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Nutrition in tomato (*Solanum lycopersicum* L) as affected by light: revealing a new role of phytochrome A

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Abstract

The *far red light insensitive* (*fri*) mutant of tomato, which is phytochrome A (phyA) deficient, displays some characteristics that have recently indicated important functions of this photoreceptor in water relations. With respect to the relationship between nutrition and water relations, we investigated the growth and nutritional status of *fri* supplied with Hoagland's complete solution and solutions with the individual omission of nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg) and sulfur (S). For this purpose, 20-day-old tomato plants of the WT (cv. Moneymaker) and *fri* mutant were transplanted into pots (one plant per pot) that contained Hoagland and Arnon (1950) solution diluted to 50 per cent in the first week and to 100 per cent from the second week of cultivation until the end of the experiment (50 DAT). Seven treatments were performed: a complete nutrient solution (KH_2PO_4, KNO_3, $Ca(NO_3)_2.5H_2O$, $MgSO_4.7H_2O$, KCl, $CaCl_2$, H_3BO_3, $MnCl_2.4H_2O$, $ZnCl_2$, $CuCl_2$, $H_2MoO_4H_2O$ and Fe EDTA) and the individual omission N (KNO_3, $Ca(NO_3)_2.5H_2O$); P (KH_2PO_4); K (KH_2PO_4, KNO_3); Ca ($CaCl_2$); Mg and S ($MgSO_4.7H_2O$) from a balanced nutrient solution. The experiment was arranged in a completely randomized factorial design with two genotypes and seven types of nutrient solutions with three replications. Upon harvest, the following measurements were performed: the height of the plants, measured from the base of the stem of each plant to the insertion of the first fully expanded leaf; the stem diameter; the total number of leaves per plant; an indirect chlorophyll measurement, which we called the green color index, and the leaf area. Statistical analysis was performed using analysis of variance (ANOVA) followed by Tukey's test. First, based on growth analyses, *fri* showed an enhanced dry weight of the shoot, root and whole plant in complete solution compared with the wild type (WT). In addition, the phyA mutant had a multifaceted response compared with that of the WT when the nutrients were omitted. For the *fri* mutant, the height and green color index were reduced without N and K; the leaf area without P, K and S; the dry weight of the root and shoot without N, P, K and S, and the root, shoot and total plant dry weight without P, K and S. On the other hand, the green color index of the *fri* mutant was enhanced without Ca and Mg. Together, these results show that in addition to revealing an altered response to nutrition in the *fri* mutant, phyA can play a role in light signaling in the nutrition and nutritional stress of tomato.

Keywords: Tomato; nutrition; abiotic stress; phytochrome; mutant.
Abbreviations: *fri_far red light insensitive mutant;* DAT_days after transplanting; HY5_LONG HYPOCOTYL 5; WT_wild type.

Introduction

Phytochromes are a widespread family of red/far-red-responsive photoreceptors that are ~120-kDa peptides (apoproteins) with a covalently linked linear tetrapyrrole bilin chromophore (forming a complex referred to as the holoprotein) (Bae and Choi, 2008). These molecules control a range of physiological responses from seed germination (Dechaine et al., 2009; Oh et al., 2009) to flowering (Andres et al., 2009; Brock et al., 2010) and each year, a considerable number of studies are published describing new biochemical and molecular roles of phytochromes. Many of these discoveries have been identified using genetic tools, mainly plant transgenics and mutants, with *Arabidopsis thaliana* as the flagship species. In this plant model, many phytochrome signaling components have been identified, revealing how, on what and where phytochromes act (Chen and Chory, 2011). Moreover, phytochrome mutants of economically important species, such as tomato (*Solanum lycopersicum*), have also permitted the discovery of agronomic traits that appear to be controlled by phytochromes. For example, the hypocotyls of the *au* tomato mutant, which is phytochrome-deficient (Muramoto et al., 2005), have reduced levels of anthocyanins, which are important antioxidant molecules (Carvalho et al., 2010). Moreover, the leaves of *au* exhibited reduced lipid peroxidation and enhanced H_2O_2 (Monteiro et al., 2012), generating strong perspectives on the biochemical and molecular manipulation of light signaling. In addition, the *far red light insensitive* (*fri*) mutant of tomato (van Tuinen et al., 1995), which is phyA-deficient, produces fruits with important qualities for the paste industry, such as an increased dry weight/fresh weight ratio, total soluble solids, and paste viscosity, and fewer seeds per fruit compared with the wild type (Alba et al., 1999). Curiously, in addition to the improved traits that are displayed by the *fri* mutant, this genotype rapidly wilts after exposure to high levels of

