Original Article

PHOTOSYNTHATE PARTITIONING AND MORPHOANATOMICAL ASPECTS OF PHOTOMORPHOGENIC MUTANTS OF TOMATO

PARTIÇÃO DE FOTOASSIMILADOS E ASPECTOS MORFOANATÔMICOS EM TOMATEIROS MUTANTES FOTOMORFOGENÉTICOS

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ABSTRACT: The aim of this study was to analyze photosynthate partitioning in tomato photomorphogenic mutants at the ends of the vegetative (40 days after emergence [DAE]) and reproductive (69 DAE) stages and to determine its interaction with morphoanatomical aspects. The mutants *aurea* (*au*), phytochrome-deficient, *high pigment-1* (*hp1*), light-exaggerated response, were studied along with the non-mutant Micro-Tom (MT) cultivar. The plants were analyzed at 40 and 68 DAE to identify photosynthate source organs and tissues as well as the target organs of remobilized photosynthate during the reproductive stage. The plants were evaluated for their internal and external morphology as well as the percentage of dry mass of their organs. Photosynthate allocation in the *hp1* mutant occurred primarily in the roots and leaves, and allocation in the *au* mutant occurred primarily in fruits. The *au* mutant showed a high capacity for photosynthate remobilization to fruit during the reproductive stage, and the predominant sources of these remobilized photosynthates were the leaf spongy parenchyma, the root vascular cylinder and the marrow stem.

KEYWORDS: *Au*. *Hp1*. Micro-Tom. Photomorphogenesis. *Solanum lycopersicum* L.

INTRODUCTION

The distribution of photosynthates among different organs of a plant is an important process inherent in the genotype and also reflects the plant's adaptability to different environmental conditions (BENINCASA, 1988; KASPERBAUER, 1988). Among environmental variables, radiation intensity and quality can induce changes in internal and external morphology as well as the allocation of photosynthates in plants (BALLARÉ et al., 1992).

In the reproductive stage of plants, fruits are strong sinks where photosynthates are preferentially allocated (PELUZIO et al., 1995), and plants that synthesize larger amounts of photosynthate tend to allocate more dry mass to fruit compared with other sinks (FLORES, 2007; PELUZIO et al., 1995). An understanding of photosynthate allocation is of fundamental importance for the cultivation of different agronomic crops, especially those in which the fruits are the exploited organ.

Light is as a fundamental factor for photosynthate production through photosynthesis and also modulates many aspects of plant development such as seed germination and flowering thorough photomorphogenesis. Although the intensity of radiation is an environmental factor that has been well explored in the commercial cultivation of plants, the exploration of radiation quality is still incipient. However, although there has been an increase in the protected cultivation of plants in under colored nets and screens that influence plant development and product quality (CORRÊA et al., 2012; OLIVEIRA et al., 2009). Studies examining the interaction between light quality and photosynthate partitioning are rare, and the tissue origin and final destination of photosynthate remobilized during plant development are unknown.

Studies of radiation quality in plants are very complex because the plant photoreceptor apparatus is interactive; phytochromes A, B, C, D and E interact among themselves, and phytochromes also interact with phototropins and cryptochromes, which are blue and ultraviolet A photoreceptors that induce or modulate photomorphogenic responses (CHEN et al., 2004). Thus, a physiological response may be determined not only by a specific spectrum of radiation but can also be altered by the influence of another spectrum. This high degree of complexity occurs because of intraspecific interactions among different phytochromes, which are red and far-red photoreceptors, and interspecific interactions with cryptochromes and phototropins, which are blue and ultraviolet A photoreceptors (CHEN et al., 2004). Because solar radiation comprises all spectra, the use of photomorphogenic mutant plants with mutations in specific photoreceptors allows for more

accurate studies regarding the influence of individual solar spectra on plant growth and development.

A series of phytochrome mutants are available for tomato (*Solanum lycopersicum* L.) that have been well characterized at the physiological and genetic level (MURAMOTO et al. 2005; PETERS et al., 1998;; SHARMA et al., 1993; SHITTENHELM et al., 2004; VAN TUINEN et al. 1997). The most well studied mutants include *aurea* (*au*), which is deficient in chromophore synthesis (MURAMOTO et al. 2005) and therefore deficient in all phytochromes (SHARMA et al., 1993), and *high pigment-1* (*hp1*), which has a mutation in a signal transduction pathway and demonstrates hypersensitivity to light (PETERS et al., 1998; VAN TUINEN et al. 1997).

Admittedly plants growing in shady environments invest more in biomass in leaves much of compared with other vegetative organs, and since because the *aurea* mutant is deficient in photoreceptors of red and infrared radiation, would expect a similar behavior this mutant may behave similarly to shade-grown plants., and because *hp1* mutant is hypersensitive to light may behave similarly to sun-grow plants. However, it is not known how the means by which a specific deficiency in phytochrome photoreceptors or its light transduction pathway would affect this response is not known.

The aim of this study was to analyze photosynthate partitioning in the tomato photomorphogenic mutants *au* and *hp1* at the end of the vegetative and reproductive stages to identify photosynthate source organs and tissues as well as the destination of remobilized photosynthate.

MATERIAL AND METHODS

This experiment was conducted at the Institute of Agricultural and Environmental Sciences, Universidade Federal do Mato Grosso, located at a latitude of 11°51'51" S and a longitude of 55°30'09" W.

Two photomorphogenic mutants of *Solanum lycopersicum* L. (Solanaceae) that were introgressed into cv. Micro-Tom (MT) (CARVALHO et al., 2011b) were used: the *aurea* (*au)* mutant, which is defective in the biosynthesis of phytochrome, and the *high pigment 1* (*hp1*) mutant, which exhibits exaggerated responses to light. Non-mutant MT plants were used as the control.

The plants were maintained in a greenhouse completely covered with a dark screen designed to create a level of 50% shading and grown in pots (150 mL) with a substrate composed of dark soil, organic matter and vermiculite (1:1:1), and 5 g of 4-14-8 NPK formulated fertilizer was added to each pot. The plants were treated weekly with a foliar fertilizer containing all macro and micronutrients and watered daily. The experiment was conducted using a completely randomized design.

