Gibberellic acid biosynthesis during dehydration phase of priming increases seed vigour of tomato

S. Seethalakshmi¹ · R. Umarani¹ · M. Djanaguiraman²

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Abstract
Priming of seed is intended to reduce the time to germination through activation of pre-germinative processes. Seed priming is controlled hydration followed by a drying (dehydration) process. The physiological processes during hydration (imbibition) were studied in detail in tomato. In contrast, gibberellic acid changes during the dehydration phase were not studied in detail. We hypothesize that there would be a change in the GA concentration during the dehydration phase of the seed priming process, which may influence the vigour characteristics of the resultant seedling. The objective of the study was to understand the influence dehydration phase of seed priming on GA biosynthesis and its subsequent effect on seed germination and seedling traits of tomato. First, the hydroprimed and unprimed seeds were re-imbibed for 3 h, 6 h, 9 h, and 12 h to initiate the germination process, and the GA concentration and seedling vigour associated parameters were recorded. In the second experiment, the imbibed seeds were dehydrated for 3 h, 6 h, 9 h, and 12 h, then re-imbibed for 3 h, 6 h, 9 h, and 12 h to understand the effect of dehydration on the GA concentration and its associated traits. Results revealed that hydroprimed seeds had a higher GA concentration and seedling vigour than unprimed seeds. The seeds that are completely dehydrated for 12 h had the highest GA and seed vigour parameters. Therefore, increased vigour of hydroprimed seeds is due to the higher levels of GA accumulated during the dehydration phase of seed priming, which can improve seed germination and seedling vigour of tomato.

Keywords Seed priming · Seed imbibition · Seed dehydration · Re-imbibition · Gibberellic acid

Abbreviations
ATP Adenosine triphosphate
ANOVA Analysis of variance
GA Gibberellic acid
HPLC High-performance liquid chromatography
LSD Least significant difference
NADH Nicotinamide adenine dinucleotide
NaOCl Sodium hypochlorite

Introduction

Tomato (Solanum lycopersicum L.) is a vegetable grown for various nutrients, protein, and carbohydrate requirements of the human diet (Rahal et al. 2014). Seed priming is a pre-sowing technique that ensures faster, uniform, and synchronized germination besides improving seedling vigour and growth under normal and adverse environmental conditions (Varier et al. 2010). The process of seed priming involves imbibition of seeds to permit pre-germinative metabolic activity to proceed, followed by dehydration to prevent actual emergence of the radicle. The imbibition phase of seed germination consists of three phases, i.e., phase I is characterized by a rapid uptake of water, phase II is categorized as a plateau in water uptake, and during phase III there will be another increase in water uptake, which permits the elongation of the embryo and the breaking of testa to complete the germination process (Finch-Savage and Leubner-Metzger 2006; Weitbrecht et al. 2011). During the phase I and II, swelling or solute leakage, activation of respiration process, biosynthesis of amino acids and sugars,
de novo synthesis of mRNA and translation, and the onset of seed reserve mobilization happens. During phase III, the rupture of seed coat occurs, which results in protrusion of the radicle (Weitbrecht et al. 2011). In the seed priming process, seeds are subjected to controlled hydration to complete phase I (imbibition) and phase II (activation) of the seed germination process, and without entering into phase III (radicle protrusion) (Bradford and Bewley 2002). Therefore, the efficiency of the seed priming technique is expected to be mostly dependent on the effective completion of phase I and phase II of the seed germination process.

Most researchers have reported that the advantage of seed priming is associated with the initiation of germination metabolism during the imbibition phase of seed priming (Heydecker et al. 1973; Simon 1984; Khan 1992; Taylor et al. 1998). However, the dehydration process is also equally important to terminate the ongoing physiological process and prevent the protrusion of radicle in the imbibing seeds. Further, Dell Aquila and Tritto (1991) have suggested that the beneficial effects of priming could be established during the drying phase since it offers sufficient time to repair and physiologically stabilize the seeds, than the imbibition phase.