evaporation compared with WT plants (Auge et al., 2012). Nevertheless, these authors verified that the stomatal density was not changed, whereas transpiration and stomatal conductance were both lower in the *fri* than in the WT plants. Moreover, in *fri*, these results were accompanied by a lower stem-specific hydraulic conductivity, which was associated with a lower xylem vessel number and transversal area, resulting in a reduction in the water supply to the leaves, which rapidly wilted under high evaporative demand. These results indicate that there are many variations in the specific responses of phytochrome A signaling during the transport of water from the roots to the leaves and fruits. Certainly, these issues are related to one of the most important themes in plant science: nutrition. In other words, is the nutritional status affected by phytochrome A? Although phytochrome deficiency in *au* can reduce nitrate and nitrite reductase in tomato seedlings (Goud et al., 1994), no nutritional study has been associated with phytochromes. Thus, in the present study, we verified the nutritional status of *fri* and found a prominent alteration in this genotype during nutrient omission.

Results and Discussion

Based on altered water relations in the *fri* tomato mutant (Auge et al., 2012), we hypothesized that this process can interfere with the way in which nutrients are translocated in the plant, which led us to use this genotype to determine a more comprehensive role of phyA in this process. We found a multifaceted response based on the results obtained from the treatments with the complete solution and the omitted nutrients. In fact, compared with the WT, *fri* had a reduced green color index and leaf area, whereas the root, shoot and whole plant dry weight was higher in this mutant. The N, Ca and Mg contents in the shoots, the N, P, K, Ca, Mg and S contents in the roots and the whole plant N, K, Ca, Mg and S contents were enhanced when *fri* was grown in the complete solution. However, when nutrients were omitted, there were strong changes in the growth and nutritional status, as discussed below.

N deficiency

Because N is an essential component of a wide range of molecules, such as proteins, amino acids, and nucleic acids, deficiency of this element most often results in stunted and slow growth as well as leaf chlorosis (Gangwar and Singh, 2011; Thangaradjou et al., 2014). Consequently, our results demonstrate that in both the WT and the *fri* mutant, N deficiency reduced the height, leaf area, green color index, and root and whole plant dry weight (Table 1). Certainly, these responses can be explained by the reduction in the macronutrient accumulation in the roots, shoots and whole plants triggered by N deficiency in both genotypes (Table 2, 3 and 4).

P deficiency

There was a severe reduction in P accumulation (78 per cent) in the roots of the phyA mutant subjected to this treatment compared with the complete solution, which indicates that the mutant may have an increased N requirement associated with an interaction with P. In accordance with this result, the most evident response to P starvation can be observed in the N accumulation in the roots of *fri*, which was reduced to 76 per cent compared with that obtained for the complete solution (a 41 per cent reduction was recorded for the WT) (Table 3). However, the green color index was not reduced under P-deficient conditions, as opposed to N-deficient conditions. Moreover, because phytochromes modulate the accumulation of pigments, such as carotenoids, chlorophylls and anthocyanins (Huq et al., 2004; Carvalho et al., 2010), the reduced green color index in *fri* grown in the complete solution reveals a predominant role of phyA in pigment accumulation, which is not dependent on P (Table 1).

K deficiency

Because K is an essential nutrient that affects most of the biochemical and physiological processes that influence plant growth and metabolism (Pettigrew, 2008; Wang and Wu, 2013; Hafsi et al., 2014), it was not surprising that K deficiency resulted in reduced height, leaf area, green color index, and root, shoot and whole plant dry weight of both the WT and *fri* (Table 1). However, under K deficiency, a more severe reduction in these parameters was observed for *fri* compared with the WT. This can be associated with a decrease in the N accumulation in the *fri* shoots and whole plants, and the P and S accumulation in the *fri* shoot, root and whole plants relative to the levels measured in the WT (Table 2, 3 and 4). Additionally, whether or not the lower K concentrations can further decrease K absorption as well as plant resistance to drought stress (Wang et al., 2013), it is reasonable to conclude that the high levels of evaporation and reduced water potential in *fri* that were observed by Auge et al. (2012) are related to the altered K response. However, a more detailed analysis of how this interplay occurs remains to be performed.