The plants were collected for analysis at the end of the vegetative stage (40 days after emergence (DAE) and at the end of the reproductive stage (69 DAE). Eight plants were selected from each genotype (mutants and wild-type) for analyzing photosynthate partitioning. For morphological and anatomical studies, the organs of five mutant and five wild-type plants were analyzed. Four sections were obtained from each organ for anatomical analysis.

At the end of the vegetative and reproductive stages, plants were harvested and their bodies were divided into root, stem, leaf and fruit. Fruits were obtained only at 69 DAE and placed in an oven with forced air circulation under a constant temperature of 65°C until a constant biomass weight was achieved. The analysis of photosynthate partitioning was based on the percentage of dry matter among the studied organs.

To investigate photosynthate partitioning, source tissues and organs containing photosynthate that was remobilized or allocated at the end of the plant reproductive stage were analyzed in addition to morphological and anatomical aspects. Plants at 40 DAE and 69 DAE were collected for the analysis of photosynthate partitioning, and tissue samples were fixed for anatomical analyses. At 40 DAE, the organs were measured for external morphology analysis.

External morphology was analyzed by measuring the following: a) plant height from the base of the stem to the apex; b) leaf width and length, width of the last leaflet, length of the last leaflet, petiole length and leaf area; and c) length of the stem internode and stem diameter. For standardizing the measurements of internode and stem diameter, the second internode from the base of the plant to the apex was consistently used. The fifth leaf from the base of the plant to the apex was adopted for studying petiole length, leaf length, leaf width, length of the last leaflet and width of the last leaflet (this last parameter was measured in the middle third of the leaflet). For analysis of leaf area, all the leaves produced by plant were used, and the measurement was performed using a plant leaf area meter (LI-3100C).

The following anatomical aspects were evaluated: a) the thickness of the epidermis, cortex

and vascular cylinder in the roots; b) the thickness of the epidermis, cortex, marrow and xylem in the stem; c) leaf thickness, thickness of the vascular bundle measured in the midrib between epidermis, width the vascular bundle measured in the equatorial direction, thickness of the abaxial and adaxial epidermis as well as the spongy parenchyma and palisade parenchyma in the leaves. The central leaflet of the leaf at the fifth node from the base to the apex was used for analysis. For the anatomical analyses, stem cuttings were made at the first mature internode from the apex, and the roots were analyzed 1 cm from the stem base. The plant material collected was fixed in formaldehyde, acetic acid and 70% ethanol (FAA 70) for 24 hours, and the material was later transferred to 50% alcohol until transverse free-hand sections were cut. One organ was obtained from five plants of each genotype, and four sections were obtained from each organ and each section was measured once for a total of 20 measurements per treatment.

The tissues were analyzed using a photomicroscope coupled with an ocular micrometer.

All the data were statistically analyzed using Sisvar software for variance analysis and Tukey averages test, adopting an error level of 5%.

RESULTS AND DISCUSSION

Except for the ratio of root dry mass to leaf dry mass (F=2.6, $p \leq 0,05$) (Figure 1C), the *hp1* mutant accumulated a higher amount of root biomass relative to total dry mass (F=12; $p \leq 0,05$) and relative to the other organs (taken together or separately) compared with MT and the *au* mutant (Figure 1). The *hp1* mutant also exhibited a higher ratio of relative leaf dry mass to total dry mass (F=4.1; $p \leq 0,05$) (Figure 2A). However, this mutant presented a lower ratio of stem dry mass to root dry mass (F=9,4; $p \leq 0,05$) (Figure 3D) as well as a lower fruit dry mass in relation to total dry mass (F=3,9; $p \leq 0,05$) (Figure 4A) and in relation to the other organs together (F=5,1; $p \leq 0,05$) (Figure 4B). *hp1* had a lower fruit dry mass in relation to leaf dry mass (F=8; $p \leq 0,05$) (Figure 4E), compared to MT and *au*, and *hp1* had a lower ratio of fruit dry mass in relation to root dry mass compared with the *au* mutant (F=12; $p \leq 0,05$) (Figure 4C).