Gibberellic acid (GA) is a phytohormone involved in various plant processes like seed germination, leaf expansion, stem elongation, flowering, and seed development (Davies 1995). During seed germination, water is imbibed, resulting in the release of bioactive gibberellin from the embryo cells, which diffuses into the aleurone layer (Fincher 1989) to induce the synthesis of hydrolytic enzymes named α-amylase (Gubler 1995). The α-amylase, in turn, diffuses from the aleurone layer into the starch-packed endosperm and converts starch molecules to glucose (Gupta et al. 2013). The glucose thus formed is utilized for the production of adenosine triphosphate (ATP) and reduced form of nicotinamide adenine dinucleotide (NADH or NADPH2), which drives rapid cell divisions of meristem cells in the embryo, resulting in seed germination (Li et al. 2018).

Ogawa et al. (2003) reported that most of the GA-upregulated transcripts of Arabidopsis, increased in abundance after imbibition relative to dry seeds, indicating imbibition activates GA synthesis. Dell Aquila and Tritto (1991) stated that the drying phase is more important because various defence enzymes and antioxidants are synthesized, which in turn can physiologically stabilize the seed. Therefore, it is not clear whether GA biosynthesis happens during the imbibition or dehydration phase, which needs to be studied in detail.

It was hypothesized that there would be a change in the GA concentration during the dehydration phase of seed priming process, which may influence the vigour characteristics of the resultant seedling. The objective of the study was to (i) understand the effect of different duration of imbibition periods on GA concentration in seed and seedling vigour traits of tomato, and (ii) quantify the effect of the re-imbibition and dehydration process on GA concentration in seeds and seedling vigour traits. This study will bridge the gap in understanding the biochemical changes that occur in the seed during both the imbibition and dehydration phase of the seed priming process.

Materials and methods

The tomato variety, Arka Vikas, a pure line selection from American variety Tip-Top, released from the Indian Institute of Horticultural Research, Bangalore, India, was used in all the experiments. The experiments were conducted at the Department of Seed Science and Technology, Tamil Nadu Agricultural University, Coimbatore, Tamil Nadu, India. Two independent experiments were conducted to understand the biochemical changes that occur (i) during the early germination phase of hydropimred and unprimed seeds of tomato seeds and (ii) during the dehydration phase of the seed priming process of tomato seeds.

Experiment 1: Effect of seed imbibition duration on moisture content, gibberellic acid content, and vigour of hydropimred and unprimed seeds of tomato

The experiment was conducted in a factorial completely randomized design. The first factor being primed and unprimed seeds. The second factor was the duration of re-imbibition. The seeds used in this experiment were thoroughly surface sterilized with 2% sodium hypochlorite (NaOCI) solution by shaking the seeds for 1 min in the NaOCI solution, then rinsed thrice with sterile water and dried in air. After sterilization, the tomato seeds were hydropimred by soaking in water for 48 h, then shade dried to bring back to original moisture content (8%) as described by Venkatasubramanian and Umarani (2007). The above described dried seeds are referred to as hydropimred seeds. In contrast, the seeds which were not primed is referred to as unprimed seeds (control). Both the primed and unprimed seeds were soaked in water to subject them to re-imbibition treatments for initiating the germination process. The re-imbibition duration was 0 h, 3 h, 6 h, 9 h, and 12 h. After the expiry of the specified imbibition duration, the seeds were collected and divided into three portions to analyze the seed moisture content, GA content and seed germination characteristics.

The first portion was used for seed moisture analysis. Five gram of seeds were transferred to a moisture bottle, then dried in a hot air oven, maintained at 103 ± 2 °C for 17 h. After cooling the bottle in a desiccator for 30 min, the seeds...
were taken out and weighed. The moisture content was calculated based on the initial and final weight and expressed in percentage.

