Chapter

Improving Tomato Productivity for Changing Climatic and Environmental Stress Conditions

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Abstract

Tomato (*Lycopersicon esculentum* Mill.) growth, cultivation and its productivity are adversely influenced by severe environmental pressures. Several environmental abiotic factors that are limited not only to drought, salinity, temperature and heat but also to mechanical stress affect tomato yield and productivity. Salinity is a persistent problem throughout the world that affects soil properties. Further, tomato productivity due to salinity stress is affected at all stages of plant development. Seed priming, a method to alleviate salinity stress is an effective technique that can improve performance and growth. It is a method that permits controlled hydration of seeds thereby, maintaining metabolic activity, without allowing the protrusion of the radicle. Mechanical conditioning, a term applied to plant stimulation by tactile stimuli through various methods like touching, brushing, or rubbing the plant material, is another environmentally friendly and simple method to regulate plant growth and also stress tolerance. Therefore, the mechanical conditioning practice primes plants for enhanced plant growth and also allows plants to defend against an impending stress factor. These two methods can be developed into successful production practices. In this chapter, we summarize current knowledge of seed priming and mechanical conditioning for plant growth, cross-tolerance and plant productivity improvement.

Keywords: tomato, abiotic stress factors, salinity, seed priming, mechanical conditioning

1. Introduction

Plants are continuously exposed to a multitude of external stress factors and, are also influenced by the ever-changing environment. These stressful environmental conditions affects both plant growth, development, strength and also productivity [1]. Salinity, drought, temperature fluctuations, light intensity are some examples of stress conditions that act alone or in combination and cause wide-spread loss to plant productivity [2]. Apart from these factors, plants are also exposed to various forms of mechanical stress including wind, rain, pathogens, animals and even plants in nature.

Such forms of mechanical stress can result in adaptive responses, that are either thigmotropic (response to touch) or discreet (wounding) responses. These adaptive responses can be applied for plant growth, cross-stress tolerance and nutritional improvement [3].

One third of irrigated land has already deteriorated by salinity stress and, it is anticipated that by 2050, more than half (50%) of the world's cultivated land would be affected by soil salinity [4]. In the last few decades, engineering salinity tolerant crops through classical breeding, transgenics have gained considerable attention [5] and recently, genome editing has also gained significant attention [6]. However, due to the complex nature of the salt tolerance trait, these approaches have resulted in limited success [7].

1.1 Salinization

Soil salinization results in deleterious consequences in plants that are primarily caused by two mechanisms – osmotic stress and ion toxicity stress. The osmotic effect is short-term and occurs due to the uptake of Na^+ and Cl^- ions thereby, reducing the osmotic potential in plants. Ionic stress effects in plants are due to the high concentrations of Na^+ and Cl^- that invariably infiltrate the roots, decreases Na^+/K^+ ratio and affect the nutrient uptake [8]. Apart from these primary effects, plants are also exposed to oxidative stress conditions that includes the production of Reactive Oxygen Species (ROS) [5]. An increase in ROS leads to lipid peroxidation, and higher degradation of macromolecules [9]. This also causes severe damage to the cellular DNA, changes in cellular membrane permeability resulting in ion leakage from the cell [10]. Plants therefore, experience a severe decline in water potential, leading to plant water deficit in salt stress conditions. Salinity also causes inhibition of plant photosynthesis [11].

Sodium chloride toxicity is related to electrical conductivity (EC), an indicator of plant tolerance to salt stress. Most of the horticultural vegetable crops including tomato have a salinity threshold that is lesser or equal to 2.5 dS m^{-1} [12]. Horticultural crops show adverse impacts of salinity characterized by poor seed germination and, also seedling growth retardation [13]. Inhibition of leaf growth has also been observed in plants exposed to excessive root zone salinity and has been attributed to decreased cell turgor, decreased photosynthetic activity, and activation of metabolic signals between stress perception and adaptation [14]. Salinity stress decreased the yield marketability of fruits, roots and tubers [15].

One of the most important horticultural crops cultivated on a global scale is *Lycopersicon esculentum* Mill. (Tomato). Tomato is considered as "moderately sensitive" to salinity [16]. It is a principal source of phytonutrients and bioactive compounds [17]. High NaCl concentration in soil reduces the rate of germination and delays germination of tomato seeds. Salinity decreases water uptake by root hairs from soil which hinders sugar metabolism inhibiting cell division and thus suppressing the leaf, flower and fruit [18]. Salinity is one among the most important abiotic stress factors threatening plant productivity and yield [19].

