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Seed Germination in Tomato: A Focus on Interaction between Phytochromes and Gibberellins or Abscisic Acid

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Abstract

Separately, it is well-documented that phytochromes (phys), gibberellin (GA) and abscisic acid (ABA) strongly control the seed germination in tomato. However, we hypothesized that phys interact with GA or ABA during this response. Thus, we make an analysis of seed germination of ABA deficient (*sit*), GA constitutive response (*pro*), phytochrome deficient (*au*) mutants as well as, specially, *au sit* and *au pro* double mutants of tomato incubated in the dark or light conditions during 120 h [12 h intervals (i)]. Compared to *au*, which severely reduced percentage germination (G_i%) and *pro*, which did not alter G_i%, *au pro* showed in the light enhanced G_i% and germination speed index (GSI) besides the reduced average germination time (AGT). Moreover, in the dark, germination of *au pro* was similar to *pro.* These results indicate that the mechanisms by which GA modulate germination in tomato are light dependent through the phy signaling, whereas intermediary values of G_i%, GSI and AGT in dark and light of *au sit* compared to *au* and *sit* single mutants indicate an additive effect of the *au* and *sit* mutations, suggesting that ABA and phy may act through the parallel signaling pathway.

Keywords

Abscisic Acid, Gibberellins, Phytochromes, Seed Germination, Tomato

1. Introduction

Classic factors that modulate seed germination in a wide range of species include the hormones gibberellin (GA)

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and abscisic acid (ABA) and phytochromes (phys), which are converted from their inactive red (R)-light-absorbing form (Pr) into its active far-red (RF)-light-absorbing form (Pfr) [1]. However, although it is well known that separately GA, ABA and phy modulate seed germination [2], these factors can strongly interact each other. For example, during seed germination in *Arabidopsis*, the degradation of PHYTOCHROME INTERACTING FACTOR 3-LIKE5 (PIL5) (also called PIF1) by phy reverses the action of PIL5, reducing ABA levels and increasing GA levels, and therefore, decreasing the DELLA proteins, GA negative signaling components [3] [4]. In addition, the DELLA-dependent accumulation of endogenous ABA levels stimulates the expression of ABI3, an embryonic transcription factor that is necessary to repress germination under FR conditions [5]-[7].

However, the regulatory loops between light and GA and ABA signaling are still very complex since the intricate molecular and biochemical signaling pathways of these molecules are dependent on species, temperature, and light [2] [8]. For example, it is known that *Arabidopsis* seeds germinate poorly in darkness, but GA can promote seed germination even in the dark [9]. In barley seeds, the expression of *GA3ox2*, a GA biosynthetic gene, increased rapidly and continued to increase up to 24-h imbibition in after-ripened grains in both light and dark conditions [10]. Thus, there are an overwhelming number of molecular and biochemical questions about the mechanisms behind seed germination. For example, which hormones and photoreceptors control the germination response, how do they do it, and how do they interact with one another? Are these interactions light dependent? In order to answer many of these questions, conducting a physiological dissection of these tools prior to following the molecular approach can provide answers to many of the above questions. Thus, hormonal and photomorphogenic mutants and hormonal-photomorphogenic double mutants have served as important tools. In the present study, we used GA constitutive response, ABA-deficient or phy-deficient mutants, as well as GA-phy or ABA-phy double mutants of tomato to explore the physiology of seed germination.

2. Materials and Methods

Plant Material and Seed Germination Assays

We used seeds of tomato (*Solanum lycopersicum*) mutants introgressed into the cultivar Micro-Tom (MT) [11]: *aurea* or *au* (phy-deficient) [12], *sitiens* or *sit* (ABA-deficient) [13], and *procera* or *pro* (GA constitutive response) [14] which were kindly provided by R. Chetelat (The C.M. Rick Tomato Genetics Resource Center, Davis, USA). We also used *au sit* and *au pro* double mutants previously constructed [15]. MT was used as control. Seed germination assays of photomorphogenic, hormonal, and double mutants and MT control were performed by sowing seeds onto two wet filter papers in transparent or black plastic boxes. The experiments were conducted in a growth chamber (25˚C, 16 h photoperiod, 55 µmol photons $m^{-2}\cdot s^{-1}$ PAR). For the dark treatment, seeds were counted in a dark room under a dim green safelight. We used three replicates of 50 seeds and calculated the daily (i) (12/12 h for 120 h) percentage of seeds that germinated (G_i%), besides the G_f%, where f is final percentage (after 120 h). The calculation may be expressed using the following formula:

$$G_i\,\%\text{ or }G_f\,\% = \left(n_i / N\right)\times 100$$

where n_i is the number of seeds germinated every 12 h, and N is the number of seeds included in the test, and then G_f% is final percentage (after 120 h) of seeds that germinated.

