an Agilent 1100 D1314A ultraviolet detector. Acetonitrile:water (40:60 v/v) was used as the mobile phase. The injected sample volume, flow rate, column temperature, and wavelength were 15 μl, 0.5 ml min^{-1}, 35°C, and 210 nm for IAA, 270 nm for Z, and 262 nm for ABA, respectively. Under these conditions, the retention times of IAA, Z, and ABA were determined as 59.02, 19.62, and 76.73 min for standards, respectively.

Measurement of Photosynthetic Parameters and Yield

The photosynthetic parameters were measured using a LI-6400 Portable Photosynthesis System (LI-COR Biosciences, Lincoln, NE). Potato productivity was assessed by determining the average weight of tubers per hill among 30 hills per plot with three replications.

Extraction and Analysis of Sucrose, Reducing Sugars, Starch, and Solanine

The contents of reducing sugars, sucrose, and starch in the apical and distal parts of tubers were analyzed using the methods of Sharma and others (1998) and Navrátil and others (2007). The content of α-chachonine was analyzed by HPLC (Tömösközi-Farkas and others 2006). α-Chachonine (Sigma) was used as the standard for solanine. The α-chachonine was extracted from 1.0 g freeze-dried potato sample with 5 ml 95% ethanol followed by incubation in water at 80–85°C for 4 h. The residue was extracted again according to the above method. After mixing the sample, insoluble constituents were removed by centrifuge (1,500 *g*, 15 min). α-Chachonine was concentrated from the potato tuber samples using a Jouan vacuum concentrator (RCT60). Finally, the α-chachonine was eluted from the deposition by applying acetonitrile:water (80:20 v/v). The HPLC separation was performed using an Agilent 1100 Series Separation Module Alliance autosampler with a 20-μl loop, with a Agilent 1100 D1314A ultraviolet detector. A YWG-C18 stainless-steel column (4.6 mm × 25 mm, 10 μm, Waters) was used with acetonitrile:water (80:20 v/v) as the mobile phase. The isocratic elution was performed at a flow rate of 1.2 ml min^{-1}. The column effluent was monitored at 205 nm, with a column temperature of 30°C and retention time of 20 min. The α-chachonine was quantitatively determined by this method with 94–98% and 99% for recovery and precision, respectively.

Data Analysis and Statistics

Data were analyzed by a data processing system (DPS ver. 7.55). Appropriate standard errors of means (SE) were calculated. Duncan's multiple-range test was applied to compare measured parameters from plants that had experienced different treatments.

Results

The contents of IAA, Z, and ABA in plant leaves showed that treatment with different concentrations of CCC had different effects on the levels of phytohormones. Spraying 1.5, 2.0, and 2.5 g L^{-1} CCC resulted in an increase in the content of IAA (11.03, 87.51, and 0.93%) and Z (10.63, 34.96, and 5.94%) in potato leaves, respectively. Changes in the ABA content induced by CCC treatment were opposite those for IAA and Z: Spraying 1.5, 2.0, and 2.5 g L^{-1} CCC decreased the content of ABA by 26.71, 35.48, and 10.88%, respectively. The contents of IAA and Z in plants treated with 2.0 g L^{-1} CCC were significantly different from those of other treatments, whereas the content of ABA differed significantly from that of other treatments (Table 2). The results also showed that 2.0 g L^{-1} CCC was the most effective spraying concentration for increasing endogenous IAA and Z contents and decreasing ABA content.

CCC changed not only the absolute content but also the content ratio of phytohormones in plant leaves. Spraying CCC caused an increase in IAA/Z, IAA/ABA, Z/ABA, and (IAA + Z)/ABA in potato leaves. The effect of 2.0 g L^{-1} CCC was more pronounced than other treatments. For

Table 2 Effects of CCC on the content of phytohormones in potato leaves

CCC treatment	IAA (ng g^{-1} FW)	Z (ng g^{-1} FW)	ABA (ng g^{-1} FW)
0, control	15.05 ± 0.94b	14.13 ± 1.00b	27.48 ± 1.81a
1.5 g L^{-1}	16.71 ± 1.35b	15.35 ± 1.09b	20.14 ± 2.20c
2.0 g L^{-1}	28.22 ± 139a	19.07 ± 2.08a	17.73 ± 2.42d
2.5 g L^{-1}	15.19 ± 0.92b	14.97 ± 0.72b	24.49 ± 2.43b

Values are mean ± standard error (SE) of three replications. Different letters within the same column indicate significant differences between treatments according to Duncan's multiple range test at $P < 0.05$ level. *FW* fresh weight

example, the ratio of IAA/ABA increased almost threefold relative to the control level. The content ratios of IAA/Z, IAA/ABA, Z/ABA, and (IAA + Z)/ABA for the 2.0 g L^{-1} CCC treatment were significantly different than those of other treatments (Table 3). CCC at 2.0 g L^{-1} was found to be the most effective spraying concentration for increasing the content ratio of IAA/Z, IAA/ABA, Z/ABA, and (IAA + Z)/ABA.