The second portion of seed was used for GA quantification using high-performance liquid chromatography (HPLC). Seeds from various re-imbibition treatments were frozen in liquid N2 and lyophilized. One gram of seeds was extracted in 100 ml of 80% methanol (v/v). The supernatant was saved, and again the residue was re-extracted overnight with 100 ml of 80% methanol (v/v). Then the methanol was decanted from the seeds, and the combined methanolic extracts were dried in a rotary flash evaporator maintained at 35 °C. The aqueous fraction was adjusted to pH 3 and loaded onto a column of 1 g charcoal and 2 g of celite. A volume of 250 ml of 80% acetone (v/v) was passed through the column. The eluate was reduced to aqueous, adjusted to pH 2.5, and partitioned five times against half-volumes of ethyl acetate. The resultant acidic fraction was subjected to analysis as described below. Appropriate fractions were methylated with ethereal diazomethane. The trimethylsilyl (TMS) ethers of the methyl esters were prepared by adding 50 µl of a solution containing pyridine-hexamethyl disilazane-trimethyl chlorosilazane (9:3:1, v/v) to methylated samples, dried in vials. Standard (GA3) were used to compare the results in the sample (Holbrook et al. 1961).

The preparative HPLC system consisted of a series of four stainless steel columns each 60 × 0.65 cm i.d., packed with Bondapak C18/Porasil B (Waters Associates, USA). Solvents used were 1% (v/v) aqueous acetic acid (solvent A) and redistilled 95% ethanol (solvent B). GA was extracted using 70% A-30% B solution, filtered through 0.45 µm type HA Millipore filters and loaded onto the column via a Waters U6K universal injector fitted with a 5-ml loop. A linear gradient of B (30-110% in 25 min) in A was delivered by two Waters 6000A pumps, controlled by a Waters 660 solvent programmer. The solvent flow rate was 9.9 ml min⁻¹, and the gradient was started 30 s after injection. Fractions were collected every min from the time of injection and dried in a fume hood. For analytical separations, a column 30 × 0.4 cm i.d. packed with Bondapak C18 (Waters Associates, USA) was used. Elution was through linear gradients of methanol in 1% aqueous acetic acid, with a flow rate of 2 ml min⁻¹. The gradient was started 2.5 min after injection and fractions were collected every min from the time of injection. The concentrations of GA in the HPLC eluate were determined by GLC. Fractions from the HPLC were methylated with ethereal diazomethane and chromatographed on a glass column 183 × 0.3 cm i.d., packed with 4% SE-33 as described previously (Beck and Ziegler 1989). The column temperature was 240 °C (for Me-GA8) and detection was by flame ionization. The results are presented as µg g⁻¹ of the sample.

The third portion was used for analyzing germination percentage, speed of germination, root length, shoot length, dry matter accumulation and vigour index. The germination test was conducted in paper towels with four replicates of 100 seeds of each treatment. The test conditions were 25 ± 2 °C and 95 ± 5% RH, illuminated with fluorescent light. On the 14th day after sowing, the number of normal seedlings was counted in each replication, and the mean percentage germination was calculated as the whole number (ISTA 1999). The root and shoot length of the normal seedlings were measured and expressed in cm. Later, the seedlings were dried in a hot air oven maintained at 85 ± 2 °C for 24 h, cooled in a desiccator, and weighed. The result was expressed as dry matter production (g 10 seedlings⁻¹). The vigour index was arrived at by multiplying germination percentage and seedling length (cm) expressed as a whole number (Abdul-Baki and Anderson 1973).

**Experiment 2: Influence of differential duration of seed dehydration of imbibed tomato seeds on the efficacy of seed priming process**

The experiment was designed in a completely randomized design with two factors and five replications. The first factor i.e., dehydration durations (3 h, 6 h, 9 h, and 12 h) was implemented after completion of imbibition process (24 h), and the second factor namely re-imbibition durations (3 h, 6 h, 9 h, and 12 h) was implemented at the end of each dehydration duration (3 h, 6 h, 9 h, and 12 h). The seeds used in this experiment were thoroughly surface sterilized with 2% sodium hypochlorite (NaOCI) solution by shaking the seeds for 1 min in the NaOCI solution, then rinsed thrice with sterile water and dried in air. After sterilization, the seeds were imbibed in water for 48 h and dried (dehydration) on filter paper for 3 h, 6 h, 9 h, and 12 h, and re-imbibed for a specific period as per the treatments mentioned above. After the stipulated time, the seeds were collected and divided into two parts and subjected to quantification of GA, as well as seed germination and seedling characteristics, respectively, as detailed in the experiment I.