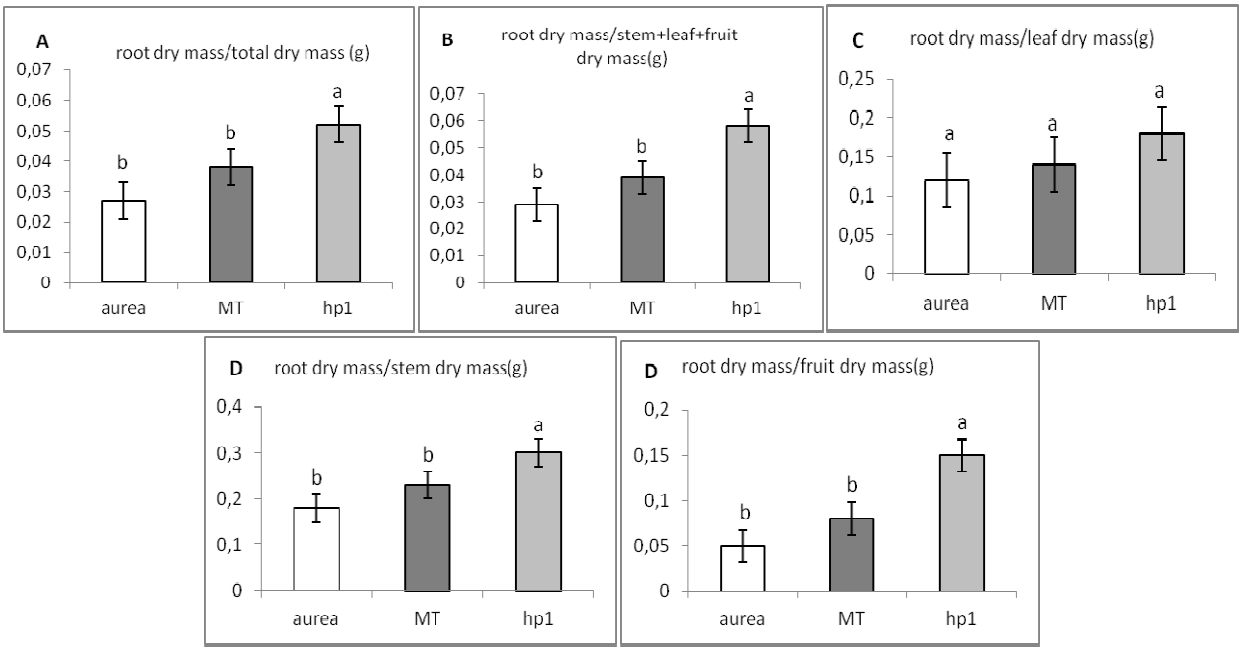

Figure 1. Root-related photosynthate partitioning in the photomorphogenic mutants aurea and hp1 as well as the Micro-Tom (MT) cultivar. Analyses were performed at the end of the reproductive stage (68 DAE). Columns with same letters do not differ by Tukey test at 5%. The bars represent standard error.

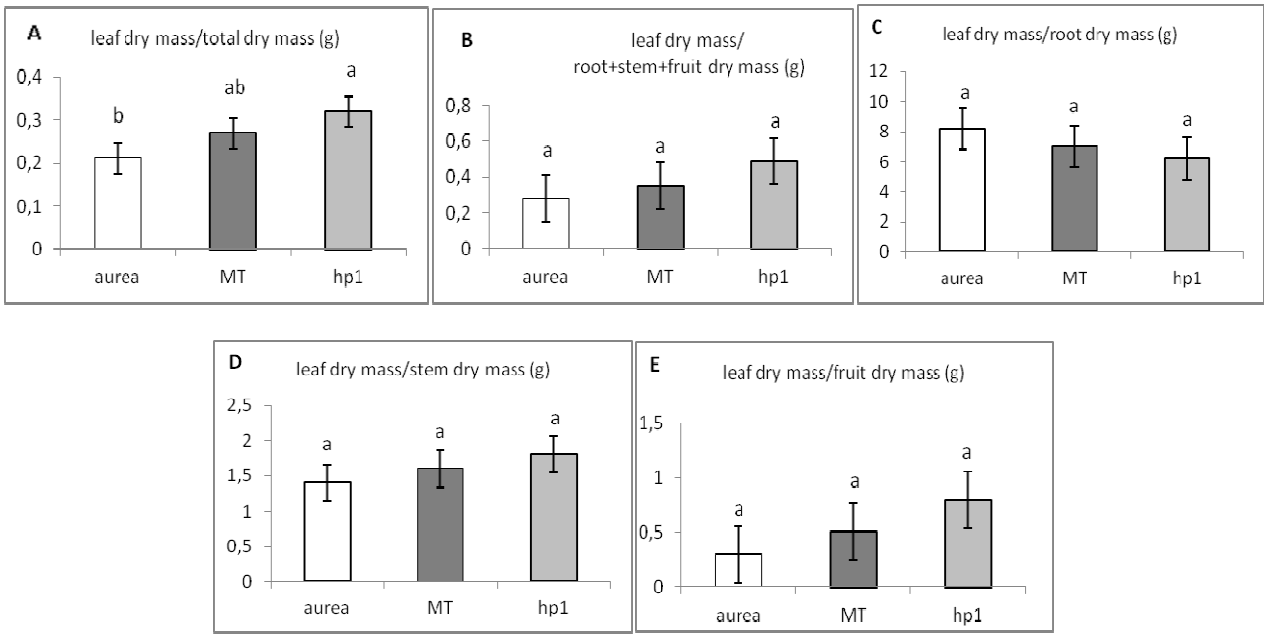

Figure 2. Leaf-related photosynthate partitioning in the photomorphogenic mutants *aurea* and *hp1* as well as the Micro-Tom (MT) cultivar. Analyses were carried out at the end of the reproductive stage (68 DAE). Columns with same letters do not differ by Tukey test at 5%. The bars represent standard error.

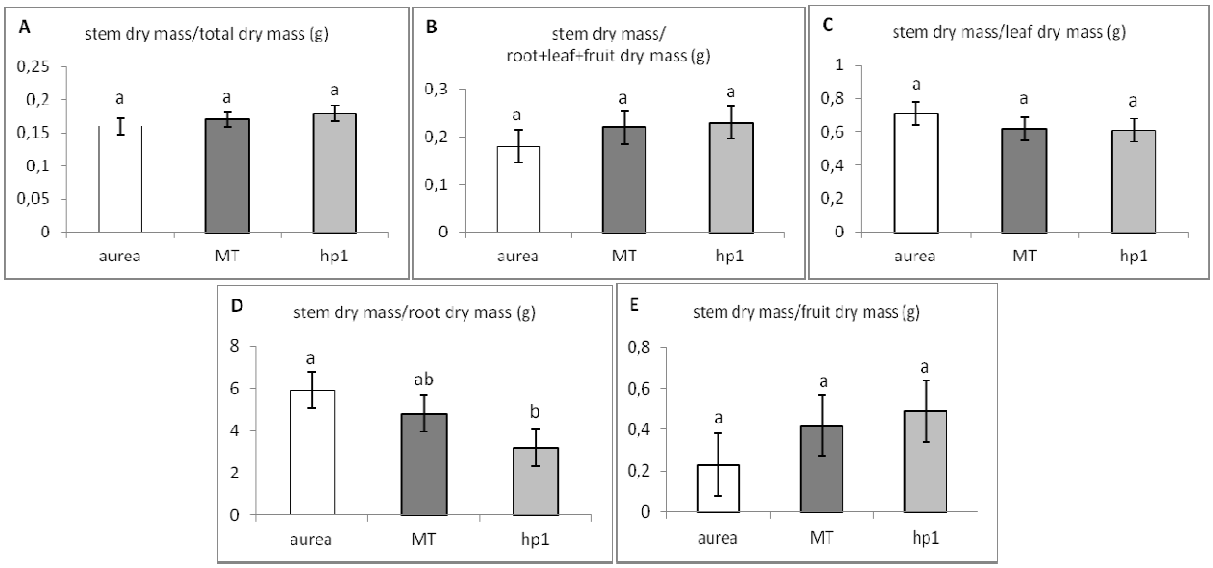

Figure 3. Stem-related photosynthate partitioning in the photomorphogenic mutants *aurea* and *hp1* as well as the Micro-Tom (MT) cultivar. Analyses were carried out at the end of the reproductive stage (68 DAE). Columns with same letters do not differ by Tukey test at 5%. The bars represent standard error.

