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ScienceDirect
Environmental and Experimental Botany 62 (2008) 160–167
Environmental and Experimental Botany
www.elsevier.com/locate/envexpbot

Stem-swelling and photosynthate partitioning in stem mustard are regulated by photoperiod and plant hormones

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Received 11 July 2007; accepted 2 August 2007

Abstract

The experiment was conducted to study the relationship between stem-swelling and photoperiod and growth hormones by comparing stem swelling with non-stem-swelling stem mustard (*Brassica juncea* var. *tsatsai*) plants about their growth characteristics and levels of endogenous gibberellin and cytokinin under different photoperiods. The results here showed that plant biomass was higher in 12-h photoperiod compared to that in long day (LD) and short day (SD), whereas stem growth was much stronger in LD compared to 12-h photoperiod and SD. Exogenous application of 1.0 mM gibberellic acid (GA_3) accelerated stem elongation in SD, but 8.9 μM benzyladenine (BA) failed. The shape of the swollen stem was also found to be associated with day length: a LD promoted stem elongation, while a 12-h photoperiod made the stem oval swollen. Also, stem was shown to have no sign of swelling in plants in SD with a relatively poor growth. The further studies showed that the largest proportion of ^{14}C photosynthate was allocated to the swelling stems in stem-swelling plants, but to expanded leaves in non-stem-swelling plants, and endogenous gibberellin A_1 (GA_1) and zeatin + zeatin riboside (ZRs) were higher in LD compared to 12-h photoperiod and SD. These results from this experiment indicate that stem growth and swelling is a physiological process of hormonal control, and the photoperiod possibly exerts its influence by altering the balance between the levels of endogenous gibberellins and cytokinins.
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Keywords: *Brassica juncea* var. *tsatsai*; Cytokinin; Gibberellin; Stem growth; Stem mustard; Photoperiod; Photosynthate partitioning; Plant hormone

1. Introduction

Stem mustard (*Brassica juncea* var. *tsatsai*) is an important vegetable, mainly grown in the Yangtze River valley in China. Stem mustard is characterized with its swollen stem, which, in eastern Asia countries, is a popular food item after pickled (Liu, 1996).

Photoperiodic regulation of storage organ formation has been investigated in several species (Austin, 1972; Sobeih, 1988; Adaniya et al., 1989; Garcia-Martinez and Gil, 2002, and references therein). A mechanism is suggested by which photoperiod evokes a series of biochemical and physiological changes including the production of plant hormones, which further result in morphological modifications in plants (Xu et al., 1997; Parks et al., 2001). It has been suggested that the level of endogenous gibberellins might be altered by a photoperiodic treatment (Dahanayake and Galwey, 1999; Kamiya and Garcia-Martinez, 1999). Also, the phenotypic differences among plants under different photoperiods as well as the modification of plant architecture are possibly controlled by the alteration in hormone levels (Zeevaart et al., 1993). Although research on the relation between plant hormones and stem swelling is rarely reported (Selman and Kulasegaram, 1967), the possible involvement of plant hormones such as gibberellins, auxins, and cytokinins in regulating the development of stem has been demonstrated (Palmer and Smith, 1969; Nishijima et al., 2005). All these studies point out the possibility that changes in endogenous hormones, gibberellins and cytokinins, involve the modification of architecture of plants, and further investigations are needed to clarify the involvement.

The development of storage organs, which acts as assimilate sinks (actively growing point), is heavily based on assimilate supply from sources (Sobeih, 1988). The carbohydrate needs of a developing organ are usually met by one or more sources:

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doi:10.1016/j.envexpbot.2007.08.001

current photosynthate, labile photosynthate pools within organs, or mobilization of carbohydrate reserves. In fact, the source–sink relations in plants generally change, with respect to the relative sink strength of different organs, number of sinks, and sink to source transitions, during plant development. Previous investigations in a variety of species have demonstrated that the partitioning of photosynthate from source to sink was affected by photoperiod (Hofstra and Nelson, 1969; Russell and Johnson, 1975; Chatterton and Silvius, 1979; Britz et al., 1985; Britz, 1990). The transport of assimilates from the sources where they produced into the sinks may be under the control of plant hormones (Roitsch, 1999). However, information is very limited regarding the effect of photoperiod on stem swelling in stem mustard, and photosynthate partitioning among organs during stem swelling is also poorly characterized. To better understand the regulation of photoperiod in stem swelling, and its possible relationships to the partitioning of photosynthates in different parts of the plant, this experiment was initiated.

