



Changes in soluble carbohydrates during phytochrome-regulated petiole elongation in watermelon seedlings

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Abstract

Changes in soluble carbohydrate composition and concentration in leaves and petioles of watermelon (*Citrullus lanatus* (Thunb) Matsum and Nakai cv. Sugar Baby) seedlings during early stages of phytochrome-regulated petiole elongation were investigated. Watermelon seedlings were grown in a controlled environment with 350 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetically active radiation (PAR) during a 12-h photoperiod. Low intensity end-of-day (EOD) light treatments (for 15 min) of red (R), far-red (FR) and FR followed by R (FR/R) were initiated when the seedlings were 14 days old. Seedling growth, and soluble carbohydrate concentration and composition in leaves and petioles were determined after 3 and 6 days of EOD light treatments. The EOD FR increased the petiole length and dry mass partitioned to petioles as early as 3 days into the treatment. This increased petiole dry mass in FR-treated plants was accompanied with an increase in reducing sugar (glucose and fructose) concentration in the petioles. Although both leaves and petioles showed this effect, the relative increase was greater in petioles than leaves. While the most abundant sugars in petioles were fructose and glucose, the predominant sugars in leaves were sucrose, raffinose, and stachyose. The photoreversion of FR induced changes in growth and sugar concentrations by R indicates the involvement of phytochrome in these processes.

Introduction

Stem and/or petiole elongation is one of the most prominent phytochrome-regulated growth responses in seedlings of many species (Casal and Smith 1989; Kasperbauer 1971; Lopez-Juez et al. 1990; Thomas and Raper 1985). Increase in FR (or low R:FR) in the light environment causes marked increases in extension growth rates of stems or petioles in some species. The increase in petiole or stem length is usually accompanied with increased dry mass partitioned to these plant parts. Rapidly elongating cells need more carbohydrates such as reducing sugars that are readily available for metabolism to meet increased demand for synthesis of structural material such as cell walls, and to maintain cell turgidity during elongation.

Several studies have shown that phytochrome regulates sugar translocation in light quality-regulated growth responses (Hoddinott 1983; Kasperbauer et al. 1970; Lercari 1982). Supplemental FR during the photoperiod increased reducing sugar accumulation in leaf blades and bulbs in *Allium cepa* L. compared to no-supplemental FR (Lercari 1982). In tobacco (*Nicotiana tabacum* L.) plants, EOD FR increased sugar concentration in leaves and stem compared to EOD R (Kasperbauer et al. 1970). Corn (*Zea mays* L.) leaves exposed at one end of the leaf with R and the other end with FR demonstrated translocation toward the FR exposed region (Hoddinott 1983). Yanovsky et al. (1995) reported that a single EOD FR treatment, compared to R, rapidly increased the activity of sucrose phosphate synthase in mustard (*Si-*

napis alba L.) leaves after the seedlings were transferred to darkness. However, these light treatments had no effects on the amounts of reducing sugars, sucrose, or starch in leaves during a 24-h dark period.

Young watermelon seedlings respond to EOD light treatments, and have been used to investigate phytochrome-mediated growth responses in several studies (Decoteau and Friend 1991; Graham and Decoteau 1997). The main phytochrome-regulated early growth response in watermelon seedlings was petiole elongation that occurred when seedlings were treated with EOD FR. Our preliminary experiments revealed that FR increased petiole elongation and dry mass partitioned to petioles in watermelon seedlings as early as 3 days of EOD light treatments compared to R or no-EOD control. These EOD light treatments did not have effects on the growth of other plant parts or dry mass partitioned to other plant parts at this stage of development. In the present study, we investigated changes in the soluble sugar composition and concentration in different parts of watermelon seedlings during early stages of petiole elongation in response to EOD light treatments. Carbohydrates were analyzed 3 and 6 days after the initiation of EOD light treatments. Since watermelon plants translocate raffinose oligosaccharides (e.g., raffinose and stachyose) in addition to sucrose, our research provides evidence on phytochrome-regulated effects on these sugars as well.

Materials and methods

Plant materials

Watermelon seedlings were grown in 250 ml styrofoam cups filled with Fafard Soilless Mix No. 3 (Fafard Inc., Anderson, SC). Two seeds were planted in each cup, watered, and grown in a controlled environment room. During the 12-h photoperiod, a constant $350 \mu\text{mol m}^{-2} \text{s}^{-1}$ of PAR was provided from four metal halide lamps (Philips Lighting Co., Somerset, NJ). Average day and night temperatures were 29 and 22 °C, respectively. After emergence, seedlings were thinned to one per cup. Fourteen-day-old (after planting), uniform seedlings of similar height with two leaves were selected for EOD light treatments.