1.2 Seed priming and mechanical conditioning practices

Two strategies, seed priming and mechanical conditioning, that are considered age-old are now gaining considerable research interest in the last decade for their role in conferring tolerance to abiotic stress conditions such as salinity, drought, chilling stress. Seed priming is a simple, cost effective and practically proven technique to accelerate rapid and also, synchronized seed germination [20]. Seed priming increased yields in many horticultural crops under adverse environmental conditions [13]. Mechanical conditioning on the other hand, is a process of physical stimulation or stress deliberately applied in order to manage plant growth and quality [21]. Studies show that the mechanical conditioning method reduce plant growth by rubbing stems, brushing shoots, shaking, vibration techniques, mechanical impedance, or even by perturbing plants with either water, wind. This method also results in cross-tolerance to stress conditions [22].

2. Seed priming

Hydration of seeds triggers the germination of seeds through three phases: imbibition, activation and radicle protrusion [23]. Seed priming is a pre-sowing hydration technique applied in a controlled condition, that results in the activation of key metabolic processes during the seed imbibition phase before the radicle emergence [24]. Seed priming transforms the seeds from a metabolically inactive state into a quasi-metabolically active state. However, this quasi-metabolically state does not support the complete emergence of the radicle [25]. The pre-sowing technique is consequently followed by seed drying and maintenance of near to original weight and moisture content of the seed (10–15%) [26]. The seed priming technique has been shown to improve salinity stress tolerance in a variety of plants (**Table 1**).

2.1 Seed priming techniques

The classification of the seed priming technique depends on the chemical nature of the priming agent. The hydropriming technique is a simple, inexpensive, and eco-friendly seed priming technique that involves imbibing seeds in distilled water [41]. In the chemical priming technique, the seeds are hydrated in salt solutions such as KH_2PO_4, KNO_3, $CaCl_2$, $MgSO_4$, NaCl, KCl while, osmopriming involves the use of osmolytes such polyamines, PEG, mannitol etc. [20]. Biopriming integrates seed uptake with biologically active bacterial inoculants such as Plant Growth Promoting Rhizobacteria [PGPRs] to enhance germination and seedling vigor [36]. Hormonal priming involves the hydration of seeds in an aerated medium of various plant growth promoting hormones such as abscisic acid, kinetin, SA [salicylic acid], GA3 and ascorbate [40]. In the solid matrix priming [SMP], the matrix potential of the priming solution is controlled during seed uptake by the addition of solid matrix substances, for example compost, clay and sand that, create matrix forces to hold water and slow solute uptake by the seeds [42]. Nutripriming improves the available nutrients and water for seed preparation of the emerging plant by adding magnesium, zinc and boron, which effectively promotes germination, growth and development, early flowering, early maturity, grain filling rate and yield of multiple crops [43]. Among all the priming techniques that is reported, hydro, osmo, chemical and hormone priming are the most commonly used, though nano-priming has stimulated intense interest in the recent years [44]. In the seed priming technique, seeds are placed in a specific, defined concentration of priming agent for a specific period [45]. The success of the priming technique relies on the water potential, priming