Ca deficiency

When Ca was omitted, reductions in the height, leaf area, green color index and root, shoot and whole plant dry weight of the WT and *fri* were observed (Table 1). However, under Ca deficiency, *fri* interestingly exhibited a substantially higher (45 per cent) green color index compared with the WT. Phytochromes modulate chlorophyll biosynthesis (Huq et al., 2004), and Ca mediates phytochrome phototransduction in a wide range of processes, including photosynthesis (Tretyn, 1999; Appenroth and Gabrys, 2003; Eprintsev et al., 2012; Pandey et al., 2013). However, whether there is some inhibitory mechanism through which phyA acts that is associated with Ca during pigment accumulation remains largely elusive. This complexity can result from a greater accumulation of P in the shoots (Table 2) and S in all tissues of *fri* compared with the WT under Ca deficiency (Table 2, 3 and 4).

Mg deficiency

Mg deficiency was directly associated with a lower green color index in the WT. This was expected given that Mg is a component of the chlorophyll molecule (Williams and Salt, 2009; Hawkesford et al., 2012). However, in this treatment, *fri* showed similar green color index values as those recorded for the complete solution (Table 1). Although Mg starvation reduced the height, leaf area, and root, shoot and whole plant dry weight of *fri* and the WT (Table 1), pigment retention in *fri* does not appear to be associated with S accumulation because these nutrients were reduced in the mutant compared with the WT (Table 2 and 3). In fact, in the case of S omission, the green color index of *fri* did not differ from that of the complete solution (Table 1). Mg-chelatase inserts an Mg ion in an ATP-dependent reaction to produce Mg-protoporphyrin IX^{13} and ferrochelatase, which synthesizes heme from protoporphyrin IX during chlorophyll biosynth-

Table 1. Growth analyses and green color index of the WT and *fri* plants grown under complete or deficient (-) solution.

	Height (cm)		Green color index		Leaf area (cm^2)		Dry weight (g per plant)					
							Shoots		Roots		Whole plant	
Nutrient solution	WT	*fri*	WT	*fri*	WT	*fri*	WT	*fri*	WT	*fri*	WT	*fri*
Complete	122.8	116.2	23.0^{A}	14.5^{B}	5146.1^{A}	3704.7^{B}	27.2^{B}	36.3^{A}	1.88^{B}	4.32^{A}	29.1^{B}	40.6^{A}
- N	29.3^{*A}	15.2^{*B}	4.9^{*}	3.2^{*}	284.1^{*}	96.7^{*}	1.9^{*}	0.5^{*}	0.42^{*}	0.30^{*}	2.3^{*}	0.7^{*}
- P	62.8^{*}	54.0^{*}	26.0^{A}	18.3^{B}	561.8^{*}	461.6^{*}	4.1^{*}	3.0^{*}	1.23^{*}	1.03^{*}	5.4^{*}	4.0^{*}
- K	47.6^{*A}	16.7^{*B}	36.5^{*A}	12.2^{B}	786.5^{*A}	182.4^{*B}	4.4^{*}	0.7^{*}	0.58^{*A}	0.15^{*B}	5.0^{*A}	0.8^{*B}
- Ca	22.5^{*}	26.0^{*}	15.2^{*B}	27.5^{*A}	339.5^{*}	674.2^{*}	3.3^{*}	5.0^{*}	0.67^{*}	0.94^{*}	4.0^{*}	6.0^{*}
- Mg	43.83^{*}	24.33^{*}	3.4^{*B}	11.9^{A}	1267.1^{*A}	494.2^{*B}	5.0^{*}	1.7^{*}	0.22^{*}	0.15^{*}	5.2^{*}	1.9^{*}
- S	99.3^{*}	67.7^{*}	13.4^{*}	10.6	3327.2^{*A}	1545.7^{*B}	28.7^{A}	11.9^{*B}	2.47^{A}	1.40^{*B}	31.2^{A}	13.3^{*B}

Asterisks within a column indicate a significant difference between the nutritional treatment and the complete solution, and different letters within a row indicate a significant difference between the genotypes according to Tukey's test at $p < 0.05$.