**Statistical analyses**

Statistical analyses were performed using SAS programs version 9.4 (SAS Institute 2003, Cary, NC). The first experiment (comparative evaluation of primed and unprimed seeds for GA and seedling characters) was set in factorial completely randomized design with five replications and the second experiment (influence of progressive stages of seed dehydration on GA and seedling characters) in a complete randomized design with two factors wherein the first factor was dehydration duration and second-factor being re-imbibition duration. There were five replications in the second experiment. Data were analyzed using an analysis of variance (ANOVA) with the GLM procedure, and Fisher’s least
significant difference (LSD) at 5% significance level was used to test differences between mean values. Percentage data were arcsine transformed before analysis.

**Results and discussion**

**Experiment 1: Effect of seed imbibition duration on moisture content, gibberellic acid content and vigour of hydroprimed and unprimed seeds**

The result of the present study indicates that there were significant \( (P < 0.05) \) differences among the treatments (re-imbibition for 0, 3, 6, 9 and 12 h) for seed moisture content (\%), germination percentage, and speed of germination (d) (Fig. 1). Similarly, there were significant \( (P < 0.05) \) differences among the priming treatments for root length (cm), shoot length (cm), total dry matter production (g 10 seedlings\(^{-1}\)), vigour index, and GA concentration (µg g\(^{-1}\)) (Fig. 2).

Among the treatments, the hydroprimed seed recorded seed moisture of > 9% at 3 h of re-imbibition, while the unprimed seeds had the same moisture content (> 9%) only after 12 h of re-imbibition (Fig. 1a). Irrespective of the duration of imbibition (3 h, 6 h, 9 h and 12 h), the unprimed seeds showed a lower speed of germination and seed germination percentage; in contrast, the hydroprimed seeds recorded a higher speed of germination and seed germination. Hydroprimed seeds showed an increased root length (cm), shoot length (cm), dry matter production (g 10 seedlings\(^{-1}\)), and vigour index compared to unprimed seeds (Figs. 1 and 2).

Similarly, the gibberellic acid concentration (µg g\(^{-1}\)) was higher in hydroprimmed seeds than unprimmed seeds throughout the re-imbibition durations (Fig. 2a–d). Further, the increased synthesis of GA was observed earlier in primed seeds (6 h) compared to unprimed seeds (9 h). The increased moisture content or rapid water imbibition, coupled with increased biosynthesis of GA in hydroprimmed seeds at 3 h, 6 h, 9 h, and 12 h of imbibition compared to respective timing of unprimed seeds, shows early biosynthesis of GA. Obviously, early or rapid biosynthesis of GA might help in a higher speed of germination and increased seed germination than unprimed seeds through higher cell division in germinating seeds (Bewley and Black 1994). Similar positive effects of hydropriming were observed in wheat (Muzaar et al. 2019), maize (Mohammadi et al. 2014), soybean (Langeroodi and Noora 2017), and sunflower (Lekic et al. 2015).

In the process of hydropriming, various pre-germination processes have to be activated without rupture of testa so that radicle does not emerge (Weitbrecht et al. 2011). The whole...
metabolism has already been initiated so that when the seeds are sown, developmental processes go on more rapidly than in the case of non-primed seeds (Kattimani et al. 1999). The increased speed of germination and synchronized seed germination in hydroprimmed seeds compared to unprimmed seeds may be associated with metabolic changes that occur during phase I and II of imbibition accomplished due to seed priming (Khajeh-Hosseini et al. 2003; Musa et al. 2001; Sadeghian and Yavari 2004). Previous studies have shown that GA produced in the embryonic axis is involved in the induction of α-amylase enzyme activity (Yamauchi et al. 2004; Seo et al. 2009) and weakening endosperm caps (Groot and Karssen 1987).