Sl No	Priming Technique and Model Plant	Priming agent and concentration/ Duration of priming	Major beneficial effects of Priming	References
1.	Chemical Priming Model: Tomato (*Lycopersicon esculentum*)	Ascorbic acid (0 and 100 mM AsA) for 1 h	• Increases water potential and water use efficiency • Modulates Antioxidant system.	[27]
2.	Nano priming Model: Tomato (*L. esculentum*)	Carbon nanotubes and graphene (50, 250 and 500 mg/L) for 24 h	• Improves the content of bioactive components in fruit • Enhances antioxidant mechanism.	[28]
3.	Irradiation Model: Tomato (*L. esculentum*)	UVC (0.85 and $3.42 kJm^{-2}$)	• Activation of photosynthetic processes • Accumulation of soluble proteins, phenolic compounds, flavonoids and carotenoid content	[29]
4.	Chemical priming Model: Tomato (*L. esculentum*)	KNO_3 (0.25, 0.50, 0.75, 1.0 and 1.25) for 24 h	• Improved final emergence and mean emergence time • Enhanced production of total soluble sugars and phenols	[17]
5.	Solid matrix Model: Tomato (*L. esculentum*)	4% Sand particles (diameter 0.5 mm to 2 mm) for 72 h	• Increased final germination percentage and vigor index • Enhanced the antioxidant defense system	[30]
6.	Solid matrix Model: Brocolli *(Brassica oleracea L. var. italica)* and Cauliflower *B. oleracea L. var. botrytis)*	Vermiculite and H_2O (1:1.5:2) for 2 days	• Enhanced antioxidant activities (POD, CAT) and osmolytes (Proline, soluble sugar and soluble protein).	[31]
7.	Osmopriming Model: Brocolli *(B. oleracea* L. var. *Italica)*	KCl	• Regulated glucosinolate metabolism and phenolic production	[32]
8.	Biopriming Model: Peas *Pisum sativum.* L	*Typha angustifolia* L. (leaf extract – 40 g/L) for 24 h	• Decreased MDA level and well maintanence of membrane integrity • Increased osmoprotectant production (Proline, total soluble sugars, K+ and P), Carotenoid and Chlorophyll content.	[33]
9.	Hydropriming Model: Napa cabbage *(Brassica rapa L. subsp. pekinensis)*	Distilled water for 10 h	Increased antioxidant activities such as POD CAT and osmoticum (Proline).	[34]
10.	Chemical priming Model: Tomato (*L. esculentum*)	Polyamines Putresine (25 mM) Spermine(2.5 mM) Spermidine(2.5 mM) 20 ml for 24 h	• Increased membrane integrity, photosynthetic pigments and proline • Enhanced enzymatic and nonenzymatic antioxidant responses	[35]

Sl No	Priming Technique and Model Plant	Priming agent and concentration/ Duration of priming	Major beneficial effects of Priming	References
11.	Bio-Priming Model: Okra *(Abelmoschus esculentus)*	*Enterobacter hormaechei* sp. (PGPR) for 1 h	• Improved germination parameters and seed vigor index • Increased K^+ and P^+ uptake • Increased chlorophyll index	[36]
12.	Hydro, chemo and hormonal priming Model: Mustard (*Brassica juncea* L.)	Water, CaCl2 (100 μM), ABA (100 μM) for 18 h	• Increased rate of germination • Enhanced SOD and GPX activity • Decreased oxidative damage	[37]
13.	Chemical and hydro Model: Sunflower (*Helianthus annuus L.*)	KNO3 (500 ppm) for 2 h and water for 18 h	• Enhanced germination characteristics, root and shoot length • Decreased mean germination time and abnormal germination percentage	[38]
14.	Chemical and Hormonal priming Model: Periwinkle *(Catharanthus roseus* L.)	KNO3 (1%) Salicylic acid (0.5 mM) for 15 h	• KNO_3 alleviated the growth of seedlings, mitotic activity and decreased chromosomal abnormalities • SA increased plumule dry weight and ratio of plumule weight: root	[39]
15.	Chemical, osmo and hormonal priming Model: Maize *(Zea mays)*	NaCl (50, 150 and 250 mM) PEG (10, 15 and 20%) GA (5, 10 and 15 mg/L) - for 24 h	• Recommended priming concentrations were found to be: • NaCl - 50 mM • PEG – 15% • GA – 10 mg/L • Increased shoot biomass (NaCl priming) • Increase grain weight (Water, NaCl and PEG)	[40]

Table 1.
Seed priming technique leading to improvement in salt tolerance in different plant species.

duration, priming agents, and also seed condition that influence subsequent seed germination and seedling emergence. Therefore, optimizing the priming technique and priming duration has been an active area of research investigation for improving seedling establishment and plant productivity under a variety of environmental conditions [45].