We used the following formulas to calculate the germination speed index (GSI) and average germination time (AGT):

$$\text{GSI} = \sum\left(n_i / t_i\right)$$

where t_i is day i

$$\text{AGT} = \sum\left(t_i \cdot n_i\right) / \sum n$$

T_{50} is the time it takes to reach 50% germination. This, in turn, is calculated according to the following formula [16] [17]:

$$T_{50} = t_i + \left[\left(N/2\right) - n_i\right]\left(t_j - t_i\right) / \left(n_j - n_i\right)$$

where N is the final number of seeds that germinated and n_i and n_j are the cumulative number of seeds germinated by adjacent counts at times t_i and t_j when $n_i < N/2 < n_j$.

To observe seed dormancy break as affected by GA in *au* mutant, seeds were incubated in light and dark conditions during 120 h with 100 µM GA.

Germination was defined as the visible emergence of the radicle through the seed coat [18] [19].

The data were submitted to statistical analysis by using analysis of variance and Tukey's test at a 5% significance level.

3. Results and Discussion

In this study, we used phy, ABA, and GA mutants, as well as double mutants displaying both phy and ABA or both phy and GA mutations, to explore the photomorphogenic and hormonal control of seed germination in tomato. As we expected, given the light treatment the ABA-deficient mutant, *sit*, showed a constant increase of G_i% after 60 h (**Figure 1(A)**) and a reduction in GSI, AGT, and T_{50} (**Table 1**) compared with the MT control. In fact, in

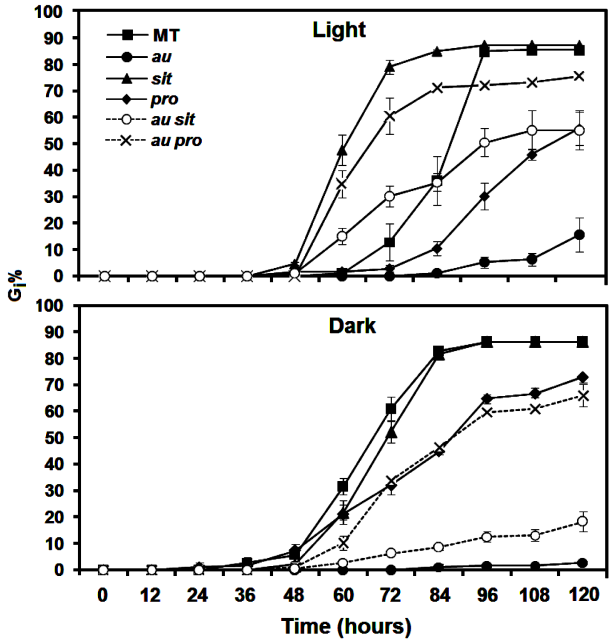

Figure 1. Seed germination percentage at 12 h intervals (i) (G_i%) of photomorphogenic and/or hormonal mutants incubated in light and dark conditions during 120 hours. Data are means ±SE.

Table 1. Germination speed index (GSI), average germination time (AGT), time to reach 50 % germination (T_{50}) and final germination percentage (G_f%) obtained from seeds of photomorphogenic and/or hormonal mutants incubated in light (L) and dark (D) conditions during 120 h.