The changes in the phytohormone status of plants induced by spraying CCC were observed against the background of changes in their photosynthetic activity. Treatments with 1.5 and 2.0 g L^{-1} CCC resulted in an increase of 26.65 and 45.84% in P_n compared with the control, respectively. Treatment with 2.5 g L^{-1} CCC decreased the P_n by 2.84% relative to the control. Treatment with 1.5, 2.0, and 2.5 g L^{-1} CCC resulted in an increase in G_s of 20.69, 54.60, and 25.86% in potato leaves, respectively. Treatment with 1.5, 2.0, and 2.5 g L^{-1} CCC increased C_i by 3.61, 7.24, and 6.49%, respectively. Treatment with 1.5, 2.0, and 2.5 g L^{-1} CCC increased T_r by 19.37, 34.56, and 22.51%, respectively. The P_n, G_s, C_i, and T_r of leaves were significantly different from each other (Table 4).

In summary, spraying CCC improved not only the photosynthetic parameters of potato leaves but also the yield and quality of tubers. The average tuber yield per hill increased 6.83, 10.10, and 3.08% after spraying 1.5, 2.0, and 2.5 g L^{-1} CCC, respectively (Fig. 1). A spraying concentration of 2.0 g L^{-1} CCC was found to be the most effective. CCC at 1.5, 2.0, and 2.5 g L^{-1} elevated the content of sucrose in tubers by 16.09, 40.65, and 7.02%, respectively (Fig. 2). Treatment with 1.5 and 2.0 g L^{-1}

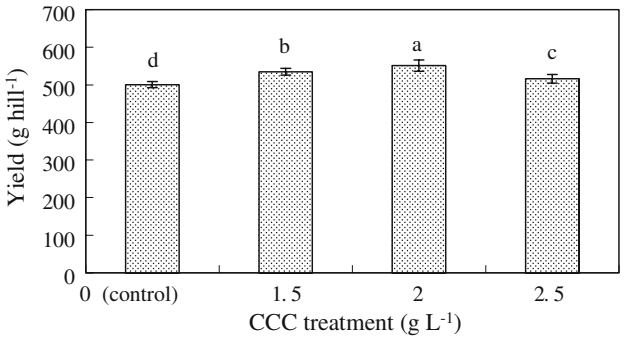

Fig. 1 Effects of CCC on the average tuber yield per hill. Different letters at each treatment point indicate significant differences between treatments according to Duncan's multiple range test at $P < 0.05$ level, $n = 3$. Vertical bars are standard error of the mean

Table 3 Effects of CCC on the content ratio of phytohormones in potato leaves

CCC treatment	IAA/Z	IAA/ABA	Z/ABA	(IAA + Z)/ABA
0, control	1.07 ± 0.08b	0.55 ± 0.07c	0.52 ± 0.06c	1.07 ± 0.12c
1.5 g L^{-1}	1.09 ± 0.11b	0.83 ± 0.06b	0.77 ± 0.12b	1.6 ± 0.17b
2.0 g L^{-1}	1.49 ± 0.10a	1.61 ± 0.20a	1.09 ± 0.16a	2.69 ± 0.34a
2.5 g L^{-1}	1.02 ± 0.05b	0.63 ± 0.09bc	0.62 ± 0.09bc	1.24 ± 0.18c

Values are mean ± standard error (SE) of three replications. Different letters within the same column indicate significant differences between treatments according to Duncan's multiple range test at $P < 0.05$ level

Table 4 Effects of CCC on the photosynthetic parameters in leaves

CCC treatment	P_n (CO_2 μmol m^{-2} s^{-1})	G_s (H_2O mol m^{-2} s^{-1})	C_i (CO_2 μL L^{-1})	T_r (H_2O mmol m^{-2} s^{-1})
0, control	10.58 ± 0.65c	0.174 ± 0.011c	277.33 ± 10.82c	0.955 ± 0.071d
1.5 g L^{-1}	13.40 ± 1.69b	0.210 ± 0.022b	287.33 ± 12.10b	1.140 ± 0.098c
2.0 g L^{-1}	15.43 ± 0.55a	0.269 ± 0.021a	297.40 ± 13.43a	1.285 ± 0.058a
2.5 g L^{-1}	10.28 ± 0.74c	0.219 ± 0.023b	295.33 ± 3.79a	1.170 ± 0.095b

