A brief overview of seed priming benefits in tomato

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Abstract

Tomato (Solanum lycopersicum L.) is one of the most important crop plants, due to its nutritional and nutraceutical qualities, as well as being of major worldwide economical importance as a source of income and a major contributor towards food security. This plant is also used as a model for studying plant physiology, biochemistry, genetics, genomics and breeding an effort to improve agronomic characteristics such as tolerance to stress factors. The purpose of this review is to highlight recent advancements in seed priming treatments resulting in improved tomato plant fitness. This review is divided into two sections focusing on: (1) benefits of tomato seed priming associated with seed germination, seedlings vigor and physiological performance of tomato plants; (2) benefits of tomato seed priming associated with improving plants tolerance to biotic stresses. Finally, we make some conclusions about the approaches that are need to further studies on this topic.

Keywords: Tomato, Seed Priming, Germination, Seedling vigor, Stress tolerance

1. Introduction

Tomato (Solanum lycopersicum L.) is one of the most important crop plants due to its ease of propagation and short life cycle (D. GOEL & al. [1]). While being a vegetable of major worldwide economical importance, the tomato is a major source of minerals and vitamins (common and nutraceuticals), as well as an anticancer agent (K. CANENE-ADAMS & al. [2], H.L. TAN & al. [3], S. FUJIMURA & al. [4], MAHIMA & al. [5], A. RAHAL & al. [6]). In addition, tomatoes are a well-known source of income and a major contributor towards food security (S. MISHRA & al. [7]). Currently, this plant is used as a model to study plant physiology, biochemistry, genetics, genomics and breeding (M.R. FOOLAD [8], S. KIMURA & N. SINHA [9]), in an effort to improve agronomic traits of interest (A. GERSZBERG & al. [10]), including plant tolerance to stress factors (J.S. BOYER [11], D. GOEL & al. [1], S.V. GUND & al. [12], C. KISSOUDIS & al. [13]).

Germination, the initial step of the plant life cycle and seedling establishment are the crucial physiological periods for plant development and the expansion of a species in a new environment (J.D. BEWLEY [14], K. WEITBRECHT & al. [15], P.O. OGBAJI & al. [16]). Rapid and uniform germination is essential for increasing tomato crop yield and quality (M. ZHANG & al. [17]), which is of economical and environmental importance in horticulture. The former allows for a higher degree of automation, easier weed control and a reduction of disease pressure in the field (B. BADEK & al. [18]) while ensuring abiotic stresses are succesfully overcome (K.C. JISHA & al. [19]).

So far, numerous research approaches have been aimed at improving crop growth and development. For instance, many priming solutions have been previously tested and used such as hydropriming, osmopriming, solid matrix priming, biopriming, chemopriming, nutripriming,
thermopriming etc. (K.C. JISHA & al. [19], R. EBRAHIMI & al. [20], T.S. LARA & al. [21], E. DELIAN & V. LAGUNOVSCHI-LUCHIAN [22], S. PAPARELLA & al. [23]); these techniques that are generally easy to apply and the results are generally very positive (A. HORII & al. [24]). Seed priming with natural and/or synthetic compounds is a physiological seed enhancement method for overcoming poor and erratic seed germination (M.K. GUPTA & al. [25]). The pre-germination seed strategy allows for partial imbibition which prevents germination (K.J. BRADFORD [26]), but controls seed hydration and the metabolic reactions before germination. This method ensures faster, uniform and synchronized germination, while improving seedling vigor and growth under a broad range of adverse conditions (W. HEYDEKKER & al. [27], K.J. BRADFORD [26], M.B. McDONALD [28], A. VARIER & al. [29]).

The purpose of this review is to highlight recent advancements in seed priming treatments leading to increased tomato plant fitness. The review will be divided into two sections focusing on: (1) benefits of tomato seed priming associated with seed germination, seedlings vigor and plants physiological performance; (2) benefits of tomato seed priming associated with improving plants tolerance to biotic stresses. Finally, we make some conclusions about the approaches that are need to further studies on this topic.