Overall, the hydroprimed seeds showed quicker water imbibition potential, concomitantly higher biochemical potential in terms of higher gibberellic acid synthesis, and increased physiological potential in terms of seed germination percentage, speed of germination, and root length compared to unprimed seeds.

**Experiment 2: Influence of differential duration of seed dehydration of imbibed tomato seeds on the efficacy of seed priming process**

Our earlier study in tomato has shown that imbibing the seeds in water for 48 h, followed by shade drying for 12 h (hydropriming) has improved the seed germination and speed of germination compared to unprimed seeds. Previous reports have established that during the imbibition phase, the pre-germinative events like the repair of mitochondria and genetic material, biosynthesis of protein, hormones, and metabolites and induction of enzymes might happen (Bewley and Black 1994). The stimulatory effect observed due to hydropromping may be associated with imbibition or dehydration period. In this study, we hypothesized that the observed positive effects of hydropriming might be related to the dehydration period. To validate this the tomato seeds were imbibed for 48 h, and then dehydrated for 3 h, 6 h, 9 h, and 12 h, and various seed germination traits like seed GA concentration, α-amylase activity and starch content were quantified by re-imbibing the seeds for 3 h, 6 h, 9 h and 12 h, to initiate the seed germination process.

The main effects of dehydration period and re-imbibition period was significant \(P < 0.05\) for speed of germination \((d)\), germination percentage, root length \((cm)\), shoot length \((cm)\), dry matter accumulation \((g\ 10\ seedlings^{-1})\), vigour index and moisture content \(\%\). However, the interaction of dehydration and re-imbibition period was significant \(P < 0.05\) for α-amylase enzyme activity \((mg\ of\ maltose\ min^{-1})\), starch content \((mg\ g^{-1})\), and gibberellic acid concentration \((\mu g\ g^{-1})\).

Among the dehydration durations \((h)\), seeds dehydrated for 12 h was found to record increased speed of germination, germination percentage, root length, shoot length, dry...
matter accumulation, and vigour index (Table 1). However, the lowest seed moisture content was recorded at 12 h of dehydration (Table 1) which was on par with 9 h. Among the re-imbibition period, the increased speed of germination, germination percentage, root length, shoot length, dry matter accumulation, and vigour index was observed at 9 h of imbibition (Table 2). There was no statistical difference between 9 h and 12 h of re-imbibition for the above-mentioned traits (Table 2). Similarly, there was no significant variation in seed moisture content from 6 h to 12 h of re-imbibition (Table 2).

The GA concentration observed at 3 h, 6 h, 9 h, and 12 h of re-imbibition duration indicated that the seeds which are dehydrated for 12 h had higher levels of GA compared with 3 h, 6 h, and 9 h of dehydration (Fig. 3). Similarly, the α-amylase enzyme activity was the highest at 12 h of dehydration and 12 h of re-imbibition (Table 3). In contrast, the starch content in the seed was the lowest at 12 h of dehydration and 12 h of re-imbibition.

The seed germination was lower in 3 h dehydrated seed (64%); subsequently, as the duration of dehydration increased, the germination percent increased from 66% to 74% (Table 1). Therefore, it is clear that advancement in dehydration increases germination potential. This phenomenon is proven by the higher seed germination potential of seeds in advanced dehydration stage observed during re-imbibition process (Table 2). Thus, complete drying of seeds after the imbibition process of seed priming improves the rate of seed imbibition and GA synthesis in seeds (Table 1; Fig. 3). GA is involved in the upregulation of α-amylase enzyme activity (Gubler et al. 1995), as a consequence, the carbohydrate stored in the endosperm will be broken down into simple sugars and will be transported to the growing embryo (Gupta and Chakrabarty 2013) to support the respiratory process, resulting in early and uniform seedling emergence and growth.