Table 2. Nutrient accumulation (mg per plant) in the shoots of the WT and *fri* plants grown under complete or deficient (-) nutrient solution.

	N		P		K		Ca		Mg		S	
Nutrient solution	WT	*fri*	WT	*fri*	WT	*fri*	WT	*fri*	WT	*fri*	WT	*fri*
Complete	665.7^{B}	929.1^{A}	117.7	116.2	903.5	963.3	497.0^{B}	614.0^{A}	129.3^{B}	186.6^{A}	162.5	179.0
- N	18.5^{*}	4.4^{*}	14.8^{*}	4.0^{*}	42.6^{*}	11.7^{*}	28.7^{*}	9.2^{*}	7.6^{*}	2.7^{*}	11.7^{*}	3.1^{*}
- P	114.8^{*}	92.4^{*}	2.9^{*}	2.2^{*}	136.9^{*}	123.2^{*}	64.1^{*}	61.8^{*}	28.3^{*}	31.6^{*}	21.5^{*}	18.4^{*}
- K	203.7^{*A}	32.8^{*B}	39.1^{*A}	7.3^{*B}	23.4^{*}	3.1^{*}	66.9^{*}	15.8^{*}	26.2^{*}	5.2^{*}	26.0^{*A}	5.4^{*B}
- Ca	129.8^{*}	210.7^{*}	35.8^{*B}	51.5^{*A}	143.6^{*}	231.4^{*}	5.3^{*}	12.8^{*}	33.8^{*}	51.1^{*}	23.8^{*}	35.5^{*}
- Mg	182.7^{*}	66.1^{*}	37.0^{*A}	10.6^{*B}	260.6^{*A}	95.7^{*B}	99.2^{*}	33.6^{*}	3.0^{*}	1.1^{*}	36.9^{*A}	12.6^{*B}
- S	640.2^{A}	317.9^{*B}	129.1^{A}	52.1^{*B}	692.9^{A}	387.7^{*B}	485.5^{A}	220.7^{*B}	150.7^{A}	51.1^{*B}	19.5^{*}	11.8^{*}

Asterisks within a column indicate a significant difference between the nutritional treatment and the complete solution, and different letters within a row indicate a significant difference between the genotypes according to Tukey's test at $p < 0.05$.

Table 3. Nutrient accumulation (mg per plant) in the roots of the WT and *fri* plants grown under complete or deficient (-) nutrient solution.

	N		P		K		Ca		Mg		S	
Nutrient solution	WT	*fri*	WT	*fri*	WT	*fri*	WT	*fri*	WT	*fri*	WT	*fri*
Complete	60.8^{B}	123.5^{A}	8.4^{B}	23.5^{A}	37.3^{B}	66.5^{A}	12.0^{B}	61.7^{A}	7.4^{B}	20.4^{A}	7.5^{B}	20.4^{A}
- N	5.2^{*}	4.3^{*}	6.4	5.0^{*}	15.3^{*}	14.1^{*}	1.9^{*}	1.9^{*}	2.0^{*}	1.7^{*}	1.4^{*}	1.3^{*}
- P	35.4	31.2^{*}	1.2^{*}	1.2^{*}	39.3	30.2^{*}	5.3^{*}	6.4^{*}	3.7	3.8^{*}	3.8^{*}	3.5^{*}
- K	21.0^{*}	5.8^{*}	5.6^{A}	1.7^{*B}	2.9^{*}	2.4^{*}	4.3^{*}	1.9^{*}	2.8^{*}	0.8^{*}	3.1^{*A}	1.0^{*B}
- Ca	25.2^{*}	35.2^{*}	6.2	7.5^{*}	23.6	35.1^{*}	1.4^{*}	1.3^{*}	1.4^{*}	3.4^{*}	2.3^{*B}	4.5^{*A}
- Mg	6.4^{*}	4.8^{*}	1.8^{*}	1.0^{*}	10.7^{*}	5.1^{*}	2.1^{*}	2.1^{*}	0.2^{*}	0.2^{*}	1.3^{*}	0.9^{*}
- S	63.6^{A}	44.0^{*B}	8.4	7.2^{*}	73.9^{*A}	52.4^{B}	16.7^{A}	11.3^{*B}	7.7	7.4^{*}	3.2^{*}	2.5^{*}

Asterisks within a column indicate a significant difference between the nutritional treatment and the complete solution, and different letters within a row indicate a significant difference between the genotypes according to Tukey's test at $p < 0.05$.