P_n, G_s, C_i, and T_r represent net photosynthetic rate, stomatal conductance, intercellular CO_2 concentration, and transpiration rate, respectively. Values are mean ± standard error (SE) of three replications. Different letters within the same column indicate significant differences between treatments according to Duncan's multiple range test at $P < 0.05$ level

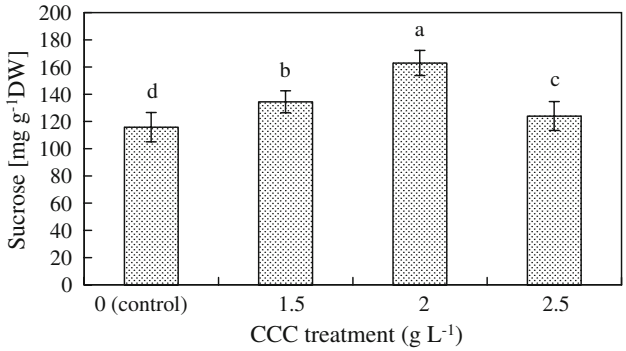

Fig. 2 Effects of CCC on the content of sucrose in tubers. Other details are as per Fig. 1

CCC increased the content of starch in tubers by 0.76 and 3.90%, respectively. Meanwhile, 2.5 g L^{-1} CCC lowered the content of starch by 0.98% (Fig. 3). The content of reducing sugars in tubers was lowered by 33.53, 74.38, and 50.53% after treatment with 1.5, 2.0, and 2.5 g L^{-1} CCC, respectively (Fig. 4). The content of solanine in tubers was lowered by 10.35, 74.33, and 67.49% after being sprayed with 1.5, 2.0, and 2.5 g L^{-1} CCC, respectively (Fig. 5). These results also showed that appropriate concentrations at 2.0 g L^{-1} CCC significantly increased the tuber yield and improved the tuber quality.

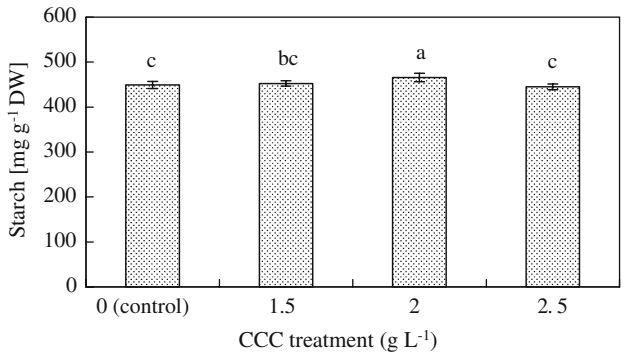

Fig. 3 Effects of CCC on the content of starch in tubers. Other details are as per Fig. 1

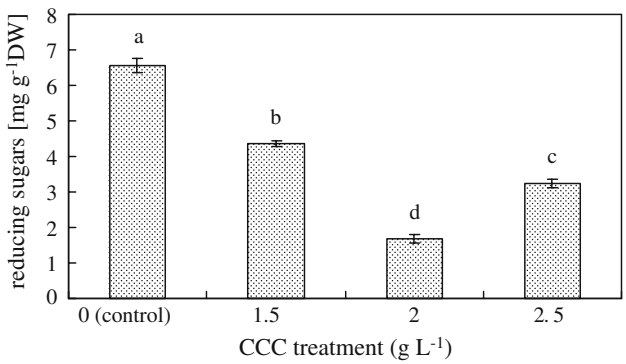

Fig. 4 Effects of CCC on the content of reducing sugars in tubers. Other details are as per Fig. 1

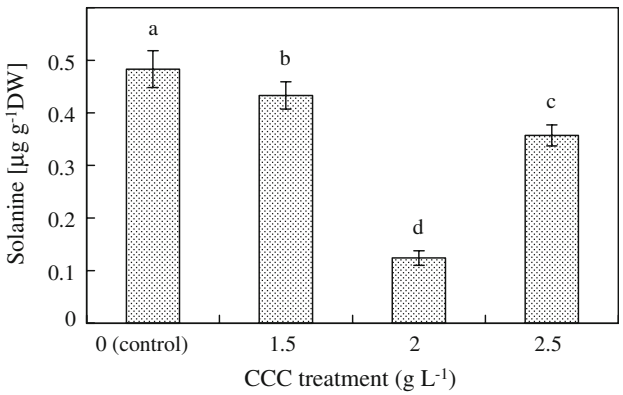

Fig. 5 Effects of CCC on the content of solanine in tubers. Other details are as per Fig. 1