2. Benefits of tomato seed priming on seed germination, seedlings vigor and plants physiological performance

Seed priming improves seeds germination, seedlings vigor and plant performance during the vegetation period as far as plant physiology and productivity is concerned. Germination comprises all the morphological, physiological and biochemical processes that occur in the seed beginning with the imbibition phase and culminating with radicle emergence from the seed coat (L. TAIZ & E. ZEIGER [30], J.D. BEWLEY & al. [31]).

Over the past 20 years, a large number of studies confirmed that various seed pretreatments triggering the so-called “pre-germinative metabolism” (S. PAPARELLA & al. [23]) have been used to improve seeds germination (B. BADEK & al. [18], A. HORII & al. [24], R. EBRAHIMI & al. [20], M.K. GUPTA & al. [25]), seedling establishment (D. HARRIS [32]) and increase plant vigor (A. HORII & al. [24], M.K. GUPTA & al. [25]), and yield (M.K. GUPTA & al. [25]). Obtaining vigorous seedlings and plants is the major premise for having a high crop yield of superior quality. Nowadays, farmers are eager to apply the most promising techniques that researchers have experimented with. While the effectiveness of these methods is of paramount importance, their ease of application, impact on health and food security, impact on the environment and not least the costs they entail are also of interest.

Generally, to evaluate the germination process is evaluated by assessing well known physiological indicators and providing adequate explanations for the obtained results. As expected, a required condition for germination is the presence of water. Increasing seed water content does not damage cells as a consequence of its rapid entry. While imbibition up to 35% followed by incubation for 1 hour leads to faster germination, matricconditioning and conditioning in limited water for 1 day results in slower germination (B. BADEK & al. [18]). In addition to providing water, different procedures, including physical methods, have been tested. For example, recent studies assessing the effect of magneto-priming cherry tomato seeds with static magnetic fields for different doses and durations (50–150 milliTesla – mT for 30 min and 1 hour) have shown that maximum germination is ensured by using 100 mT for 30 min (M.K. GUPTA & al. [25]). Numerous studies have focused on other priming methods such as osmopriming, salinity priming, hormonal priming, and chemical priming. Studies performed by T.S. LARA & al. [21] emphasized that tomato seeds priming with a solution of
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potassium nitrate (KNO₃) (50 mM) resulted in an increased germination time and rate compared to other treatments (i.e., polyethylene glycol (PEG 6000) -1.1MPa and PEG+KNO₃). A likely possibility is that the absorbed nitrate enters seed embryo metabolism at through the nitrate reductase enzyme pathway resulting in the production of nitrite/nitric oxide, which in turn promotes faster germination. According to the authors of this study, KNO₃ priming did not affected the percent, uniformity or synchrony of germination. Regarding the germination rate of tomato seeds after priming with natrium chloride (NaCl) and gibberellic acid (GA), M. NAKAUNE & al. [33] reported values of 4.9 and 4.6 times higher at 36 hours after sowing compared to hydro-primed seeds, with endogenous abscisic acid levels being similar after sowing. These results suggest that the effect of NaCl is caused by an increase of the GA₄ content via GA biosynthetic genes activation, and a subsequent increase in the expression of genes related to endosperm cap weakening. In addition, osmopriming of tomato seeds in 10% (w/v) polyethylene glycol (PEG) solution for 2 days at 20±1°C in the dark followed by exposure at 25±1°C for 7 days under normal (water) and 100 mM NaCl conditions, respectively, demonstrated that seeds germination could be improved under aging and salinity conditions (M. ZHANG & al. [17]).