EOD light treatments

The EOD light treatments began when seedlings were 14 d old and continued for 9 consecutive days. The following four light treatments were imposed immediately after the photoperiod each day. After the light treatments, seedlings were returned to the dark until the next photoperiod. There were 30 seedlings (replicates) per each light treatment.

1. R: 15 min of $9 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the 600–700 nm waveband provided by filtering radiation from six cool-white, 40-W fluorescent lamps (Philips Lighting Co., Somerset, NJ) through a Roscolux #19 acetate filter (Rosco Inc., Port Chester, NY)
2. FR: 15 min of $68 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the 700–780 nm waveband provided by filtering radiation from two 150-W internal-reflector, incandescent lamps (Philips Lighting Co., Somerset, NJ) through a polyacrylic sheet of cast acrylic #2711, dark red (Rohm and Hass, Bristol, PA)
3. FR/R: 15 min of FR treatment (as above) immediately followed by 15 min of R treatment (as above). This treatment was included to test the photoreversibility of phytochrome-regulated responses.
4. Control: No EOD light treatments (seedlings were immediately placed in the dark at completion of regular photoperiod)

After 3 and 6 days of EOD treatments, seedlings were sampled for growth measurements and carbohydrate analysis. Sampling was done 9 h after the initiation of the photoperiod. The first 2 or 3 leaf blades (counted from the bottom of the seedling and designated as leaf 1, 2, and 3, respectively) and their petioles (petiole 1, 2, and 3, respectively) were dissected. Leaf area, using a LI-COR 3100 area meter (Lincoln, NE), and petiole length were measured. Dry mass of leaves and petioles were determined separately after oven drying for 5 days at 70 °C. For carbohydrate analysis, tissues from 3 seedlings were pooled to make one replicate, and there were 4 replicates per treatment. These tissues were immediately frozen in liquid nitrogen and stored at –70 °C. Frozen tissues were then freeze-dried and ground to a fine powder in a mortar with a pestle.

The entire experiment was repeated twice, and similar growth effects were observed for EOD light treatments. Carbohydrate analysis was done with tissues from one representative experiment, and growth

Table 1. End-of-day (EOD) light treatment effects on growth and dry mass partitioned to plant parts of watermelon seedlings after 3 days of EOD light treatments

EOD light treatment ^z	Length (cm)			Area (cm ²)		Dry Mass (mg)				
	H ^y	P1	P2	L1	L2	H	P1	P2	L1	L2
R	6.1 a ^x	3.3 b	2.0 b	24.8 a	15.4 a	21.1 a	8.4 b	7.8 b	90.3 a	54.3 a
FR	6.7 a	5.0 a	6.3 a	29.8 a	18.8 a	27.6 a	14.2 a	17.2 a	110.0 a	64.7 a
FR/R	6.2 a	3.3 b	2.5 b	27.6 a	17.7 a	21.8 a	9.8 b	8.8 b	97.6 a	55.9 a
Control	5.8 a	3.0 b	2.3 b	26.0 a	16.8 a	21.2 a	9.1 b	6.4 b	95.1 a	60.6 a

^z R – red (15 min), FR – far-red (15 min), FR/R – FR (15 min) immediately followed by R (15 min), and C – control (without EOD light).

^y H – hypocotyl, P1, P2 – petiole 1, 2, respectively, L1, L2 – leaf 1, 2, respectively, (counted from the bottom of the seedling). ^x Values are means of five replicates. Mean separation in columns by LSD (P=0.05).

and carbohydrate data of that experiment are presented. Analysis of variance was performed to test treatment effects, and least significant difference (LSD) was calculated for mean comparison.

Extraction and analysis of soluble carbohydrates

Soluble carbohydrates were extracted from freeze-dried tissue with methanol:chloroform:water (12:5:3, v:v:v) as described by Miller and Langhans (1989). Extracted carbohydrates were dissolved in HPLC-grade water and subjected to high-performance anion exchange chromatography coupled with pulsed amperometric detection (HPAE-PAD) using a Dionex (DX-300) system. The chromatography system was equipped with a Carbopac PA-1 column and a gold electrode. The waveform potentials were: +0.05 V, 0.00–0.30 s; +0.60 V, 0.31–0.43 s; –0.80 V, 0.44–0.74 s. Sugars were eluted for 20 min at a flow rate of 1.0 ml min⁻¹ at 9.6 MPa, using the following gradients of eluents: a linear gradient from 0 to 20 mM sodium acetate in 200 mM NaOH (0 to 15 min); a linear decreasing gradient from 20 to 0 mM sodium acetate in 200 mM NaOH (15 to 16 min); 200 mM NaOH (16 to 20 min). All the soluble carbohydrates in the extracts were completely resolved with the above elution profile except that glucose and galactose were co-eluted. Samples were eluted with 20 mM NaOH for 40 min (all other conditions as above) to separate and quantify glucose and galactose. Sugars were identified by retention time and quantified according to calibration curves derived for peak areas corresponding to different amounts of authentic standard sugars (Sigma, St. Louis, MO).