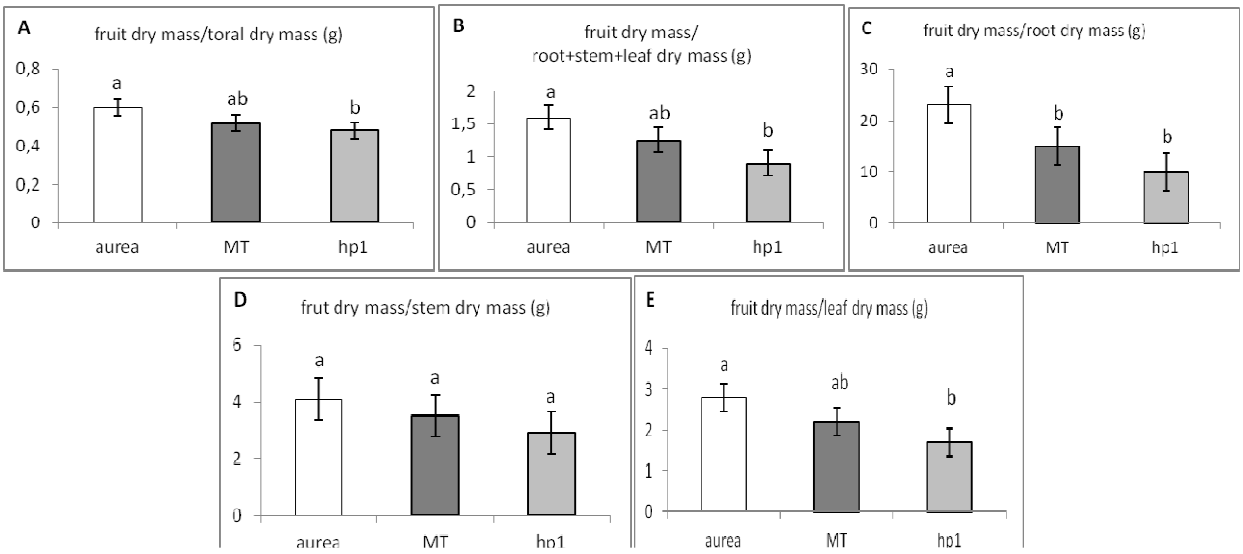

Figure 4. Fruit-related photosynthate partitioning in the photomorphogenic mutants *aurea* and *hp1* as well as the Micro-Tom (MT) cultivar. Analyses were carried out at the end of the reproductive stage (68 DAE). Columns with same letters do not differ by Tukey test at 5%. The bars represent standard error.

Although the *hp1* mutant is hyper-responsive to light-mediated events and has increased levels of photosynthetic pigments (chlorophyll and carotenoids) as well as higher rates of potential photosynthesis in relation to the MT cultivar and the *au* mutant (MELO et al., 2009), we did not find evidence that this was related to the higher biomass accumulation in fruits (Figure 4). In tomato plants, the organ of greatest interest is the fruit; however, the high photosynthetic potential of this mutant was not reflected by an increase in fruit productivity because the root and leaf were the preferential organs for photosynthate allocation (Figures 1 and 2). The *hp1* mutant is more often referenced as having an exaggerated light signal transduction pathway rather than as a mutant that overexpresses phytochrome (AZARI et al., 2010; CARVALHO et al., 2011a; PETERS et al., 1998; VAN TUINEN et al., 1997), and it is possible to compare the response of this mutant to that of other mutants known to overexpress phytochromes. Compared to other genotypes, the *hp1* mutant allocated less photosynthate to fruits in this study (Figure 4); this result was also observed for the tomato mutant *Dara-5*, which has a higher content of phytochrome B and did not exhibit a significant increase in biomass fruit production despite a quantitative increase in plant biomass (SHITTENHELM et al., 2004).

The high capacity for responses to events mediated by the phytochromes may suggest that the *hp1* mutant is a sun plant. According to Nakazono et al. (2001), *Euterpe edulis* Mart. tended to exhibit higher biomass accumulation in roots when grown under 50% shading, which is similar to what was observed in *hp1* tomato mutants grown under 50% shading (Figure 1). The preferential accumulation of photosynthate in roots is a typical characteristic of a plant grown in bright sunlight (RAMOS et al., 2004); higher root biomass is needed to absorb water and nutrients from the soil to meet the demand of the aerial parts, which also tend to increase in mass under bright conditions due to the accumulation of photosynthate. This response was also shown in this work based on the high ratio of leaf dry mass to total dry mass (Figure 2). According to Carvalho et al. (2011a), Moraes et al. (2003) and Nakazono et al. (2001) such behavior is a strategy to support a higher photosynthetic capacity and high transpiration rate. According to Liu et al. (2004), in addition to roots, the large investment in leaf biomass (as noted in Figure 2) is due to high levels of pigments such as chlorophylls and carotenoids, which are characteristic of this mutant (MELO et al., 2009).