Discussion

It is generally believed that phytohormonal regulation provides the basis for assimilate distribution and productivity of potato. It was shown in our study that the pathways and directions of physiologic processes depend not only on the content but also on the content ratio of phytohormones. Treatment with CCC had a prolonged impact on the plants, which was manifested by changes in the endogenous phytohormonal balance of leaves. As in the case of leaves, it is generally believed that CCC greatly decreased the contents of gibberellins. In agreement with earlier findings (Agăr and others 2006; Navrátil and others 2007), our research found that CCC completely inhibited GA synthesis in potato (unpublished). In addition, CCC induced a noticeable decrease in the content of ABA. It has been suggested that ABA has a signaling function that underlies the physiologic activity of CCC (Biemelt and others 2000; Shen and others 2006). Clearly, different species may use different phytohormones or rely on different interactions among them to accomplish their various functions.

It was found that the lower ratio of IAA/Z can promote flower-bud differentiation of plants. The reduction of ABA content and the enhancement of Z/ABA, IAA/ABA, and (IAA + Z)/ABA ratios are probably beneficial to the growth of tubers at the tuber bulking stage. The ratio Z/ABA is of considerable importance because its value is characteristic of the activity of stomata. Both Z and ABA regulate the opening of stomata. The activity of stomata has a significant effect on water balance, the P_n, G_s, C_i, and T_r of leaves, and the growth rate of plants. It was shown that treatment of potato plants with CCC increased the opening of stomata, with 2.0 g L^{-1} CCC having the most prominent effect. This is because treatment with 2.0 g L^{-1} CCC caused the highest increase in the Z/ABA ratio.

The use of CCC induced an increase in the rate of photosynthetic assimilation of carbon dioxide. It was noted that this phenomenon largely depends on the physiologic

state and age of plants as well as on the concentration of CCC (Kirillova and others 2003). CCC-induced stimulation of photosynthetic processes may also be due to its resistance to stress factors and its metabolism mechanism in plants, as stated in the Introduction.

The changes in the net photosynthetic rate in potato plants induced by spraying CCC resulted in changes in plant productivity. It was shown that the growth rate of potato plants treated with CCC increased. The CCC-induced increase in the productivity of the plants can be attributed to the acceleration of the process of photophosphorylation and an increase in the photosynthetic rate. The results of this study imply that treatment of plants with CCC may increase the number of chloroplasts, elevate the concentration of chlorophyll and carotenoids, accelerate the process of photophosphorylation, and stimulate the photosynthetic rate. This was accompanied by an increase in the growth rate of leaves, their thickness, and weight, and ultimately in the productivity of the plants. The major fraction of products of photosynthesis relies not only on the net photosynthetic rate in mature leaves but also on the photosynthetic products in mature and aging leaves being exported to other organs. In our experiments, plants were treated with CCC at the tuber iniatition stage, that is, when the growth rate of leaves had declined to moderate levels. It is also important to note that plants were cultivated under short-day conditions. Further studies are necessary to clarify whether the early effects of CCC application are mainly due to modification of activity of photosynthetic enzymes or other mechanisms.

The results of quality assessment of potato tubers of a given harvest revealed that CCC exerted long-term or secondary effects, including changes in the contents of sucrose, starch, reducing sugars, and solanine. The promotion of soluble carbohydrate contents helps the growth and development of tubers after spraying CCC. Presumably, these results are due to the fact that CCC enhances mobilization of these compounds as substrates for respiration, thereby significantly increasing the respiration rate. The CCC-induced increase in the content of sucrose in tubers may account for the CCC-induced increase in the content of dissolved sugars in the plant and could promote the process of polymerization of sucrose to starch. Hence, the content of solanine as a secondary product of respiration could be depressed.

The results of our study found that phytohormonal metabolism and photosynthetic physiology of potato leaves affected early after application of CCC were significantly improved. CCC was also found to be capable of increasing the resistance of potato to stress factors, and consequently the productivity of potato is increased (Rabha and Dey 1993; Sharma and others 1998), and tuber yield and quality are also increased. These findings, together with the observed productivity enhancement and quality improvement, suggest that the use of CCC in potato production is promising.

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