### Conclusions

The major findings from this study are (i) throughout the re-imbibition durations, the hydroprimed seeds had higher levels of seed moisture, gibberellic acid concentration, speed of germination, germination percentage, and seedling vigour traits than unprimed seeds, (ii) dehydration of imbibed seeds for 12 h resulted in an increased GA concentration in seeds, and seedling vigour traits compared to other dehydration treatments (3, 6, and 9 h), and (iii) higher GA concentration in seeds increased the α-amylase activity resulting in improved seed germination. The present study showed that the seed dehydration process is more critical in the seed priming process because the physiological processes required for early and uniform germination are happening during that time. However, further experiments to study

### Table 1

Main effect of dehydration period (h) on seedling traits of tomato seeds

| Stages of dehydration (h) | Speed of germination (d) | Germination percentage | Root length (cm) | Shoot length (cm) | Dry matter production (g 10 seedlings−1) | Vigour index | Moisture content (%) |
|---------------------------|--------------------------|------------------------|------------------|------------------|-----------------------------------------|-------------|---------------------|
| 3                         | 3.07d                    | 64 (53.19)†            | 11.54d           | 5.25d            | 0.018b                                  | 1075d       | 10.33 (18.74)a      |
| 6                         | 3.39c                    | 66 (54.28)†            | 12.25c           | 5.40c            | 0.018b                                  | 1160c       | 9.68 (18.11)b       |
| 9                         | 4.09b                    | 72 (57.95)†            | 13.17b           | 5.63b            | 0.021a                                  | 1354b       | 9.00 (17.46)c       |
| 12                        | 4.36a                    | 74 (59.19)†            | 13.97a           | 5.96a            | 0.021a                                  | 1470a       | 8.93 (17.37)c       |
| LSD (P ≤ 0.05)            | 0.085                    | 0.89                   | 0.30             | 0.12             | 0.0005                                  | 24.87       | 0.16                |

*LSD* Least significant difference; value in parenthesis is arcsine transformed value. †The means with different letters in each column are significantly different at *P* < 0.5

### Table 2

Main effect of re-imbibition period (h) on seedling traits of tomato seeds

| Stages of re-imbibition (h) | Speed of germination (d) | Germination percentage | Root length (cm) | Shoot length (cm) | Dry matter production (g 10 seedlings−1) | Vigour index | Moisture content (%) |
|-----------------------------|--------------------------|------------------------|------------------|------------------|-----------------------------------------|-------------|---------------------|
| 3                           | 3.59b                    | 68 (55.80)†            | 12.35c           | 5.46a            | 0.02a                                   | 1219c       | 9.20 (17.65)b       |
| 6                           | 3.65b                    | 69 (56.27)†            | 12.58b           | 5.54b            | 0.02a                                   | 1256b       | 9.48 (17.91)a       |
| 9                           | 3.80a                    | 69 (56.22)†            | 12.81ab          | 5.59a            | 0.02a                                   | 1274b       | 9.60 (18.03)a       |
| 12                          | 3.87a                    | 69 (56.32)†            | 13.19a           | 5.65a            | 0.02a                                   | 1309a       | 9.65 (18.09)a       |
| LSD (P ≤ 0.05)              | 0.085                    | NS                     | 0.30             | NS               | NS                                      | 24.8        | 0.16                |

*LSD* Least significant difference; value in parenthesis is arcsine transformed value. †The means with different letters in each column are significantly different at *P* < 0.5

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the effect of dehydration on other metabolic events such as enzyme synthesis, breakdown of stored food reserves and protein synthesis are needed.

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Author contributions SS and RU designed the experiment, carried out the research, analyzed the data and wrote the paper. MD helped in revising the manuscript and preparing it for submission. All of the authors read and approved the final manuscript.

Declarations

Conflict of interest The authors declare that they have no competing interests.

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