In the *hp1* mutant, the thickness of the spongy parenchyma at 40 DAE (Table 2) and 68 DAE (Table 3) as well the total leaf blade thickness at 40 DAE (Table 2) were increased compared with those of the other genotypes, and these data corroborate the work of Melo et al (2011). Therefore, it is expected that the higher biomass accumulation in the leaves of this mutant in relation to the total dry mass of the plant (Figure 2) occurs specifically as a result of mesophyll parenchyma characteristics because there was no significant

difference between the leaf area among genotypes (Table 1) apart from the fact that the leaf length was decreased in this mutant compared with MT and *au* (Table 1). The increased thickness of mesophyll chlorenchyma is a typical feature of sun plants and serves as both a mechanism to provide homogeneous canalization of the incident radiation and an avoidance mechanism to prevent photo-oxidative damage (TERASHIMA et al., 2001). According to Gondim et al. (2008), leaves grown under high light intensities tend to be smaller and thicker with increased mesophyll per unit area, fewer intercellular spaces in the mesophyll and greater stomatal and vein density when compared with leaves exposed to shade. Considering that the *hp1* mutant exhibits an exaggerated response to light, it is expected to behave like a sun plant even when cultivated in the shade.

Table 1. External morphology of the photomorphogenic mutants *aurea* and *hp1* as well as the Micro-Tom cultivar at the end of the vegetative stage (40 DAE).

	Leaf morphology (mm)				
Genotype	Petiole length	Leaf width	Leaf length	Width of the last leaflet	Length of the last leaflet
Micro-Tom	6,75 a ± 0,29	37,71 a ± 0,19	41,75 a ± 0,13	12,89 a ± 0,16	23,37 a ± 0,19
aurea	7,50 a ± 0,27	39,16 a ± 0,17	49,63 a ± 0,13	12,98 a ± 0,20	24,47 a ± 0,17
hp1	5,99 a ± 0,31	29,30 a ± 0,16	32,26 b ± 0,12	12,02 a ± 0,16	20,00 a ± 0,18
	Stem morphology				
	Stem diameter (mm)	Internode length (mm)	Plant height (mm)	Leaf area (cm^2)	
Micro-Tom	4,08 a ± 0,20	4,40 b ± 0,25	84.36 ab ± 0,12	37,55 a ± 0,20	
aurea	3,89 a ± 0,20	6,50 a ± 0,26	102.19 a ± 0,16	51,40 a ± 0,22	
hp1	3,70 a ± 0,18	2,55 b ± 0,24	74,06 b ± 0,14	36,61 a ± 0,21	

Among genotypes, averages followed by the same letter do not differ by the Tukey test ($p \leq 0.05$). Averages are followed by percentage of variation coefficients.

Table 2. Tissue thickness of the photomorphogenic mutants *aurea* and *hp1* as well as the Micro-Tom cultivar at the end of the vegetative stage (40 DAE).

	Leaf and leaf epidermis thickness (µm)			
Genotypes	Abaxial epidermis	Adaxial epidermis	Leaf blade	
Micro-Tom	19,46 b ± 0,20	25,20 a ± 0,09	260,07 b ± 0,16	
aurea	22,80 a ± 0,21	25,92 a ± 0,08	282,99 b ± 0,13	
hp1	19,10 b ± 0,21	25,60 a ± 0,10	328,51 a ± 0,13	
	Leaf vascular bundle and leaf parenchyma thickness (µm)			
	Palisade parenchyma	Spongy parenchyma	Polar vascular bundle	Equatorial vascular bundle
Micro-Tom	110,44 a ± 0,15	157,10 b ± 0,20	648,64 b ± 0,16	279,45 b ± 0,14
aurea	122,72 a ± 0,18	158,35 b ± 0,19	777,59 a ± 0,17	396,96 a ± 0,16
hp1	124,24 a ± 0,18	196,96 a ± 0,24	618,40 b ± 0,15	273,45 b ± 0,12
	Stem tissue thickness (µm)			
	Epidermis	Cortex	Marrow	Xylem
Micro-Tom	40,65 b ± 0,17	296,93 a ± 0,22	2794,91 a ± 0,10	634,06 a ± 0,12
aurea	36,12 b ± 0,17	312,21 a ± 0,20	2866,26 a ± 0,09	624,37 a ± 0,12
hp1	54,30 a ± 0,20	248,51 b ± 0,24	2855,28 a ± 0,12	558,23 b ± 0,15
	Root tissue thickness (µm)			
	Epidermis	Cortex	Vascular cylinder	
Micro-Tom	86,88 a ± 0,26	448,91 a ± 0,28	2163,38 a ± 0,19	
aurea	60,57 b ± 0,25	468,39 a ± 0,25	1917,93 ab ± 0,17	
hp1	67,32 b ± 0,22	345,78 b ± 0,23	1812,93 b ± 0,21	

Among genotypes, averages followed by same letter do not differ by the Tukey test ($p \leq 0.05$). Averages are followed by percentage of variation coefficients.

Table 3. Tissue thickness of the photomorphogenic mutants *aurea* and *hp1* as well as the Micro-Tom cultivar at the end of the reproductive stage (68 DAE).

Micro tomato	Leaf tissue thickness (µm)					
	Abaxial epidermis	Adaxial epidermis	Palisade parenchyma	Spongy parenchyma	Polar vascular bundle	Equatorial vascular bundle
Micro-Tom	19,20 b ± 0,41	27,24 b ± 0,20	111,99 a ± 0,31	167,99 ab ± 0,30	912,30 b ± 0,29	441,45 a ± 0,22
aurea	29,40 a ± 0,43	33,24 a ± 0,21	103,73 a ± 0,32	156,33 b ± 0,33	1191,00a± 0,29	483,92 a ± 0,24
hp1	22,32 ab ± 0,42	28,44 b ± 0,19	113,88 a ± 0,30	209,06 a ± 0,33	745,24 b ± 0,29	328,99 b ± 0,21

	Stem tissue thickness (µm)			
	Epidermis	Cortex	Marrow	Xylem
Micro-Tom	31,32 b ± 0,33	318,75 a ± 0,25	3.379,57 a ± 0,15	671,98 a ± 0,24
aurea	47,88 a ± 0,36	328,54 a ± 0,23	2.636,31 b ± 0,15	505,38 b ± 0,22
hp1	38,88 ab ± 0,36	259,95 b ± 0,26	2.912,46 b ± 0,13	632,78 a ± 0,24

	Root tissue thickness (µm)		
	Epidermis	Cortex	Vascular cylinder
Micro-Tom	61,68 a ± 0,35	616,91 a ± 0,29	1.681,80 a ± 0,19
aurea	49,92 a ± 0,38	566,51 a ± 0,27	1.260,88 b ± 0,22
hp1	58,20 a ± 0,35	620,18 a ± 0,28	1.658,01 a ± 0,22

Among genotypes, averages followed by same letter do not differ by the Tukey test ($p \leq 0.05$). Averages are followed by percentage of variation coefficients.