2.2 Mechanism of seed priming induced salinity stress cross-tolerance

2.2.1 Seed water uptake and seed physiology

Seed priming ensures maintenance of optimal moisture levels before sowing through controlled hydration process. It allows physiochemical processes (metabolic activities) to be carried out in treated seeds prior to germination, but limits the emergence of radicle prior to sowing. The seed priming process is accomplished in three phases [24]. The first phase is phase of imbibition where uptake of water is controlled in primed seeds [23]. Controlled hydration takes place in the first phase, limiting the seed moisture sufficient to initiate early phase of germination [23]. This is subsequently followed by the activation phase, in which a series of DNA repairing and metabolic activities commences at the cellular level. In this phase, synthesis of proteins, activation of enzyme, antioxidant system and DNA repair takes place [24]. Priming is thought to increase the activity of several enzymes involved in metabolism of carbohydrates (alpha and beta amylases), proteins (proteases) and lipid mobilization that are involved in the stored reserve mobilization. Seed priming also permits early DNA replication and repair, increased RNA and also decreases the leakage of metabolites [46]. Priming also enhances antioxidant synthesis for re-orienting the seeds to defend against oxidative damage [47]. In the third stage, the uptake of water is rapid and protrusion of the radicle commences [24]. This is then followed by the dehydration process or drying. The seed drying procedure is critical as it can affect seed vigor and longevity and needs ideal conditions for seed storage [23]. The ideal conditions for maintenance of seed integrity are usually done by bringing the seeds to its original moisture content (**Figure 1**). Varier et al. [48] reported that, since the seed priming technique leads the seeds to advanced physiological status in comparison to unprimed seeds, the primed seeds are more prone to seed deterioration, and therefore a major bottle-neck in the commercialization of primed seeds. However, recent studies show that mimosine, a chemical inhibitor of cell cycle, identified from a large screen of biologically active compounds, resulted in the development of green cotyledons and prevented seed deterioration after the seed priming technique. The identification of a cell cycle inhibitor suggests that the cell-cycle is an important checkpoint in maintenance of seed integrity during priming. However, to be applicable commercially, the optimization of concentration of chemicals for seed priming needs to be carried out [49].

Seed priming mainly improves salinity stress tolerance through cross-tolerance, through two main mechanisms. In the first well- understood mechanism, seed

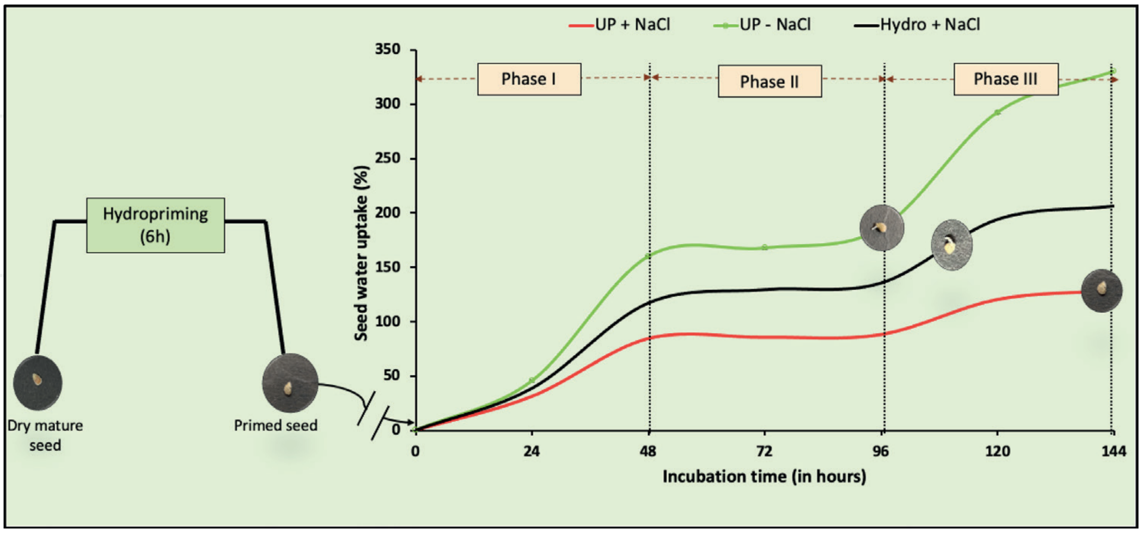

Figure 1.

Rate of seed water uptake (%) in the three phases of seed germination after exposing the hydroprimed and unprimed seeds of Lycopersicon esculentum mill. To 100 mM NaCl stress conditions. Tomato seeds (Lycopersicon esculentum mill.) belonging to variety Arka Rakshak was procured from the Indian Institute of Horticultural Sciences (IIHR, Hesaraghatta, Bengaluru, Karnataka). Dry seed lots were weighed initially. Healthy seeds were surface sterilized using routine methods. Sterilized seeds were imbibed in distilled water for 6 h and subsequently dried (room temperature). Seeds were then allowed to germinate in petri plates layered with filter paper soaked in distilled water or 100 mM NaCl alone. Each treatment (unprimed or hydroprimed) consisted of 60 seeds.

priming activates germination through enhanced energy metabolism, early reserve mobilization, embryo expansion and endosperm weakening. Secondly, seed also priming leads to abiotic stress that represses the radicle protrusion. This re-programming results in "priming memory" in seeds. The "priming memory" is mainly epigenetic in nature. These two mechanisms together mediate the improved stress tolerance of the primed seeds [25].

