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Chlorocholine chloride application effects on photosynthetic capacity and photoassimilates partitioning in potato (*Solanum tuberosum* L.)

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ABSTRACT

Treatment of potato (*Solanum tuberosum* L.) with chlorocholine chloride (CCC) applied twice as a foliar spray 25 and 30 days after planting has shown to decrease shoot and stolon growth but increase tuber yield. However, the regulatory role of CCC on translocation of recently fixed photoassimilates into different parts of potato plants has not been fully illustrated. In this study, ^{14}C-isotope labelling technique was used to estimate the photosynthetic capacity and photoassimilate partitioning among leaves, stems, roots + stolons, and tubers of potted potatoes treated with 1.5 g l^{-1} CCC. CCC treatment significantly increased tuber dry mass but reduced leaf dry mass. CCC-treated leaves had significantly higher chlorophyll and carotenoid contents and assimilated 22.0% more $^{14}CO_2$ per leaf dry mass than the controls. Compared with the control, CCC treatment reduced the translocation of ^{14}C-photoassimilates into leaves, stems and roots + stolons but increased that into tubers. CCC-treated leaves exported 14.6% more ^{14}C-photoassimilates into other parts of the plants. In addition, CCC treatment reduced ^{14}C-soluble sugar and ^{14}C-starch accumulation in leaves and stems but enhanced them in tubers and roots + stolons. Collectively, the results indicate that CCC treatment significantly improves the photosynthetic capacity of potato leaves and promotes photoassimilates partitioning into tubers thereby enhancing tuber growth.

1. Introduction

Potato (*Solanum tuberosum* L.) rates fourth among the world's various agricultural products in production volume, after wheat, rice and corn (Fabeiro et al., 2001). It is an important crop in terms of human food and starch industry. In countries with agriculture based economies, potato production is an important contributing factor to the overall agricultural produce (Sharma et al., 1998a).

Chlorocholine chloride (2-chloroethyltrimethyl-ammonium chloride, CCC) is an anti-gibberellin growth retardant (Sharma et al., 1998a). It is well known that CCC treatment could induce changes in the morphogenesis of potato plants cultured *in vitro* (Bandara et al., 1998) and may increase potato tuber yield and quality (Yamamoto and Nakata, 1997; Caldiz et al., 1998). Several effects of CCC treatment may account for such an improvement of tuber yield. First, CCC treatment could depress the growth of stems, leaves and stolons, but promote tuber initiation and tuber bulking (Dyson, 1965; Menzel, 1980; Tezuka et al., 1989; Hussain et al., 2006). Second, CCC treatment could promote tuber initiation in potato plants growing under non-inducing long day conditions and could completely reverse the inhibitory effect of high temperature on tuberisation (Pruski et al., 2001; Tekalign and Hammes, 2004). Third, CCC treatment may increase photosynthetic capacity by increase of leaf chlorophyll content and thus enhancing tuber growth (Sharma et al., 1998a). In addition, CCC treatment can enhance plant nutrient uptake from soil, improve water balance and protein synthesis in growing organs (Grossmann, 1990). Furthermore, a study by Sharma et al. (1998b) showed that CCC treatment could promote starch accumulation in potato tubers presumably through enhancing sucrose synthase (SS) activity in the tubers during the tuber bulking stage. Despite rich literature is available in this subject, until now the effects of CCC on the translocation of recently fixed photoassimilates to different parts of potato plants has not been fully illustrated.

In this study, the effect of foliar spray of CCC on the partitioning of recently fixed photoassimilates among leaves, stems, roots + stolons, and tubers of potato plants were investigated using the ^{14}C-isotope labelling technique. Our purposes were to reveal the regulatory role of CCC on photoassimilates partitioning between source and sink organs; and to provide a theoretical basis of CCC application for high-yield and good-quality potato production.

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2. Materials and methods

2.1. Plant material and growing conditions

Virus-free plants of potato (*S. tuberosum* L. cv. Zhongshu 3, supplied by Hunan Provincial Virus-free and Rapid Propagative Center of Potato of China) were grown in plastic pots (15 cm diameter and 16 cm deep) in a greenhouse at Hunan Provincial Key Laboratory of Phytohormones and Growth Development from October to December 2007. The pots were filled with 0.25 kg dry organic soil. Only one plant was allowed in one pot. The climate conditions in the greenhouse were: $20/14 \pm 2$ °C day/night air temperature, 15 h photoperiod and >500 μmol m^{-2} s^{-1} photosynthetic active radiation (PAR) supplied by sunlight plus metal-halide lamps. Before planting, pots were water saturated and allowed to drain freely until there was no change in weight. The full pot-holding capacity was then calculated as the difference between in this weight and soil dry weight plus pot weight. During the experiment, all pots were randomly arranged and were watered daily to 90% of full pot-holding capacity via weighing.

2.2. CCC treatment

In the greenhouse, plantlets were grown under optimal conditions during the first 4 weeks after planting. At tuber initiation stage, CCC treatment was performed twice on 25 and 30 days after planting (DAP), respectively. During the treatment, half of the plants were foliar sprayed with 1.5 g l^{-1} CCC until considerable run-off on the leaf surface occurred; the rest of the plants were sprayed with the same amount of distilled water and were served as control. Each treatment had 12 replicates. After the treatment all plants were well-watered and cultured under the same condition until tuber bulking (i.e. 60 DAP).