Results

EOD light effects on seedling growth

Compared to the control, R did not affect growth of seedlings, whereas FR significantly increased petiole length and dry mass partitioned to petioles. After 3 days of EOD, FR, compared to the control, increased lengths of petiole 1 and 2 by 167% and 274%, respectively, and dry mass partitioned to petiole 1 and 2 by 156% and 340%, respectively (Table 1). Similar treatment trends on petiole growth existed at 6 days of EOD (data not shown). Although the values were not statistically significant, a slight increase in the leaf area and leaf dry mass was apparent in leaf 1 and leaf 2 of FR-treated seedlings.

Soluble carbohydrates in leaves

The soluble carbohydrates in leaves were composed of glucose, galactose, fructose, sucrose, raffinose, and stachyose. Sucrose was the most abundant soluble carbohydrate in leaves followed by stachyose. Galactose was present at very low concentration (less than 1 mg g⁻¹ DW). After 3 days of EOD treatments, FR increased total soluble carbohydrate (TSC) concentration in leaf 1 and 2 by 16% and 12%, respectively, compared to the control or R (Table 2). Among individual sugars, significant effects of EOD treatments were seen only in glucose and fructose, where FR significantly increased their concentrations in both leaves compared to all other treatments. The increase in glucose and fructose in leaf 1 was 23% and 47%, respectively, while in leaf 2, it was 35% and 49%, respectively. The FR effects were photoreversed by R (FR/R treatment) in the case of glucose and fructose concentrations, whereas effects were variable in the case of TSC, sucrose and raffinose.

Table 2. Soluble carbohydrate concentrations in leaves (counted from the bottom of the seedling) of watermelon seedlings after 3 or 6 days of end-of-day (EOD) light treatments.

EOD treatment ^z	Carbohydrate concentration (mg g ⁻¹ dry mass)						
	Glu ^y	Gal	Fru	Suc	Raf	Sta	TSC
3 days after EOD – Leaf 1							
R	4.6 b ^x	0.13 a	5.6 b	14.2 bc	2.4 c	8.8 c	35.8 c
FR	5.9 a	0.13 a	8.4 a	15.4 b	3.6 ab	11.1 a	44.5 a
FR/R	4.1 b	0.11 a	5.2 b	17.2 a	3.4 b	9.6 bc	39.6 b
C	4.8 b	0.09 a	5.7 b	13.6 c	3.8 a	10.5 ab	38.4 bc
3 days after EOD – Leaf 2							
R	3.0 c	0.10 a	3.1 c	13.7 c	3.2 c	9.6 a	32.7 c
FR	4.6 a	0.10 a	6.1 a	18.2 ab	4.5 b	9.8 a	43.3 a
FR/R	2.5 d	0.10 a	2.8 c	20.2 a	5.1 a	9.9 a	40.6 ab
C	3.7 b	0.11 a	4.1 b	16.2 bc	4.2 b	10.7 a	38.8 b
6 days after EOD – Leaf 3							
R	6.6 b	0.11 b	8.7 b	25.6 a	5.9 a	8.6 a	55.6 b
FR	17.5 a	0.32 a	22.9 a	25.6 a	6.4 a	7.8 a	80.4 a
FR/R	3.5 b	0.13 b	4.9 b	24.2 a	6.9 a	9.4 a	48.9 b
C	7.0 b	0.14 b	8.8 b	27.6 a	6.5 a	8.8 a	58.8 b

^z R – red (15 min), FR – far-red (15 min), FR/R – FR (15 min) immediately followed by R (15 min), and C- control (without EOD light). ^yGlu – glucose, Gal – galactose, Fru – fructose, Suc – sucrose, Raf – raffinose, Sta – stachyose, TSC – total soluble carbohydrates. ^xValues are means of 4 replicates. Mean separation in columns by LSD (P=0.05).

At 6 days of EOD, TSC concentration increased by about 20% compared to 3 days of EOD treatments in all leaves in all treatments. However, significant light treatment effects were seen only in leaf 3, therefore, carbohydrate data were presented for leaf 3 only at 6 days EOD (Table 2). The FR increased TSC in leaf 3 by 37% compared to the control. Among individual sugars, the most prominent changes occurred in glucose and fructose levels in leaf 3. The FR increased glucose and fructose concentrations in leaf 3 by 151% and 160% respectively, compared to the control, whereas R or FR/R treatment had no effect.