Table 4. Total (shoot+root) nutrient accumulation (mg per plant) in the WT and *fri* plants grown under complete or deficient (-) nutrient solution.

	N		P		K		Ca		Mg		S	
Nutrient solution	WT	*fri*	WT	*fri*	WT	*fri*	WT	*fri*	WT	*fri*	WT	*fri*
Complete	726.5^{B}	1052.6^{A}	126.1	139.7	940.8	1029.8	509.1^{B}	675.7^{A}	136.7^{B}	207.0^{A}	170.1^{B}	199.4^{A}
- N	23.7^{*}	8.7^{*}	21.2^{*}	9.1^{*}	57.8^{*}	25.8^{*}	30.7^{*}	11.1^{*}	9.6^{*}	4.4^{*}	13.1^{*}	4.4^{*}
- P	150.2^{*}	123.6^{*}	4.1^{*}	3.4^{*}	176.2^{*}	153.4^{*}	69.3^{*}	68.3^{*}	32.0^{*}	35.4^{*}	25.3^{*}	21.9^{*}
- K	224.7^{*A}	38.5^{*B}	44.7^{*A}	9.0^{*B}	26.3^{*}	5.5^{*}	71.2^{*}	17.7^{*}	28.9^{*}	6.0^{*}	29.1^{*A}	6.4^{*B}
- Ca	155.0^{*}	245.4^{*}	41.9^{*B}	59.0^{*A}	167.2^{*}	266.5^{*}	6.7^{*}	14.1^{*}	35.2^{*}	54.5^{*}	26.1^{*}	40.0^{*}
- Mg	189.2^{*}	70.9^{*}	38.8^{*A}	11.5^{*B}	271.3^{*A}	100.8^{*B}	101.2^{*}	35.7^{*}	3.2^{*}	1.3^{*}	38.2^{*A}	13.4^{*B}
- S	703.8^{A}	361.9^{*B}	137.5^{A}	59.3^{*B}	766.8^{A}	440.1^{*B}	502.2^{A}	231.9^{*B}	158.4^{A}	58.5^{*B}	22.7^{*}	14.3^{*}

Asterisks within a column indicate a significant difference between the nutritional treatment and the complete solution, and different letters within a row indicate a significant difference between the genotypes according to Tukey's test at $p < 0.05$.

esis, and is under the control of phytochromes in *Arabidopsis* (Stephenson and Terry, 2008). However, in addition to inferring that phyA is part of the inhibitory signaling of pigments during biosynthesis, the reduced green color index in *fri* opens a number of new avenues for researching the role of phyA in tomato during this process.

S deficiency

The green color retention of *fri* under S starvation was similar to that of the complete solution. However, this mutant had a lower leaf area and root, shoot and whole plant dry weight, as well as a lower accumulation of N, P, K, Ca and Mg in the shoots and whole plant compared with the WT (Table 1 and 2). These results provide evidence that *fri* has an altered nutritional mechanism based on the interaction between phyA and S. In accordance with this, the transcription factor LONG HYPOCOTYL 5 (HY5), which acts downstream of phyA in *Arabidopsis* (Ang et al., 1998; Ulm et al., 2004), is involved in the regulation of adenosine 5'-phosphosulphate reductase (APR), a key enzyme for sulfate assimilation (Lee et al., 2011; Huseby et al., 2013). Thus, our results reinforce the idea that phyA plays a role in light signaling in S nutrition, but how this is achieved remains unknown.