2.3. Measurements of leaf photosynthetic pigments contents

At tuber bulking stage (i.e. 60 DAP), six plants of each treatment were selected for measurement of leaf photosynthetic pigments content. The contents of Chl a, Chl b, and carotenoid (Car x) were determined on the second fully expanded upper canopy leaves and followed the methods described by Lichtenthaler (1987) and Wellburn (1994).

2.4. $^{14}CO_2$ labelling

In order to trace the translocation of recently fixed photoassimilates into different parts of the plant, six plants of each treatment were used for ^{14}C-isotope labelling. This was conducted at 62 DAP. The plants were moved from the greenhouse into a transparent assimilation chamber (117 l) with an air circulation system linked to a $^{14}CO_2$ generator. In the generator, $^{14}CO_2$ was produced by adding perchloric acid into $Ba^{14}CO_3$ (0.607 g) + Na_2CO_3 (2.266 g) powder mixture (the amounts of the chemicals were calculated based on the chamber and tuber volume and the desired $^{14}CO_2$ concentration); such that the $^{14}CO_2$ concentration was achieved at a ^{14}C-radioactivity of 185 kBq l^{-1}. The chamber was kept at a photosynthetic active radiation of 500 μmol m^{-2} s^{-1} for a 1.5 h period for $^{14}CO_2$ assimilation, and the residue $^{14}CO_2$ + CO_2 was subsequently absorbed by NaOH solution. After $^{14}CO_2$ labelling, the plants were moved back to the greenhouse and grown under normal conditions.

2.5. Assay of ^{14}C-radioactivity

Three plants of each treatment were harvested at the third day after $^{14}CO_2$ assimilation, i.e. 65 DAP and the other three plants were used for other purposes. The plants were washed by distilled water and leaves, stems, tubers, roots + stolons were harvested. The plant materials were dried in an oven at 80 °C to constant weight, i.e. the dry mass (DM) of plant materials were obtained. The distribution of DM (%) among leaves, stems, tubers, and roots + stolons was calculated as the ratio of DM of each part of the plant to the total DM of the plant. The dried plant materials were finely grounded for the measurement of ^{14}C-photoassimilates radioactivity.

40 mg dry samples for each plant part, respectively, were enveloped by a small lens wiping paper and put on a small iron loop in a 250 ml own-made burning conical flask. Oxygen gas was injected into the flask facilitating the sample burning. Then the flask was sealed. The sample was burned by electric fire starter from the outer iron thread. 3 ml carbinolamine was injected into the flash from the rubber cork for absorbing the $^{14}CO_2$ after the sample burned completely. The carbinolamine solute was used for radioactivity assay.

100 mg dry samples of each plant part, respectively, added into a 10 ml cuvette sealed with a rubber cork were incubated in a water-bath at 80 °C for 30 min using 5 ml of 80% ethanol to extract soluble sugars. The extracts were centrifuged at 2000 × *g* for 10 min and the resulting supernatants were transferred to a 5 ml tube and used for the assays of ^{14}C-soluble sugar radioactivity. For starch extraction, 50 mg dry samples of each plant part, respectively, added into a 10 ml cuvette sealed with a rubber cork were incubated in a water-bath at 100 °C for 2 h using 5 ml of 6 M HCl. The extracts were centrifuged at 2000 × *g* for 10 min and the resulting supernatants were transferred to a 5 ml tube and used for the assays of the radioactivity of ^{14}C-starch.

The total ^{14}C-photoassimilates, ^{14}C-soluble sugar and ^{14}C-starch were measured by a liquid scintillation counter (TRI-CARB2100TR, USA) as described by Osaki et al. (2004).

2.6. Data analysis and statistics

Data were subjected to analysis of data processing system (DPS) (version 7.55). Appropriate standard errors of means (S.E.) were calculated. Duncan's multiple range test was applied to compare measured parameters from plants that had experienced different treatments. The ^{14}C-partitioning (%) was calculated as the ^{14}C-photoassimilates radioactivity in one organ divided by the total ^{14}C-photoassimilates radioactivity in the whole plant. The leaf $^{14}CO_2$ assimilability was calculated as the sum of ^{14}C-radioactivity of the whole plant divided by the leaf DM of the plant. The leaf ^{14}C-photoassimilates exporting ratio was calculated as the sum of ^{14}C-radioactivity in stems, tubers, and roots + stolons divided by the total ^{14}C-radioactivity of the whole plant. The ^{14}C-soluble sugar and ^{14}C-starch distribution (%) is calculated as the percentage of ^{14}C-radioactivity of soluble sugar and starch in one organ divided by the total soluble sugar and starch radioactivity of the whole plant.

3. Results

3.1. Effect of CCC treatment on leaf photosynthetic pigments contents and plant dry mass production

CCC treatment significantly increased the contents of photosynthetic pigments in potato leaves (Fig. 1). The contents of Chl a, Chl b, and carotenoid (Car x) of the CCC-treated plants was 119.6, 79.5, and 79.3%, respectively, higher than those of the control plants (Fig. 1).

The DM of stems and roots + stolons was similar for the CCC-treated plants and the controls; however, CCC treatment resulted