The beneficial effects of seed pretreatment are not only reflected in the outcome of the germination process. To be more specific, seed priming is not only beneficial under normal culture conditions, but is also an appropriate means for the plant to successfully overcome the action of stressors. Among different abiotic stress factors, salinity is one of the most important in many arid and semiarid regions (E.A. IBRAHIM [34]). Salinity has a negative impact from the initial stages of seed germination and seedling growth and ultimately affects all the physiological and biochemical processes in a mature plant (A. NAWAZ & al. [35]). K. CHEN and R. ARORA [36] summarized two priming strategies to improve seed stress tolerance, with one that ensuring an advanced status of the germination and the second providing a priming-induced ‘stress imprint’. Together, these two strategies establish a ‘priming memory’ in seeds. In recent years, D.X. TAN & al. [37]) reported that melatonin, a molecule known for its benefits to human health, is one of the first lines of defence and an internal sensor of oxidative stress in plants. Furthermore, very recent research highlighted that the tomato seedling health index was improved by 44.11% compared to control when seeds were soaked in 0.1 mM melatonin. Accordingly, root dry weights were as high as 0.483 g for pre-treated seedlings, versus 0.364 g for untreated ones (J. LIU & al. [38]). The authors of these studies have indicated however that additional investigations are needed, in order to know the mechanism by which melatonin confers tolerance to drought to tomato plants. Sand priming of two tomato varieties for 72 hours at 25°C improved germination and vigor indicators under salinity stress (0, 50, 100 and 150 mM NaCl) coinciding with an increased activity of antioxidant enzymes such as malondialdehyde (MDA), catalase (CAT), peroxidase (POD), superoxide dismutase (SOD) and ascorbate peroxidase (APX) (A. NAWAZ & al. [35]). Recently, M.K. GUPTA & al. [25] reported that cherry tomatoes seedlings vigor was enhanced by 23% following seed exposure to pulsed magnetic field (PMF). As far as using fish protein hydrolysates (FPH) (a proline precursor-rich) for priming (2.5 mL/L) is concerned, A. HORII & al. [24] noticed a positive increase of tomato seedling weight following 2.5 mL/L and 5.0 mL/L FPH treatment during early and late germination. However, only data for 2.5 mL/L FPH at day 6 were significantly higher. Instead, plant height increased under the action of the FPH treatment, with values not being significantly higher compared to those recorded in the control variant. According to the A. HORII & al. [24] study, tomato seed germination percentage was not affected by FPH treatment, but further research is necessary to better understand the action of this compound on seedling metabolism. Treatments designed to improve plant vigor
were also undertaken in China by P.O. OGBAJI & al. [16]. In the context of a negative pressure hydraulic auto-irrigation systems, an experiment on three cultivars of tomato (Jiafen No-18, Jiahong No-5, and Jiahong No-4) emphasized that the application of 50% soil + 50% diatomite (a siliceous sedimentary rock, mainly comprised of SiO2) generated the highest radicle length, coleoptiles length, fresh leaf weight and dry leaf weight for Jiafen No. 18, an appropriate cv. under such conditions. A remarkable increase in the radicle length, shoot length and total fresh weight was also reported by M. ZHANG & al. [17] for tomato seedlings obtained from seeds osmoprimed with PEG in salinity conditions. In addition, 0.05 M NaCl priming and seed priming and irrigation with 0.05 M NaCl starting from sowing, prior to salt stress application, positively affected germination and seedling vigor, as demonstrated by an increase in root and hypocotyl lengths and fresh weight (F.I. SAHIN & al. [39]).

Enhanced tolerance to high osmotic stress during seeds germination has also been achieved by biopriming seeds with *Enterobacter* (a commonly occurring rhizosphere bacteria) strains, hence termed osmotolerant plant growth promoting bacteria (PGPB). Seeds of two tomato cultivars have been used for the experiments, with one being grown under irrigated conditions and one without irrigation. As R.M. BHATT & al. [40] noticed, the application of biopriming for a period of 24 h followed by incubation at 25°C under different mannitol induced osmotic stresses (0, -0.2, -0.4, -0.6, -0.8, -1.0 MPa) proved to be successful for both cv., as far as seed germination and the seedling vigor index are concerned, when compared to untreated or hydro-primed seeds at up to -0.6 MPa.

