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Response of potato dry matter assimilation and partitioning to elevated CO_2 at various stages of tuber initiation and growth

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ABSTRACT

Plants are able to adjust their development of sink organs in response to elevated atmospheric CO_2, but there is an incomplete understanding of the processes responsible for alteration in sink capacity and carbon partitioning among alternative sinks. In potato (*Solanum tuberosum* L.), studies have shown that elevated CO_2 increases partitioning to tubers. The objectives of the current studies were to elucidate growth response to elevated CO_2 at discrete stages before and after imposition of tuber-inducing photoperiods, and test whether tuber sink development responds to elevated CO_2 primarily by altering tuber initiation, cell proliferation or enhancement of tuber cell size. Contrary to the hypothesis that an initial phase of CO_2 enrichment would have carry-over effects, plants pre-treated for four weeks with elevated CO_2 before tuber initiation increased whole-plant biomass during tuber initiation to a similar extent as those receiving a control pretreatment, though partitioning was shifted toward stems. Elevated CO_2, whether imposed before or after a tuber-inducing photoperiod, did not increase tuber number. Flow cytometry of tuber nuclei was used to determine cell numbers and nuclear DNA endoreduplication. Elevated CO_2 imposed at both the initial two weeks after the start of tuber-inducing photoperiod and in the next two weeks of tuber bulking substantially increased tuber size by enhancing cell proliferation, not by increasing average cell volume or nuclear DNA size-class (endoreduplication). We conclude that the ability of tubers to stimulate cell proliferation throughout tuber initiation and tuber-bulking stages contributes to enhanced partitioning into tubers in elevated CO_2 environments.

1. Introduction

Sustained stimulation of net photosynthesis and growth in response to elevated atmospheric CO_2 requires sufficient sink organ development to utilize and store additional photosynthate (Ainsworth and Rogers, 2007; Rogers et al., 1998). In long-term studies representative of elevated-CO_2 conditions of future climates, plants often lack sufficient sink capacity such that carbohydrates accumulate in leaves and photosynthetic activity is inhibited. Plants are able to adjust their development of sink organs in response to altered photosynthetic rates (Gibson, 2005), but the processes involved in such responses differ depending on the species, growth stage, and organs. Elevated CO_2 during vegetative growth prior to 100% canopy light interception, can enhance leaf area production and theoretically provide a compound interest benefit to whole-canopy photosynthesis (Gifford et al., 1973). Also during the vegetative stage, some excess photoassimilate can accumulate as starch in stem and other vegetative organs and later be remobilized and exported to reproductive organs (Ho, 1988). Thus, studies of sink-organ development at particular stages have helped to explain whole-season growth outcomes.

In potatoes, whole-season studies have shown that elevated atmospheric CO_2 alters carbon partitioning so that a higher proportion of carbon accumulates into developing tubers (Fleisher et al., 2008b; Miglietta et al., 1998), especially the largest tuber size-class (Högy and Fangmeier, 2009). But little is known about the processes that occur at various stages of tuber development, which may be responsible for alteration in sink capacity and carbon partitioning among alternative sinks.

Potato tuberization is elicited by a short-day photoperiod through the participation of phytochrome signals (Jackson, 1999). From early research it has been known that tuberization is enhanced when nitrogen fertility is not excessive and plants are well illuminated to increase photosynthesis, thus creating a high C:N ratio (Krauss, 1985). Studies of in vitro-grown shoot explants have shown that tuberization is induced by sucrose feeding (Garner and Blake, 1989; Raices et al., 2003). Tuber expansion and expression of metabolic machinery for starch accumulation are also

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regulated by carbohydrate supply (Fernie and Willmitzer, 2001; Jackson, 1999).

Studies of the effects of elevated CO_2 on plant growth have indicated that cell proliferation and expansion growth in sink organs are important contributors to the development of sink capacity. For example studies of tomato (*Lycopersicon esculentum* Mill.) fruit (Cong and Tanksley, 2006), *Arabidopsis thaliana* L. leaves (Horiguchi et al., 2006) and maize (*Zea mays* L.) kernels (Setter and Flannigan, 1989), indicate that regulation of cell number and cell size can be important mechanisms by which sink capacity is regulated.

In the present studies we examined the effects of elevated CO_2 applied during various discrete stages of potato development before and after tuber initiation on partitioning of dry matter among potato plant parts. Our objectives were to test the hypothesis that elevated CO_2 before tuber sink-organ development would alter whole plant growth and partitioning in subsequent stages of elevated CO_2, and to determine whether elevated CO_2 affects tuber sink development primarily by affecting tuber initiation, cell proliferation or enhancement of tuber cell size. These studies provide insight on the processes involved in favored partitioning toward the tuber sink in plants grown in elevated CO_2.