Soluble carbohydrates in petioles

At 3 days of EOD, the TSC concentrations were higher in petioles than in leaves (Table 3). All the sugars identified in leaves were also present in petioles. However, the relative proportion of individual sugars in the petioles was different compared to the leaves. The most abundant sugar in petioles was fructose followed by glucose. Sucrose, raffinose, and stachyose concentrations in petioles were lower than those of in leaves. Galactose concentration was higher in petioles than in leaves, but it was still less than 1 mg g⁻¹ DW.

At 3 days of EOD, FR significantly increased TSC concentration in petioles compared to other light

treatments (Table 3). This increase in petiole 1 and 2 was 55% and 80%, respectively, compared to the control. Consistent with its effects in leaves, FR increased glucose and fructose concentrations significantly in petioles compared to R or control. The FR almost doubled glucose and fructose concentrations compared to the control. At 6 days of EOD, petiole TSC concentrations were greater than that at 3 days of EOD in all treatments (Table 4). For example, at 6 days of EOD, TSC in petiole 1 increased by 74% in FR treated seedlings while it was increased by 100% in control seedlings compared to those of at 3 days of EOD. The effects of FR on increasing glucose and fructose concentrations in petioles were further increased at 6 days of EOD compared to those of at 3 days of EOD. In petioles, FR effects were greater in the younger petiole (petiole 3) than the older petiole (petiole 1). For example, at 6 days of EOD, FR increased glucose concentrations by 52%, 161% and 254%, and fructose concentrations by 57%, 150% and 179% in petiole 1, 2 and 3, respectively, compared to the control. On the other hand, FR decreased sucrose, raffinose, and stachyose concentrations in all petioles compared to the control at 6 days of EOD.

Table 3. Soluble carbohydrate levels in petiole 1 and petiole 2 (counted from the bottom of the seedling) of watermelon seedlings at 3 days of end-of-day (EOD) light treatments

EOD treatment ^z	Carbohydrate concentration (mg g ⁻¹ dry mass)						
	Glu ^y	Gal	Fru	Suc	Raf	Sta	TSC
	Petiole 1						
R	14.7 b ^x	0.24 a	22.4 b	10.4 a	3.5 bc	4.2 a	55.4 b
FR	27.7 a	0.31 a	41.5 a	9.8 a	3.1 c	4.4 a	86.8 a
FR/R	15.3 b	0.31 a	21.6 b	11.3 a	4.7 a	4.8 a	57.9 b
C	15.8 b	0.30 a	21.0 b	10.3 a	4.0 b	4.6 a	56.0 b
	Petiole 2						
R	16.7 b	0.39 bc	24.1 b	8.5 a	3.1 a	3.6 a	56.3 b
FR	34.1 a	0.56 a	49.3 a	9.1 a	2.7 a	3.3 a	99.1 a
FR/R	13.2 c	0.41 b	20.8 b	8.3 a	3.6 a	4.8 a	51.1 b
C	14.4 bc	0.29 c	21.5 b	8.3 a	4.3 a	4.6 a	55.1 b

^z R – red (15 min), FR – far-red (15 min), FR/R – FR (15 min) immediately followed by R (15 min), and C – control (without EOD light).

^yGlu – glucose, Gal – galactose, Fru – fructose, Suc – sucrose, Raf – raffinose, Sta – stachyose, TSC – total soluble carbohydrates. ^xValues are means of 4 replicates. Mean separation in columns by LSD (P=0.05).

Table 4. Soluble carbohydrate concentrations in petioles of watermelon seedlings after 6 days of end-of-day (EOD) light treatments

EOD treatment ^z	Carbohydrate concentration (mg g ⁻¹ dry mass)						
	Glu ^y	Gal	Fru	Suc	Raf	Sta	TSC
	Petiole 1						
R	33.7 b ^x	0.38 b	42.9 b	17.1 a	7.1 a	6.0 a	107.3 b
FR	56.4 a	0.55 a	70.4 a	15.6 a	4.0 b	4.2 b	151.3 a
FR/R	40.0 b	0.42 b	48.2 b	18.4 a	7.2 a	5.8 a	120.0 b
C	37.1 b	0.27 c	44.7 b	16.2 a	6.9 a	6.6 a	111.8 b
	Petiole 2						
R	25.1 b	0.44 b	33.5 b	15.6 ab	5.7 a	4.6 a	84.9 b
FR	63.7 a	1.07 a	79.6 a	12.4 b	3.7 b	3.3 b	163.8 a
FR/R	28.3 b	0.52 b	36.7 a	18.6 a	5.4 a	5.1 a	94.7 b
C	24.4 b	0.49 b	31.9 b	17.3 a	5.8 a	4.9 a	84.7 b
	Petiole 3						
R	36.5 b	0.52 b	47.4 b	15.6 a	3.8 b	3.5 b	107.3 b
FR	93.9 a	0.80 a	102.3 a	11.1 b	2.3 c	2.9 b	213.2 a
FR/R	32.3 b	0.50 b	45.7 b	16.3 a	4.0 b	3.3 b	102.1 b
C	26.5 b	0.47 b	36.7 b	16.5 a	5.2 a	4.3 a	89.6 b