Previous reports have explored the effect of phytochromes on plant morphology, which can result in changes in tissue thickness, as presented by this study. Smith (1995) proposed that phyA and phyB predominantly control the polar elongation of cells, which may be responsible for the growth of non-directional cells. Tsukaya et al. (2002) suggest that a phyB mutation affects not only cell elongation but also the number of cells in a leaf blade. These authors, working with leaves of an *Arabidopsis thaliana* phyB mutant, observed that this mutation was responsible decreases in the size and number of mesophyll cells, resulting in leaves that were thinner than those produced by control plants.

The *au* mutant, although deficient in phytochrome content (SHARMA et al., 1993), presented ratios of root dry mass to total dry mass and root dry mass to other organs (taken together or separately) that were statistically similar to those of MT; however, this accumulation was lower than that observed in the *hp1* mutant with the exception of the ratio of root dry mass to leaf dry mass, which was similar among the three genotypes (Figure 1).

The *au* mutant showed a lower ratio of leaf dry mass to total dry mass compared with the MT cultivar and the *hp1* mutant (F=4.1, $p \leq 0,05$) (Figure 2A) and showed the highest stem dry mass/root dry mass ratio compared with the other genotypes (F=9.4; $p \leq 0,05$) (Figure 3D). Additionally, the *au* mutant showed a greater accumulation of fruit dry mass in relation to total dry mass (F=3.9; $p \leq 0,05$) and in relation to the mass of other organs (analyzed together or separately) with the exception of the ratio of fruit dry mass to stem dry mass, which was equal among the three genotypes (Figure 4).

Once the *au* mutant exhibits a deficiency in its photoreceptor apparatus (MURAMOTO et al. 2005), it is presumed that this mutant can behave as a shaded sun-plant. Typically, plants that require long periods of sunlight exposure tend to be capable of stretching further to capture light; consequently, such plants needs to invest more photosynthate in their stems (LARCHER et al., 2012), which may be the reason why the *au* mutant showed a higher allocation of photosynthate to the stem in relation to the roots (Figure 3D). This explanation is also supported by the fact that this mutant stem has a greater internode length and a greater plant height at 40 DAE compared with other genotypes (Table 1). It is known that phytochromes are involved in the inhibition or stimulation of stem growth, and the data obtained in this study are in accordance with those of Kerckhoffs et al. (1997), who reported greater elongation in *au* mutant stems compared with other mutants and wild-type plants.

The finding that the *au* mutant allocates the largest amount of photosynthate to fruits in relation to other organs when compared with other genotypes (Figure 4) is most likely related to its decrease in allocation of photosynthate to leaves and

roots, especially compared with the *hp1* mutant (Figures 1 and 2). This indicates that the *au* mutant has a high capacity for remobilizing photosynthates from the leaves and roots to the developing fruits, which can be confirmed by the data in Figures 5A and 5B. These data show that at the end of the vegetative stage (40 DAE), there was no difference between the genotypes with respect to photosynthate partitioning in roots and leaves in relation to total plant dry mass, and when these same parameters were verified at the end of the reproductive stage (68 DAE), there was a significant decrease in the ratio of root dry mass to total dry mass in the *au* mutant compared with the *hp1* mutant (Figure 1). This significant decrease was accompanied by a decrease in the ratio of leaf dry mass to total dry mass in the *au* mutant compared with the other genotypes (Figure 2). Thus, it can be inferred that the *au* mutant has a high capacity for remobilization of photosynthate during its reproductive stage, prioritizing photosynthate relocation to fruits.

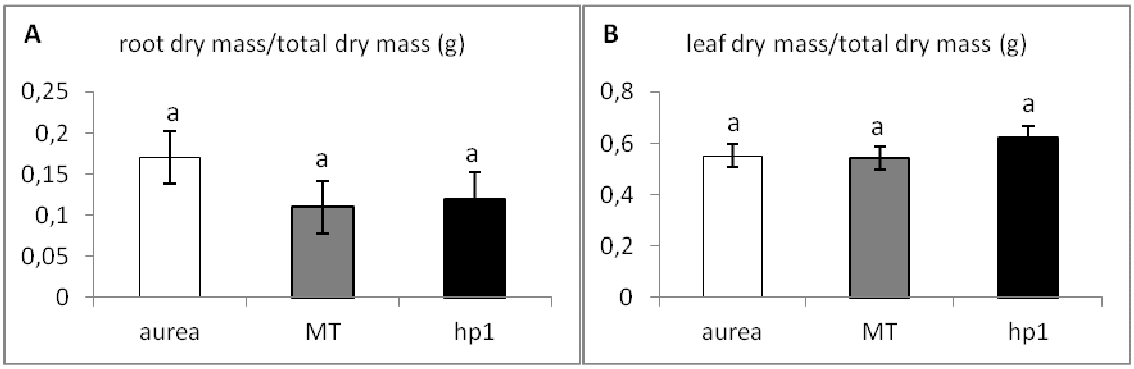

Figure 5. Photosynthate partition in the photomorphogenic mutants *aurea* and *hp1* as well as the Micro-Tom (MT) cultivar in relation to roots and leaves. Analyses were carried out at the end of the vegetative stage (40 DAE). Columns with same letters do not differ by the Tukey test at 5%. The bars represent standard error.