Genotypes	GSI		AGT		T_{50}		G_f%	
	L	D	L	D	L	D	L	D
MT	0.56^{bc*}	0.74^{a}	89.08^{ab}	70.40^{b}	84.82^{ab}	64.89^{b}	98.00^{a}	100.00^{a}
au	0.08^{e}	0.02^{d}	103.95^{a}	104.00^{a}	-	-	18.00^{c}	3.33^{d}
pro	0.33^{d}	0.58^{b}	100.00^{a}	80.39^{b}	105.93^{a}	82.04^{a}	64.00^{b}	84.67^{b}
sit	0.76^{a}	0.69^{a}	67.04^{c}	74.00^{b}	59.17^{c}	68.44^{b}	100.00^{a}	100.00^{a}
au pro	0.63^{ab}	0.49^{b}	70.46^{c}	81.15^{ab}	64.71^{bc}	80.71^{a}	86.67^{ab}	76.67^{b}
au sit	0.42^{cd}	0.12^{c}	78.33^{bc}	89.53^{ab}	98.5^{a}	-	63.33^{b}	21.33^{c}

*In a column, means followed by the same letter are not significantly different by the Tukey test at 5% of probability. Following N/2 (Coolbear *et al*., 1984; Farooq *et al*., 2005) [16] [17], the absent data mean that genotypes did not reach T_{50}.

contrast with wild-type seeds, seeds of *sit* always readily germinate and even exhibit viviparous germination in overripe fruits [20]. Although the GSI and AGT data show the rapidity with which *sit* can germinate despite its ABA deficiency, G_f% and G_i% after 120 h did not differ from that of MT (**Table 1**). Moreover, in the dark condition, G_i% from 48 to 120 h (**Figure 1(B)**), AGT, T_{50}, and especially GSI (**Table 1**) did not differ from MT. This finding indicates that ABA deficiency in *sit* has a complex mechanism that is light dependent during germination and that remains to be explored using molecular and biochemical approaches.

To investigate whether the constitutive GA response conferred by the *pro* affected germination, Bassel *et al*. [13] dissected the embryo axes from the endosperm after 4 h of imbibition and verified that the *pro* germinated the fastest of all the wide types. However, we observed that in both the dark and the light condition in intact seeds, *pro* reduced G_i% from 60 to 120 h (**Figure 1**) and also reduced GSI and G_f%. The AGT was similar to that in MT (**Table 1**), and T_{50} was increased in the dark. Thus, irrespective of whether constitutive GA response is the mechanism by which *pro* accelerates germination in dissected seeds, the *pro* mutation is not fully capable of mediating a rapid breaking of coat dormancy. In other words, although GA profoundly influences seed germination and the *pro* mutation regulates GA responses within the embryo [13], the coat modifications for radicle protrusion appear not to depend on the GA constitutive response. Further detailed inspections of seed biochemistry and the anatomy of *pro* are necessary to explain the delayed germination in this mutant.

One of the more noticeable effects of the *au* mutation is a severe delay in seed germination [15] [21] due to a deficiency in phytochrome chromophore biosynthesis. We present novel observations relating to this effect regarding G_i% (**Figure 1**), GSI, and G_f% (**Table 1**), all of which were reduced in the light and the dark, whereas AGT increased compared to that in MT (**Table 1**). It is remarkable to note that the severity of the germination delay in the *au* mutation is intensified in the dark, indicating that although *au* is phytochrome deficient, either the low phytochrome signaling or the presence of other photoreceptors such as cryptochromes is sufficient to promote germination in this mutant.

Intriguingly, compared with *au* and *pro*, the *au pro* double mutant in the light condition showed an enhanced G_i% from 60 to 120 h (**Figure 1(A)**), increased GSI (**Table 1**), and reduced AGT (**Table 1**). In the dark, this genotype showed a similar GSI and AGT to *pro* and *au*, on top of the existing similarity between AGT and *pro*. One might expect to see an additive effect of reduced germination of *au* and *pro* in double mutants, but in the light, the phy deficiency and GA constitutive response improve seed germination. Certainly, these results need to be interpreted carefully, as there is interaction between light and GA at virtually every stage of plant growth [13] [22]. Furthermore, and particularly during seed germination, the mechanisms by which GA is involved in light signaling are quite complex. For example, previous findings in *Arabidopsis* indicate that phytochromes promote seed germination by lowering the level of DELLA proteins and increasing the level of bioactive GA [3] [4].