^z R – red (15 min), FR – far-red (15 min), FR/R – FR (15 min) immediately followed by R (15 min), and C – control (without EOD light).

^yGlu – glucose, Gal – galactose, Fru – fructose, Suc – sucrose, Raf – raffinose, Sta – stachyose, TSC – total soluble carbohydrates. ^xValues are means of 4 replicates. Mean separation in columns by LSD (P=0.05).

Discussion

The main growth effect of EOD FR in watermelon seedlings was the increase in petiole length and dry mass partitioned to the petioles. This increased petiole dry mass in EOD FR treated plants was accompanied with an increase in reducing sugar (glucose and fructose) concentration in the petioles as early as 3 days of EOD. Although both leaves and petioles showed this result, the degree was greater in petioles

than leaves. Increased metabolic activities and the synthesis of structural polysaccharides such as cell walls in elongating petioles of FR treated plants require increased supply of hexose sugars as substrates. These effects were not observed in either R or FR/R treatments. The photo-reversibility of the results suggests that the reducing sugar amounts are under phytochrome control in young leaves and petioles.

Consistent with the FR effects on petiole growth, the effects of FR on soluble carbohydrates was greater

in younger petioles (especially petioles formed or became visible after the EOD treatments were initiated) than older petioles. The greatest effects of FR on both elongation growth and increased levels of glucose and fructose were observed in petiole 3, at 6 days of EOD treatments. The greater effects on younger leaves and petioles may be due to the greater surface area directly exposed to the light stimulus (older leaves may have been shaded by young leaves) (Graham and Decoteau 1997; Yanovsky et al. 1995). Another possibility is that the phytochrome control is more pronounced in actively growing and expanding young leaves and petioles where a rapid influx of reducing sugars is essential.

Raffinose family oligosaccharides (e.g., raffinose and stachyose) are important transport sugars in addition to sucrose in plants of Cucurbitaceae family including watermelon (Chrost and Schmitz 1997; Gross and Pharr 1982). In the present study, considerable amounts of stachyose and raffinose were detected in watermelon seedlings. The concentrations of these sugars were higher in leaves than in petioles. Once these oligosaccharides are translocated to sink tissues, galactose is removed by α -galactosidase to result in sucrose. Sucrose is hydrolyzed by either invertase or sucrose synthase to result in glucose (UDP-glucose in the case of sucrose synthase) and fructose, and then utilized for metabolic and synthetic activities of the sink tissues. There were relatively lower amounts of galactose present in petioles compared to raffinose, stachyose, glucose, and fructose. These results imply that galactose released by raffinose or stachyose is rapidly converted to other sugars or utilized for metabolic activities.

Increased activity of sucrose hydrolyzing enzymes is required to attract more reducing sugars to sink tissues (Ho 1988). The increased expression of these enzymes may increase the sink strength of petioles, and thereby increase sucrose (or raffinose or stachyose) translocation into petioles. Hormones such as gibberellins often regulate the expression and activity of these sucrose hydrolyzing enzymes in plant tissues. In several elongating tissues, such as bean (*Phaseolus vulgaris*) internodes (Morris and Arthur 1985), *Avena* internodes (Kaufman et al. 1968), and elongating dwarf pea (*Pisum sativum* L.) shoots (Wu et al. 1993), gibberellin has been shown to increase invertase activities.

Gibberellin biosynthesis has been reported to be under phytochrome control in several species such as bean (Beall et al. 1996), cowpea (Garcia-Martinez et

al. 1987), and pea (Murfet 1988). Our parallel experiments conducted with the present study indicated that phytochrome-regulated petiole and stem elongation in watermelon seedlings was mediated by an increase in active gibberellin biosynthesis (our unpublished data). Those observations support the possibility that the increase in reducing sugars in elongating petioles of FR treated watermelon seedlings is a result of increased invertase activity mediated by increased GA biosynthesis.

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