The tissue source of photosynthate that is remobilized from the leaves into the fruits in the *au* mutant is most likely the spongy parenchyma because although its thickness did not differ significantly from that of MT at 40 DAE (Table 2), it decreased significantly at 68 DAE (Table 3). In roots, the most likely origin of remobilized photosynthate is the vascular cylinder for the same reason given for the spongy parenchyma (Tables 2 and 3). This significant reduction in the ratio of tissue thickness between 40 and 68 DAE can also be observed in the marrow stem (Tables 2 and 3).

It is intriguing that the *au* mutant, which has defects in the photoreceptor apparatus and decreased levels of photosynthetic pigments (MURAMOTO et al., 2005, SHARMA et al., 1993), accumulates more fruit dry mass than the MT cultivar and the *hp1* mutant. However, previous studies have shown that, regardless of its deficiencies, the *au* mutant exhibits high rates of photosynthesis that are equivalent to those observed in the MT cultivar and has more total nitrogen and total protein than the MT cultivar and the *hp1* mutant (MELO et al., 2009). Therefore, in addition to the high capacity for remobilization of photosynthate into fruit during the reproductive stage that was observed in this study, the large amount of nitrogen allocated to protein could subsidize the high rates of photosynthate production, thus justifying the enhanced ability of *au* to accumulate biomass in fruits. It is estimated that approximately 20% of total foliar nitrogen in C3 plants is present in the enzyme ribulose 1,5-bisphosphate carboxylase-oxygenase (Rubisco), a key enzyme involved in carboxylation in the Calvin-Benson cycle (EVANS & SEEMANN, 1984).

CONCLUSIONS

At the end of the plant life cycle, photosynthate was allocated primarily to roots and leaves in the *hp1* mutant, whereas the *au* mutant allocated photosynthate primarily to fruits.

The *au* mutant showed a high capacity for remobilization of photosynthate from vegetative organs to fruits during the reproductive stage.

The remobilized photosynthate in the fruits of *au* mutants originates from the spongy leaf parenchyma and the root vascular cylinder of the marrow stem.

Based on the results obtained from *au* and *hp1* mutants, it can be concluded that phytochrome content and alterations in the pathway of red and far-red light transduction, respectively, influence the partitioning of photosynthate among plant organs.

RESUMO: O objetivo deste estudo foi analisar a partição de fotoassimilados em tomateiros mutantes fotomorfogenéticos ao final da fase vegetativa, aos 40 dias após a emergência (DAE), e ao final da fase reprodutiva, aos 69 DAE, e sua interação com aspectos morfoanatômicos. Foram estudados os mutantes aurea (*au*), deficiente em fitocromo, e *hp1*, o qual expressa resposta exagerada à luz, e o tomateiro selvagem cultivar Micro-Tom (MT). As plantas foram analisadas 40 dias após a emergência (DAE) e 68 DAE, tentando identificar os órgãos e tecidos dos fotoassimilados remobilizados e seus órgãos de destino durante o estádio reprodutivo. As plantas foram avaliadas quanto à sua morfologia interna e externa e percentagem de massa seca entre os órgãos. A alocação de fotoassimilados no mutante *hp1* ocorreu prioritariamente em raízes e folhas comparativamente aos demais órgãos, e no mutante *au* ocorreu prioritariamente em frutos comparativamente aos demais órgãos. O mutante *au* deteve alta capacidade de remobilização de fotoassimilados durante sua fase reprodutiva para os frutos e os fotoassimilados remobilizados tiveram origem preponderante do parênquima lacunoso foliar, do cilindro vascular radicular e da medula caulinar.

PALAVRAS-CHAVE: *Aurea*. H*p1*. Micro-Tom. Fotomorfogênese. *Solanum lycopersicum* L.

REFERENCES

AZARI, R.; EVENOR, D.; NAHON, S.; SHLOMO, H.; CHEN, L.; LEVIN, I. Overexpression of *UV-DAMAGED DNA BINDING PROTEIN 1* links plant development and phytonutrient accumulation in high *pigment-1* tomato. **Journal Experimental Botany**, Oxford, v. 61, n. 13, p. 3627-3637, 2010.

BALLARÉ, C. L., SCOPEL, A. L., SÁNCHEZ, R. A. Photomorphogenic processes in the agricultural environment. **Photochemistry and Photobiology**, Oxford, v. 56, p. 777-788, 1992.

BENINCASA, M. **Análise de crescimento de plantas**. Jaboticabal: Funep/UNESP, p. 42, 1988.

CARVALHO, R. F.; AIDAR, S. T.; AZEVEDE, R. A.; DODD, I. C.; PRES, L. E. P. Enhanced transpiration rate in the high pigment 1 tomato mutant and its physiological significance. **Plant Biology**, Berlim, v. 13, p. 546-550, 2011a.

CARVALHO, R. F.; CAMPOS, M. L.; PINO, L. E.; CRESTANA, S. L.; ZSOGON, A.; LIMA, J. E.; BENEDITO, V. A.; PERES, L. E. P. Convergence of developmental mutants into a single tomato model system: 'Micro-Tom' as an effective toolkit for plant development research. **Plant Methods**, London, v. 7, p. 18-32, 2011b

CORRÊA, R.M.; PINTO, J. E. B.; REIS, E. S.; MOREIRA, C. M. Crescimento de plantas, teor e qualidade de óleo essencial de folhas de orégano sob malhas coloridas. **Global Science and Tecnology**, Rio Verde, v. 5, n. 1, p. 11-22, 2012.

CHEN, M.; CHORY, J.; FANKHAUSER, C. Light signal transduction in higher plants. **Annual Review Genetics**, Palo Alto, v. 38, p. 87-117, 2004.

EVANS, J. R.; SEEMAN, J. R**.** Differences between wheat genotypes in specific activity of RuBP carboxylase and the relationship to photosynthesis. **Plant Physiology**, Victoria, v. 74, p. 759-765, 1984.

FLORES, M. E. P. **Variabilidade genética de acessos de tomateiro (*Lycopersicon esculentum* Mill.) com base na avaliação de fotossíntese, partição de fotoassimilados e produção.** 2007, 48f.. Dissertação (Mestrado em Fitotecnia). Curso de Pós-Graduação em Melhoramento de Plantas e Biotecnologia, Universidade Federal de Viçosa, Viçosa, MG, 2007.