Besides the aforementioned benefits, seeds primed with KNO3 displayed an increase in the antioxidant system activity (e.g. SOD and CAT) (T.S. LARA & al. [21]). The beneficial effect of KNO3 was explained by the nitrate reductase enzyme activity in the production of nitrite/nitric oxide, which acted to remove dormancy and promote faster germination. On the one hand, F.I. SAHIN & al. [39] noticed a favorable effect of NaCl priming on the accumulation of osmoregulating defense molecules (e.g. proline and anthocyanin), and on the induction of the antioxidative enzyme system of the plant. On the other hand, A. HORII & al. [24] reported that in the case of FPH treatment, phenolic content decreased with the free radical-scavenging activity following a similar trend. The results obtained by M. ZHANG & al. [17] regarding the decline in electrolyte leakage and malondialdehyde activity in PEG-primed seeds during the imbibition period, by comparison to unprimed seeds under aging and salinity stress, suggest that the improved vigor could be associated with a decrease in seed lipid peroxidation. The overall antioxidant system dynamics during osmopriming, post-priming germination, and early seedling establishment emphasized significant conclusions. A reduction of CAT and SOD activity, coupled with an increased ascorbic acid activity and reduced glutathione (AsA-GSH) cycle during osmopriming suggests a repression of protective programs present in dry seeds and a stimulation of germination-related activities in imbibed seeds. A renewal of the antioxidant system is apparent during the late stages of germination, coinciding with potential repair and the development of organelles. In addition, osmopriming improved stress tolerance of germinating seeds, possibly by increasing the germination potential of the primed seeds (e.g. mediating a more robust antioxidant system) (K. CHEN and R. ARORA [41]). In the case of static and pulsed magneto-primed seeds, an activation of antioxidant enzymes system, as a tool to scavenge reactive oxygen species, was also recorded (M.K. GUPTA & al. [25]).

Despite numerous studies, experimental results regarding the priming impact on plant performance during the growing season and yield quality are limited. However, M.K. GUPTA & al. [25] highlighted that the field performance of cherry tomatoes was influenced by both static magnetic field (SMF) and pulsed magneto field (PMF)-priming. To be more specific, a 17% and 27% increase in plant yield was recorded for SMF and PMF-primed seeds, respectively.
respectively. A major change in the mean fruit weight, rather than in fruit numbers, accounted for the yield increase observed. Better fruit quality as a result of priming was also recorded. For example, lycopene content increased by 1.3 and 2.4-fold and total soluble solids by 10 and 21% in SMF and PMF treatments, respectively, compared to control. In addition to biotechnological measures, application of 2-chloro-6-(3-methoxyphenyl) aminopurine [an inhibitor of cytokinin degradation (INCYDE)] at 10 nM, compared with exogenous applications of cytokinin (CKs) as a means to maintain CK homeostasis, could be a better and more efficient approach to counteract abiotic stress (A.O. AREMU & al. [42]). A.O. AREMU & collaborators [42] also stated that from the economical point of view, foliar application of such treatment is advisable, although optimizing the number of treatments and specific application period is necessary. INCYDE enhanced the antioxidant defence system, as well as photosynthesis efficiency. In addition to the beneficial effects of exposing seeds and seedlings of ‘Jinpeng No. 1’ tomato to 0.1 mM melatonin as measured by the seedling health index, a significantly positive impact as far as the mitigation of stress related damage was also recorded. The results obtained by J. LIU & al. [38] showed that such treatment increased stomata conductance and photochemical efficiency, coinciding with the activation of the antioxidant system. Furthermore, NaCl seed priming and irrigation at the seedling stage enhanced the response of 5-leaf stage tomato to 10-day high salt stress as shown by the beneficial effects on chlorophyll contents, chlorophyll to carotenoid ratios, lipid peroxidation and electrolyte leakage (F.I. SAHIN & al. [39]). Many physiological and biochemical processes underpin germination vigor, with seed quality also being characterized by new markers derived from studies using “-omics” approaches, as a tool for breeding programs and/or biotechnological means to obtain better crop yields (L. RAJJOU & al. [43]).