Thus, at least in the light, it is plausible to suggest that in tomato the *au* mutant shows reduced germination because the phy deficiency does not induce GA activities; however, a hormonal quantification was not carried out in this mutant. So far, although exogenous GA did not recover *au* germination in the light to MT levels, *au* seems trigger more sensitivity to GA in the dark (**Figure 2**), indicating that tomato does not have a linear induction of GA by phy during germination. In fact, although the GA constitutive response of *pro* recovers *au* germination in *au pro*, the delayed germination in *pro* shows that the GA modulation of seed germination in tomato occurs only under specific conditions or that GA functions are highly redundant. Further evidence is that in the dark, G_i% (**Figure 1(B)**), GSI, AGT, and G_f% (**Table 1**) are similar in *pro* and *au pro*. In addition, there is an intricate GA signaling pathway in *pro* or *au pro*, as *pro* contains reduced concentrations of GAs despite its constant response to this hormone [23].

In the light and dark conditions, the intermediary values of G_i% (**Figure 1**), GSI, and G_f% (**Table 1**) of *au sit* compared with *au* and *sit* suggest that there is an additive effect of both mutations on germination. However, only in the light condition, AGT of *au sit* seemed to show an epistatic effect of *sit*, as *sit* and *au sit* are similar (**Table 1**). Thus, although an additive interaction indicates that light and ABA have independent pathways during tomato germination, AGT of *au sit* revealed that the mechanisms by which phy and ABA control germination can be dependent on one another. However, data regarding how ABA is part of light signaling are still very scarce in tomato. Majority of the currently available information relates to the separate effects of phy [24] [25] or ABA [26] [27].

A more detailed analysis of particular aspects of *pro*, such as the reduced concentrations of GA and constitutive responses to this hormone [23], will clarify the mechanism for such responses and will improve our knowledge of the role of GA in seed germination in tomato. The results of *au pro* raise questions about the mechanisms

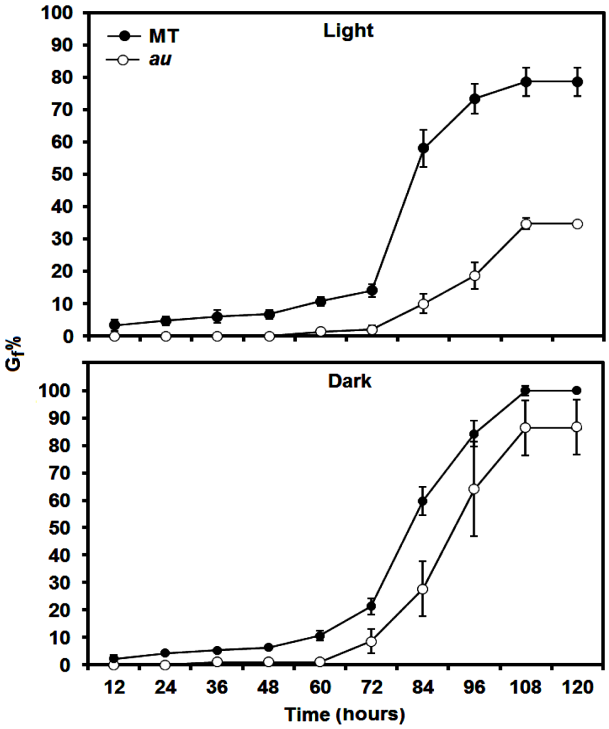

Figure 2. Seed germination percentage at 12 h intervals of *au* mutant incubated in light and dark conditions during 120 hours. Over time, seeds were treated with 100 µM GA. Note that GA did not induce dormancy break to MT levels, but seems trigger more sensitivity to GA in the dark. Data are means ± SE.

of GA participation in light signaling during germination. For example, which photoreceptors interact with GA, how do they interact, and can they regulate GA levels? These questions may be asked about ABA and other hormonal classes as well, as brassinosteroids, auxin [28] [29], cytokinin [30], and ethylene [31] are clearly involved in germination. However, the most important issue of the molecular interpretation of light signaling and hormone interactions during germination remains to be elucidated by future research.

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Abbreviations

AGT: average germination time
GSI: germination speed index
GA: gibberellin
ABA: abscisic acid
phy: phytochrome

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