GONDIM, A. R. O.; PUIATTI, M.; VENTRELLA, M. C.; CECON, P. R. Plasticidade anatômica da folha de taro cultivado sob diferentes condições de sombreamento. **Bragantia**, Campinas, v. 67, n. 4, p. 1037-1045, 2008.

KASPERBAUER, M. J.; HUNT, P. G. Far-red light affects photosynthate allocation and yield of tomato over red mulch. **Crop Science**, Madison, v. 38, p. 970-974, 1998.

KERCKHOFFS, L. H, J.; SENGERS, M. M. T; KENDRICK, R. E. Growth analysis of wild-type and photomorphogenic-mutant tomato plants. **Physiologia Plantarum**, Copenhagen, v. 99, p. 309-315, 1997

LARCHER, l.; BOEGER, M. R.. T.; MARQUES, M. C. M. Biomass allocation and shade tolerance in three species of Atlantic Forest. **Botany**, Ottawa, v. 90, n. 9, p. 830-838, 2012.

LIU, Y.; ROOF, S.; ZHIBIAO, Y.; BARRY, C.; TUINEN, A. van; VREBALOV, J.; BOWLER, C.; GIOVANNONI, J. Manipulation of light signal tranduction as a means of modifying fruit nutritional quality in tomato. **PNAS Plant Biology**, Washington, v. 101, n. 26, p. 9897- 9902, 2004.

MELO, H. C.; CASTRO, E. M.; ALVES, E.; PERINA, F. J. Anatomia foliar de microtomaterios fitocromo-mutantes e ultraestrutura de cloroplastos. **Ciência e Agrotecnologia**, Lavras, v. 35, n. 1, p. 11-18, 2011.

MELO, H. C.; CASTRO, E. M.; SORARES, A. M.; OLIVEIRA, C.; RAMOS, S.J. Características fisiológicas de microtomateiros fitocromo-mutantes. **Ciência e Agrotecnologia**, Lavras, v. 33, n. 5, p. 1213-1219, 2009.

MORAES, H.; MARUR, C. J.; CARAMORI, P. H.; RIBEIRO, A. M. A.; GOMES. J. C. Características fisiológicas e de crescimento de cafeeiro sombreado com guandu e cultivado a pleno sol. **Pesquisa Agropecuária Brasileira**, Brasília, v. 38, n. 10, p. 1131-1137, 2003.

MURAMOTO, T; KAMI, C.; KATAOKA, H.; IWATA N, L. P. J.; MUKOUGAWA K, Y. A.; KOHCHI, T. The tomato photomorphogenetic mutant, aurea, is deficient in phytochromobilin synthase for phytochrome chromophore biosynthesis. **Plant Cell Physiology**, Kyoto, v. 46, p. 661–665, 2005.

NAKAZONO, E. M.; COSTA, M. C.; FUTATSUGI, K.;PAULILO, M.T.S. Crescimento inicial de *Euterpe edulis* Mart. em diferentes regimes de luz. **Revista Brasileira de Botânica**, São Paulo, v. 24, n. 2, p. 173-179, 2001.

OLIVEIRA, M. I.; CASTRO, E. M.;COSTA, L. C. B.; OLIVEIRA, C. Características biométricas, anatômicas e fisiológicas de *Artemisia vulgaris* L. cultivada sob telas coloridas. **Revista Brasileira de Plantas Medicinais**, Botucatu, v. 11, n. 1, p. 56-62, 2009.

PELUZIO, J. M.; CASALI, V. W. D.; LOPES, N. F. Partição de assimilados em tomateiro após a poda apical. **Horticultura Brasileira**, Brasília, v. 13, p. 41-43, 1995.

PETERS, J. L.; SZELL, M.; KENRICK, R. E. The expression of light-regulated genes in the high-pigment-1 mutant of tomato. **Plant Physiology**, Victoria, v. 117, p. 797-807, 1998.

RAMOS, K. M. O.; FELFILI, J. M.; FAGG, C. W.; SOUSA-SILVA, J. C.; FRANCO, A. C. Desenvolvimento inicial e repartição de biomassa de *Amburana cearensis* (Allemao) A.C. Smith, em diferentes condições de sombreamento. **Acta Botanica Brasilica**, São Paulo, v. 18, n. 2. P. 351-358, 2004

SCHITTENHELM, S.; MENGE-HARTMANN, U.; OLDENBURG, E. Photosynthesis, Carbohydrate Metabolism, and Yield of Phytochrome-B-Overexpressing Potatoes under Different Light Regimes. **Crop Science**, Madison, v. 44, p. 131-143, 2004.

SHARMA, R. ; LÓPEZ-JUEZ, E.; NAGATANI, A.; FURUYA, M. Identification of photo-inactive phytochrome A in etiolated seedlings and photo-active phytochrome B in green leaves of aurea mutant of tomato. **Plant Journal**, New Jersey, v. 4, p. 1035-1042, 1993.

SMITH, H. Physiological and ecological function within the phytochrome family. **Annual Review Plant physiology Plant Molecular Biology**, Palo Alto, v. 46, p. 289-315, 1995

TERASHIMA, I.; MIYAZAWA, S.-I.; HANBA, Y. T. Why are sun leaves thicker than shade leaves? Consideration based on analyses of CO_2 diffusion in the leaf. **Journal Plant Research**, New York, v. 114, p. 93-105, 2001.

TSUKAYA, H.; KOZUKA, T.; KIM, G.-T. Genetic control of petiole length in *Arabidopsis thaliana*. **Plant Cell Physiology**, Kyoto, v. 43, p. 1221-1228, 2002.

VAN TUINEN, A.; CORDONNIER-PRATT, M. M.; PRATT, L. H.; VERKERK, R.; ZABEL, P.; KOORNEEF, M. The mapping of phytochrome genes and photomorphogenic mutants of tomato. **Theoretical and Applied Genetics**, New York, v. 94, p. 115–122, 1997.