In this study, we reported the responses of plant weight, stem weight, and the ratio of stem width to length to different photoperiodic treatments and the endogenous gibberellin A_1 (GA_1) and zeatin + zeatin riboside (ZRs) levels in plants grown in different photoperiods as well as the effect of exogenous application of GA_3 and BA on the induction of stem swelling in a short photoperiod. Also, we investigated the distribution of ^{14}C photosynthates in stem-swelling and non-stem-swelling plants.

2. Materials and methods

2.1. Plant material and growth conditions

The experiment was carried out in a greenhouse at the Experimental Farm of Zhejiang University, located in Hangzhou (30°16′N, 120°16′E), China. Seeds of stem mustard were sown in late August. Four weeks after sowing, plants having three to four true leaves with uniform growth, they were transplanted from seedling bed to pots (25 cm × 20 cm) filled with nursery soil mixture, each pot having one plant. One week later, after the plant stand was recovered, the pots were transferred to the greenhouse for photoperiodic treatment. The 16 h light/8 h dark photoperiod (LD) was imposed on the plants by adding fluorescent tubes (460 μmol m^{-2} s^{-2} light intensity), while the 8 h light/16 h dark photoperiod (SD) was achieved by using black curtains. The control plants were grown in a photoperiod of 12 h light/12 h dark (CK). At least 80 plants were used in each photoperiodic treatment. The greenhouse provided an ambient a day/night temperature ranging from 26/18 °C in September to 15/5 °C in December. The plants were regularly irrigated and fertilized throughout the period of study.

Samples of the leaves and stems from the potted plants were collected at different times. There was an exception to this: for plants subjected to LD condition, the sampling for these plants was terminated, when the plants started to flower, in week 12 after treatment. The maximum length and width of stems, the aboveground plant fresh weight, and stem fresh weight were measured at each sampling, and then the leaves and stems were used to quantify the endogenous hormone levels.

2.2. $^{14}CO_2$ photosynthate analysis

Feeding of $^{14}CO_2$ was conducted in week 12 after photoperiodic treatment. At this period of time, plants grown under the 12-h photoperiod were at the middle stage of stem swelling, whereas stems of plants grown in SD did not start to swell. The third youngest, fully expanded leaf of each plant was fed with 10 μCi $^{14}CO_2$ for approximately 20 min. Labeled $^{14}CO_2$ was liberated from $NaH^{14}CO_3$ in the presence of excess lactic acid and recirculated in a feeding chamber enclosing the fed leaf during the feeding period. At 48 h after the feeding, three plants for each treatment were harvested and their roots were removed. The plants were separated into young leaves (<6 cm), fully expanded leaves (≥6 cm), and stems, and the plant parts were then dried at 80 °C for 48 h. After weighed, the dried plant parts were burnt in a Parkard Tri-carb oxidizer, and the combustion products were bubbled through and trapped in a 10 ml solution (methylbenzene 600 ml + methanol 100 ml + ethanol amine 150 ml + ethylene glycol 150 ml + POPOP 2 g + PPO 5 g). The absolute radioactivity of these samples was measured using a Model 1900TR Packard Tri-carb liquid scintillation counter.

Data from three plants in each treatment were averaged.

2.3. Effect of GA_3 and BA application on stem swelling

Seedlings were grown in the greenhouse. At the four to five leaf stage, they were transferred to a greenhouse at 20 °C under a 8-h photoperiod for 4 weeks. During this period, 25 μl of 1.0 mM GA_3 and 8.9 μM BA were respectively applied to the base of petiole of each plant every day for 4 weeks. The plants then grew for 2 weeks after the GA_3 and BA application. The control plants were continuously grown in 12-h photoperiod at 20 °C.

The top biomass, underground biomass, stem height, and stem width of at least 16 plants in each treatment were recorded.

2.4. Endogenous hormone determination

One gram of the leaves from the third completely expanded leaf from the top of the plant, and the swollen stems of middle portions was collected, which contained at least five plants grown under different photoperiods. The samples were immediately homogenized in 3 ml of 80% cold methanol (containing 10 mg l^{-1}-butyl hydroxytoluene) and 50 mg of polyvinyl pyrrolidione per gram fresh material under dark conditions for 10 min. The tissue residues were removed by centrifugation at 10,000 × *g* for 30 min after extraction at 4 °C for 24 h. The pellet was re-extracted as mentioned above. Then the supernatant pH was reduced to 3.0, and the gibberellins were extracted with ethyl acetate. After ethyl acetate was removed *in vacuo*, the extracts were separated by chemical partitioning in conjunction with elution through a Sep-Pak C_{18} cartridges (Waters Association). The endogenous GA_1 were then identified by comparing the ratios of molecular ion following the procedure described by Guo et al. (2004).

Analyses of endogenous hormone ZRs were carried out as described previously by Guo et al. (1994). The cytokinins were purified by Sep-Pak C_{18} cartridges (Waters Association), and

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