Final considerations

Phytochrome mutants have revealed important roles of photoreceptors from germination to flowering, as well as in abiotic stress responses (Carvalho et al., 2011). Thus, in this work, we demonstrate that a phyA mutant of tomato exhibited varied growth and nutritional status under the omission of N, P, K, Ca, Mg and S, indicating that phyA plays a prominent role in the signaling response associated with these elements. Curiously, in the complete solution, *fri* had higher dry matter as well as N, Ca and Mg in the shoots, N, P, K, Ca, Mg and S in the roots, and N, Ca, Mg and S in the whole plants compared with the WT. This improved nutritional status in *fri* could explain the enhanced horticultural traits, such as the dry weight/fresh weight ratio, total soluble solids, and paste viscosity, that were found by Alba et al., (1999). Although it is reasonable to suggest that the altered growth and nutritional status can be associated with modifications of the water relations of *fri*, such as lower stem-specific hydraulic conductivity, xylem vessel number and transverse area, which lead to a reduction in water supply to the leaves (Auge et al., 2012), new approaches can be used to understand the changes that occur in *fri*, stimulating intensive research for a better understanding of phyA signaling during water and nutritional stress.

Materials and Methods

Plant cultivation

The experiment was conducted in a greenhouse at the Faculdade de Ciências Agrárias e Veterinárias – Unesp, Jaboticabal, São Paulo, Brazil, using tomato (*Solanum lycopersicum L.*) cv. Moneymaker, which was used as the wild type (WT), as well as the *fri* mutant. The plants were grown for 49 days (between August and October 2013) in pots containing 8 L of nutrient solution. The seeds were provided by the "Tomato Genetics Resource Center, Davis, CA, USA" (TGRC).

Experimental Design

Seven treatments were performed: a complete nutrient solution (KH_2PO_4, KNO_3, $Ca(NO_3)_2.5H_2O$, $MgSO_4.7H_2O$, KCl, $CaCl_2$, H_3BO_3, $MnCl_2.4H_2O$, $ZnCl_2$, $CuCl_2$, $H_2MoO_4H_2O$ and Fe EDTA) and the individual omission of N (KNO_3, $Ca(NO_3)_2.5H_2O$); P (KH_2PO_4); K (KH_2PO_4, KNO_3); Ca ($CaCl_2$); Mg and S ($MgSO_4.7H_2O$) from a balanced nutrient solution. The experiment was arranged in a completely randomized factorial design with two genotypes and seven types of nutrient solutions with three replications. In this experiment, 20-day-old WT and *fri* mutant tomato plants were transplanted into pots (one plant per pot) containing Hoagland and Arnon (1950) solution diluted to 50 per cent in the first week and to 100 per cent from the second week of cultivation until the end of the experiment. The nutrient solutions were prepared with deionized water and replaced every 15 days. The pH was adjusted twice daily to 5.5 ± 0.5 using NaOH or HCl 0.1 M. To replace the transpired water, deionized water was used, and the nutrient solution was constantly oxygenated with the aid of one air compressor.

Biochemical, physiological and nutritional analysis

The plants were harvested 50 days after transplanting (DAT). Upon harvest, the following measurements were performed: the height of the plants, which was measured from the base of the stem of each plant to the insertion of the first fully expanded leaf; the stem diameter; the total number of leaves per plant; an indirect chlorophyll measurement, which we called the green color index, on ten leaves per experimental unit using the OPTI-Sciences® model CCM-200 Hudson, Boston, USA; and the leaf area using an LI-3100C Area Meter Lincoln, Nebraska, USA. The harvested plant material was washed with deionized water, separated into shoots and roots and placed in an oven with forced ventilation at 65 °C to dry to a constant weight to determine the dry mass. Then, the macronutrient concentration in the dry shoots and roots was determined according to the method described by Bataglia et al. (1983). The dry matter of the shoots increased with the dry matter of the roots, and these values were added to obtain the whole plant dry matter. The nutrient concentration was used to calculate the accumulation of nutrients in the shoots, roots and whole plants.

Statistical analyses

Statistical analyses were performed using analysis of variance (ANOVA) followed by Tukey's test ($P \leq 0.05$) using Assistat software (www.assistat.com).

Conclusion

This work is the first report that addresses the role of phytochromes in plant nutrition. The growth and nutrient data allow us to conclude that in addition to revealing an altered response to nutrition in the *fri* mutant, phyA can play a role in light signaling in the nutrition and nutritional stress of tomato. However, this is just the beginning because light modulates plant growth through the complex phototoreceptor system that in tomato, in particular, involves phy B1, phy B2, phy E and phy F.

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