3. **Benefits of tomato seed priming on improving plants tolerance to biotic stresses**

In general, when discussing priming we refer to the treatments applied to seeds (the most common practice that are reported also in the literature) to produce plants tolerant to various stresses (W.G. PILL & al. [44], D. GOEL & al. [1], S. FATEMY & al. [45], A. NAWAZ & al. [35], A.S. MUTAR & F.A. FATTAH [46], K.C. JISHA & al. [19], R.M. BHATT & al. [40]). Nevertheless, the fact that plants are also primed at seedling stage, especially to induce resistance to biotic stress, should not be overlooked (R.M. BHATT & al. [40]).

As we have mentioned previously, seed priming can be also be used to achieve tolerance to some pathogens and pest attacks, using different natural (S. AIMÉ & al. [47], S.V. GUND & al. [12], N. THAKUR & A. TRIPATHI [48]), or synthetic compounds, such as jasmonic acid (JA) (L.E. SMART & al. [49], P. KRÓL & al. [50]), salicylic acid (SA) (A. GHOOHESTANI & al. [51], E. MIRABI & M. HASANABADI [52]), β- aminobutiric acid (BABA) and benzothiadiazol (S. FATEMY & al. [45], A.S. MUTAR and F.A. FATTAH [46]). Such treatments can induce responses in plants similar to those caused by systemic acquired resistance (SAR). These compounds acting as elicitors (S. PAUDEL & al. [53]) or beneficial microorganisms (R. SRIVASTAVA & al. [54]) can induce the physiologically “primed” state in the plant (U. CONRATH [55], P. FILIPPOU & al. [56]). Current progress made in terms of equipment has provided unprecedented investigative possibilities and has opened promising prospects toward 'prime-omics' (see review A. BALMER & al. [57]). The rhizosphere is a particularly important reservoir which allows for the detection, isolation and exploitation of the beneficial effects of the microorganisms’ bank, including in connection with the induction of resistance to biotic stress factors. The selection of an appropriate and effective microbial strain is one of the first and most important steps of applying biological
control methods, with the clear identification of the biological agent also being important (S.V. GUND & al. [12]). In this context, S.V. GUND & al. [12] tested the effect of fifteen *Pseudomonas* and five actinomycetes isolates on controlling the leaf curl virus by applying seed priming, soil and foliar treatments to tomatoes in greenhouse conditions. An inoculation with the AUDP326(4), AUDP360(2), AUDP 139, AUDT217 and AUDT152 isolates resulted in a disease reduction of up to 60-80%. Consequently, the observed reduction of the viral infection and suppression of the viral multiplication led to recommending these isolates as part of an integrated programme for specific virus management in tomato. Similarly, A.N. BABU & al. [58] reported that growth promoting rhizobacteria (PGPRs) can be used to enhance tomato defense against blight disease caused by *Alternaria solani*, resulting in enhanced accumulation of antioxidant peroxidase and polyphenol oxidase enzymes, that may be exploited in the field of genetic engineering.