2.2.2 Seed priming induced salt stress response in plants

Salt stress affects plants leading to both osmotic and ionic stress. High concentration of Na^+ and Cl^- ions in the environment causes plant water deficit. The osmo protectants such as proline, amino acids, soluble sugars and proteins can regulate the cellular osmoticum in response to the reduced external water potential [23]. Seed priming is shown to improve osmotic adjustment when plants are exposed to salt stress condition. Yan 2016 conducted hydro priming of *Brassica rapa* subsp. *pekinensis* cultivar Xiaoza 56′ seeds which is considered salt sensitive (Napa cabbage). The seeds were hydroprimed for 10 h and germinated under different NaCl concentration (0, 50, 100, 150, 200 or 250 mM). Hydropriming increased the germination percentage and early seedling growth which was however, delayed in unprimed seeds grown under similar NaCl conditions. There was a significant increase in proline in 100, 150 and 200 mM NaCl concentrations, resulting in reduction in osmotic stress. However, in 50 mM NaCl there was a decrease in proline content. This study also concluded that an increase in salinity also gradually increased the proline contents [34]. Similar results were also obtained by biopriming Peas (*Pisum sativum*). Biopriming of *Pisum sativum* L, var. Lincoln with extract of *Typha angustifolia* for 48 h and exposed to 120 mM NaCl concentration resulted in enhancement in osmoprotectants such as proline, total soluble sugars along with K^+ ion concentration [33]. Therefore, seed priming regulates the osmotic potential and alleviates salt stress conditions by improving water absorption by the cell, aiding seed germination [50].

Accumulation of Na^+ ions under saline condition results in ionic stress, causing the structural damage to cell membrane and inhibiting embryo activity [51]. Increase of Na^+ in the cytoplasm also hinders the entry of other ions particularly K^+ which affects the physiology in plants [51]. Inorganic ions such as Ca^+ mitigates the negative effect of Na^+ and maintains ion homeostasis under NaCl stress conditions. This was corroborated from research performed in *Sorghum bicolor* (L.) Moench [51]. In this study, $CaCl_2$ was used as priming agent to ameliorate salt stress toxicity in sorghum. It was shown that $CaCl_2$ priming resulted in upregulation of antiporter genes such as NHX_2, NHX_4, SOS1 and the K^+ transporters AKT_1, AKT_2, HKT_1, HAK_1 and KUP which may be responsible for decreasing the Na^+ levels and increasing of K^+ levels in tissues [51]. Calcium is also a vital element for maintenance of cell-wall structure, cell elongation and cell-division [23]. Ben Youssef [52] reported that NaCl negatively affects the Membrane Stability Index (MSI) (37%) and disrupts the membrane integrity. MSI is a physiological index that estimates the percentage of membrane injury based on the electrolyte leakage [53]. Further, the authors have shown that priming with $CaCl_2$ **decreased MSI in** *Hordeum vulgare* **(L. Manel) and** *Hordeum maritimum* **seedling**s [52]. Calcium chloride signaling also plays a vital role in activating SOS pathway by directing Na^+ efflux [51] resulting in minimal leakage of ions from the plant cell and also, decreases the extent of damage to the cell membrane.

Salinity also induces membrane damage by the accumulation of inhibitory levels of reactive oxygen species (ROS) [54]. ROS scavenging can be achieved by two complex systems: the enzymatic comprised of superoxide dismutase (SOD), peroxidase (POD), catalase (CAT) and the nonenzymatic consisting of ascorbic acid, alkaloids, carotenoids and tocopherols [54]. In a case study, solid matrix seed priming (using vermiculate and water) of *Brassica oleracea* var. *italica* (Broccolli) increased the SOD, POD, CAT activities along with proline, sugars and proteins [31]. These studies demonstrate that ROS homeostasis is critical for plant responses to salt stress conditions. There is a negative relationship between antioxidant activity and MDA levels. Seed priming reduced MDA by enhancing antioxidant activity [25, 30].