2. Materials and methods

2.1. Plant material

Potato (*Solanum tuberosum* L. cv. Katahdin) tubers were cut into pieces containing one to two eyes and placed into a foil-covered and humidified container for 48 h to allow development of a cork layer of cells. Six to eight pieces were sown in 12-L pots containing a mix of vermiculite/perlite/peat (1:1:1; v:v:v) supplemented with $CaSO_4$ (4 g L^{-1}) and powdered limestone (0.7 g L^{-1}), and covered with 2 cm of soil. Plants were grown in a greenhouse with 14 h supplemental lighting (1000 W metal halide, Duraglow, GE, Hendersonville, NC), and drip irrigated with an aqueous solution applied at 2 h intervals during the light period containing 1.08 g L^{-1} Peter's 15-16-17 complete fertilizer (W.R. Grace and Co., Fogelsville, PA), which supplied the following elemental nutrients: 33 mg L^{-1} of NO_3-N, 86 mg L^{-1} of NH_4-N, 42 mg L^{-1} of urea-N, 74 mg L^{-1} of P, 151 mg L^{-1} of K, and small amounts of minor and micronutrients. Controlled-environment chambers (Model CEL-63-10, Sherer Inc., Marshall, MI, USA) with 112 cm × 74 cm (width × depth) internal space had a 25/18 °C (day/night) temperature regime and 600 μmol photons [400–600 nm] m^{-2} s^{-1} at the top of the canopy, supplied by fluorescent/incandescent lamps. Young plants emerged from eyes by 10 to 14 days after sowing. Two weeks after emergence, young plants, about 15 cm in height, were trimmed to include one shoot, the mother tuber piece was removed, and plants were re-sown in new pots with one plant/pot. After transplanting, plants were grown in the greenhouse for various periods depending on the treatment schedule (Fig. 1), then moved into growth chambers for CO_2 and light treatments as described below.

2.2. CO_2 treatments

Elevated CO_2 treatments were imposed at three stages (Fig. 1) with respect to the shift from 14-h to 10-h day length which stimulates tuber initiation: (1) four weeks before tuber initiation (pre-tuber initiation, PTI), (2) the first two weeks after the start of imposing a 10-h photoperiod, which is hereafter called tuber initiation stage (TI), and (3) two weeks after TI, during tuber bulking stage (TB). Tuber initiation was stimulated by transferring plants from the greenhouse to growth chamber, and thereby switching the day length from 14 to 10 h (short day). Nutrient solution and watering regime were the same as in the greenhouse. The duration of the

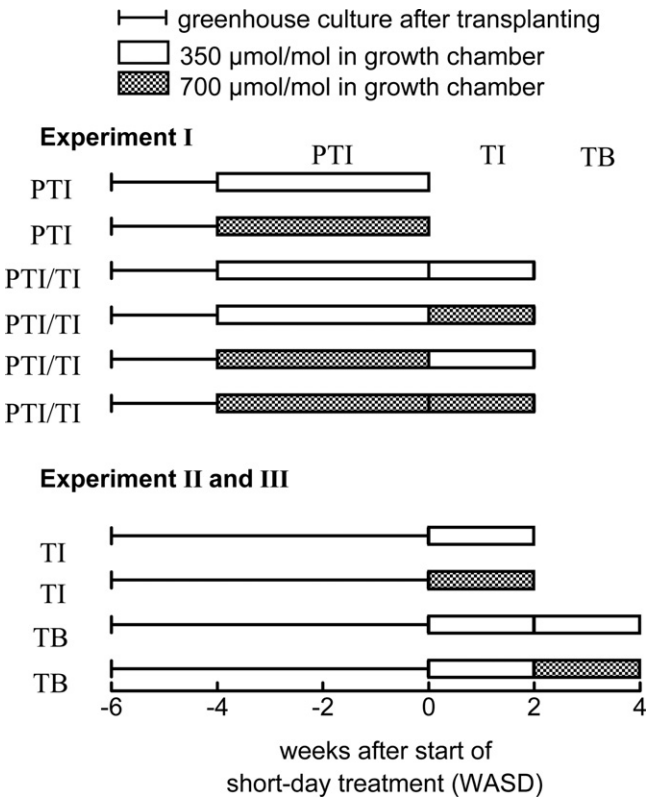

Fig. 1. Diagram of CO_2 treatment time frames at various developmental stages with respect to the switch from long day (14 h) to short day (10 h). PTI, pre tuber initiation stage, TI, tuber initiation stage, TB, tuber bulking stage.

elevated CO_2 treatment was 4 weeks for PTI and two weeks for TI and TB. Three experiments were conducted (Exp-I, Exp-II, and Exp-III), as shown in Fig. 1. For each batch in Exp-I, 16 greenhouse-grown plants (pre-tuber initiation) were randomly assigned to four identical growth chambers (4 plants/growth chamber) to which CO_2 treatments (350 or 700 μmol/mol) were randomly assigned. Eight plants (experimental units) were harvested at the end of PTI; the remaining plants were reassigned randomly to the growth chambers and associated CO_2 treatments and continued growth until the end of TI. For each batch in Exp-II and Exp-III, eight greenhouse-grown plants were randomly assigned to four chambers with CO_2 treatments according to the schedule shown in Fig. 1. There were two batches in Exp-I, 6 batches in Exp-II, and 3 batches in Exp-III. A two way ANOVA was used to partition the total sums of squares into batch, treatment, and error sources of variation. The 5% confidence intervals were calculated as $t_{(0.05,\upsilon)} \times \sqrt{\mathrm{MSE}/n}$, where t is the significant studentized ranges, υ is the error degrees of freedom, MSE (mean square of error) = SSE/υ, and n is the replication of treatment. Students' t-tests were used for comparisons of paired treatments. Multiple-range LSD tests were used for multiple comparisons.

Chamber CO_2 concentration was monitored with a calibrated infrared gas analyzer (Nova 421P, Nova Analytical Systems Inc., Niagara Falls, NY) that alternately sampled each of the chambers using computer-controlled valves. The gas analyzer output was interfaced to a computer data acquisition and control system (EnviroMac, Remote Measurement Systems Inc., Seattle, WA) which supplied CO_2 to both the 350 and 700 μmol/mol chambers as needed from a compressed CO_2 cylinder to maintain the CO_2 concentration within 30 μmol/mol of the desired levels. At the end of CO_2 treatments, plants were harvested and separated into leaves, stems and tubers (including stolon). All materials were oven dried at 70 °C to a constant weight before determining dry weight (DW).