As shown by R. SRIVASTAVA & al. [54], tomato seeds biopriming by combinations of arbuscular mycorrhizal fungi, fluorescent *Pseudomonas* and *Trichoderma harzianum* significantly reduced the incidence of *Fusarium oxysporum* f.sp. *lycopersici* by 74% in pots and 67% in field experiments. Moreover, yield was higher by 25% when compared the non-inoculated variants. In addition to the positive effect of the three microorganisms regarding on reducing disease incidence and the increasing yield, the addition of compost led to a disease reduction by 87% in pots and 74% in the field, with the yield being 33% higher. Furthermore, tomato seeds biopriming with antagonistic fungal agents (*Trichoderma viridae* and *T. harzianum*) and *Pseudomonas fluorescens* (bacterial antagonist) improved tomato germination (93.1%) and seedling vigor (953.33) both in nursery and field conditions. Furthermore, seedling emergence increased (54.4%) and seedling vigor was augmented (95.23%) (N. THAKUR & A. TRIPATHI [48]). In addition, microbial biocontrol agents reduced the level of important diseases incidence such as damping off (*Pythium aphanidermatum*), bacterial wilt (*Ralstonia solani*) and fusarial wilt (*Fusarium oxysporum*). Moreover, the combined application of seed treatments that include biocontrol agents, biofertilizers, and compost can provide control of various pathogens and also lead to increased plant productivity. *In vitro* application of methyl jasmonate (MeJA) as a seed treatment at 0.01, 0.1 and 1 mM provided tomato seedlings with protection against the soil-borne fungal pathogen *Fusarium oxysporum* f.sp. *lycopersici*. Assessments carried out on 15 day old seedlings revealed a significant increase in the levels of phenolic compounds such as salicylic acid, kaempferol and quercetin, associated with an increase of phenylalanine ammonia-lyase, chalcone synthase and flavonol synthase/flavanone 3-hydroxylase-like genes (P. KRÓL & al. [50]). Previous studies performed by L.E. SMART & al. [49] also demonstrated the effects of jasmonic acid seed treatment on indirect defence against pests, such as *Tetranychus urticae*. Most importantly for tomato growth in greenhouses, predatory mites were strongly attracted to odors of treated plants compared to control ones, due to the emission of methyl salicylate and TMTT (E,E-4,8,12-trimethyl-1,3,7,11- tridecatetraene). Similar positive findings about the induction of plant defense were obtained by S. PAUDEL & al. [53]. The effect of tomato seed priming with methyl jasmonate was assessed in connection with fruit worm (*Helicoverpa zea*) larval growth and the activity of the polyphenol oxidase; a determination carried out on leaves revealed an increase in enzyme activity coupled with a reduction in larval growth. However, there was registered a reduction of seeds germination, seedlings growth, fruis ripening time and fruit quantity, once the dose of MeJA was increased. As a result, the authors emphasized care must be taken when the treatment is designed. To be more specific, it is necessary to maintain a balance between the resistance level required, the projected amount of herbivory and the resulting fitness costs or benefits experienced by plants. The research carried out in vitro by S. FATEMY & al. [45] using soil
drench and/or seed treatment using of DL-β-Amino butyric acid (BABA) (25 mg/l) led to promising results for the control of the Meloidogyne javanica nematode. Both techniques applied reduced the number of galls and egg mass by 82% and higher concentrations (200 and 500 mg/l) led to a further reduction in nematode numbers, although the differences were not significant. Furthermore, final nematode density was reduced by almost 87% and plant growth was improved, with plant mass being increased.

4. Conclusions

Classical seed priming methods, as well as seed biopriming techniques, have beneficial effects on tomatoes, in terms of improving seed germination, emergence, seedling vigor, as well as ensuring the optimal evolution of all physiological processes throughout the seasons, both in greenhouse and field environments, under normal and/or stress conditions. However, research done in recent years has led to the necessity of optimizing seed priming, refining existing techniques and developing better priming protocols in order to achieve maximum benefits. Additional research is required to elucidate their impact on metabolism, as part of multidisciplinary translational studies, made possible due to recent progress in analytical techniques and newly emerging technologies.

Further experiments need to be undertaken, including the promising prospects of 'prime-omics', to improve yield and productivity, while ensuring a positive impact on the environment.

In the context of sustainable horticulture, it is necessary to translate successful experimental tests performed in vitro, in greenhouses and/or in field conditions into an environmentally friendly and economically viable tool to improve tomato plant growth and development.

References

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