2.3 Amelioration of salinity by seed priming

Seed priming is as cost-effective practice in establishing uniformity of germination [55]. In an experiment conducted in our laboratory with tomato, the dry seeds were primed in distilled water for 6 h (hydropriming). The dried hydroprimed seeds were allowed to germinate in control, unstressed conditions (0 mM NaCl). Seeds undergo re-imbibition and enters into phase I of the seed water uptake process during which rapid initial water uptake takes place, triggering all cellular processes. Imbibition of water takes place rapidly in control tomato seeds as they are not exposed to NaCl stress conditions. However, there was a decline in the percentage of water absorption in the seeds exposed to NaCl stress (100 mM) (84.5%) in comparison to control seeds (159.9%) at 48th h. In tomato, the first phase was shown to last from 0th h- 48th h, after imbibition. However, hydroprimed seeds that were exposed to NaCl conditions (100 mM) showed seed water content of 116.9% (at the 48th h) water in comparison to stressed seeds during phase I (0–48 hr). This confirms that hydropriming of tomato seeds improves the water uptake mechanism in tomato (**Figure 1**). The second phase, the lag phase, of the seed germination process is characterized by a plateau where there is limited water uptake, but increased metabolic and cellular activity. This phase is marked by metabolic activities such as protein synthesis, activation of antioxidant system and enzymes, DNA repair mechanism and ATP production [24]. All macromolecules such as carbohydrates, proteins and lipids are mobilized by enzyme to nourish the newly developing embryo. For instance, α- amylase activity and total soluble sugars increased in wheat, when primed with benzyl amino purine and sorghum water extract [56]. Further, with the onset of favorable environmental conditions in nature, these nutrients are redirected to the next phase (Phase-III) of seed germination i.e., radicle emergence. Hydroprimed seeds exposed to NaCl stress (100 mM) exhibits 135.3% of seed water uptake when compared to unprimed (88.1%) seeds grown under similar conditions (100 mM NaCl). The surge in water uptake resulted in hydrolysis of macromolecules aiding in early radicle emergence in comparison to unprimed stressed seeds (**Figure 1**). It is now understood that with seed priming, the lag time of imbibition is reduced [57]. The swelling of the embryo in primed seeds speeds up the germination by facilitating water absorption [55]. Seed priming also reduced physical resistance of the endosperm, stimulates pre-germinative re-orientation of metabolic processed and leaches out the chemical inhibitors of germination [58]. In summary, the seedlings emerge faster, show vigor and performs better in NaCl stress conditions (**Figure 1**). In another experiment, seeds of *Lycopersicon esculentum* (tomato) of two varieties (var.205 and var.206) were primed with sand (solid matrix priming) (4%) at 25°C for 72 h. The treatment improved germination by increasing the antioxidant enzyme activities in laboratory conditions. *Lycopersicon esculentum* var.206 showed higher activities of CAT, POD, SOD, APX (4.5, 15.3, 6.6 and 4.1% respectively) with high salt stress (150 mM) in comparison with var.205. The increase in the activities of antioxidant enzymes is understood to improve the innate defense mechanism in the primed seeds leading to enhancement in the seed vigor in tomato [30].

Garcia et al. reported that nanoparticles can be used as effective priming agents in tomato. The authors showed that nanopriming of tomato seeds with Graphene based-Graphene 500 (GP500) and carbon based-Carbon nano tube 500 (CNT 500) for 24 h resulted in enhancement in chlorophyll content by 8.75 and 13.3% when compared with untreated seeds in 50 mM NaCl stress conditions. The authors reported that the ion leakage decreased by 10.71% with the addition of CNT 500 when compared to non-sonicated control. All these studies suggest that priming with nanoparticles can cause subtle to marked changes in biochemical, physiological, and biological properties. The carbon nanomaterials (priming agent) penetrate the seed coat by forming new pores allowing the entry of water, oxygen, nutrients into the cytosol. This facilitates the seed germination process [28].

Further, green house experiment conducted in tomato with two different concentrations of ascorbic acid (hormonal priming; AsA-0 and 100 mM) for an hour enhanced leaf water potential (LWP) and water use efficiency (WUE) in NaCl stress conditions. LWP increased by 25% when seeds were primed with 100 mM AsA exposed to NaCl (100 Mm) and showed lower LWP in the absence of NaCl. Water Use Efficiency (WUE) increased by 37.7 and 21.6% with 0 mM and 100 mM NaCl. There was a significant interaction effect of NaCl and AsA within and between NaCl concentrations. LWP is directly correlated to WUE as water availability affects stomatal opening. The dry mass of leaves and fruits increased with AsA priming by 19.5 and 17.9% respectively in plants subjected to NaCl [27].

Abdel-Aziz et al. 2019 demonstrated the positive effect of nanopriming on the growth and productivity of *Phaseolus vulgaris* cv. Contender (French bean). The authors investigated the possible effects of two different methods (foliar spray and seed priming) using nanoparticles on French bean. The two nanomaterials nanochitosan (Cs) and carbon nanotubes (CNTs) were applied either by foliar spray or by seed priming technique. There was significant increase in the biochemical composition of yielded seeds of foliar spray than in seed priming in comparison to control seeds. The days to harvest decreased to 80 days through foliar spray without compromising the yield, whereas seed priming resulted in 110 days to harvest. Therefore, it was concluded that Cs nanoparticles improved growth and yield more than CNTs through foliar application. The differences in stress responsive effects in *Phaseolus vulgaris* between the two modes of application (foliar vs. seed priming) was explained on the basis that, nanoparticles are best absorbed by the stomata when they are foliar sprayed, providing more nutrients [59].

Alamer et al., evaluated the efficiency of seed priming by irradiating tomato seeds with a dose of 0.85kJm^{-2} and 3.42kJm^{-2} under laboratory conditions. UV-C priming enhanced root and leaf biomass by 51 and 36% with 0.85 kJm^{-2} and 10 and 25% with 3.42kJm^{-2} respectively. UV-C priming with 0.85 kJ m^{-2} and 3.42kJm^{-2} also decreased Na$^+$ content by 33 and 20% in roots and 30 and 40% in leaves respectively. K$^+$ accumulation on the other hand, decreased in roots by 38% (with 0.85kJm^{-2}) and 22% (with 3.42kJm^{-2}) compared to untreated controls. Interestingly, treatment with 0.85kJm^{-2} alleviated NaCl-induced stress by maintaining root biomass, root potassium supply and leaf protein content in comparison to controls. On the contrary, treatment with 3.42kJm^{-2} stimulated the NaCl resistance of the tomatoes by maintaining the protein, total polyphenol and tannin content of the roots in comparison to controls. This, points to the fact that different concentration of priming agents can influence the resistance of plants to salinity stress to varying degrees [29].

3. Mechanical conditioning methods for stem length reduction

The principal benefit of mechanical conditioning strategy for farm application is to produce plant transplants that are strong, more elastic, sturdier and shorter. The plant stem supports the weight of branches, fruits and therefore, requires adequate strength to withstand wind, lodging, rain and other environmental stress damages. Chemicals that are widely used as plant growth inhibitors have the drawback of toxicity and also, continuous inhibition [60]. Mechanical conditioning in plants is therefore, a much effective method to control and regulate the plant height. Among all the methods used for mechanical conditioning, brushing treatment has received the most significant research interest in vegetables crops due to the ease of its application and the possibility of automation for field applications. Brushing provides for the tactile stimulation of the plant growing points. In most of the research reported, brushing provides a mechanism to reduce plant height, but is has also been shown to increase stem and petiole strength. The device used for brushing treatments must also be robust and strong enough to manipulate the shoots in a plant. In an interesting study, experiments were performed to compare chemical treatment using paclobutrazol (a chemical bases plant growth retardant) with physical stimulation (40 brush strokes per day) or cold air (air flow of 2 m sec^{-1}, at 18°C each day). Both paclobutrazol and mechanical stimulation provided the best results in terms of stem reduction of 25% in comparison to control plants. Brushing treatment also resulted in reduced plant biomass. However, paclobutrazol treated seedlings grew better than the brushed or cool air flow treated seedlings after they were transplanted to the field [61].

Mechanical stimulus (MS) has also been done by gentle rubbing. For instance, mechanical stimulus was applied to 3-week tomato plants at the 4th internode by mechanical rubbing between the thumb and fore-finger and rubbed back and forth, once for 10s. Internode length was measured thereafter after 14 days. Results showed that rubbing of internodes resulted in significant reduction in the elongation of the stressed internode (4th) and also, the neighboring internode (5th internode). This was also corroborated with increased lignification (7.68% in the control to 10.08% in the mechanically stressed sample). It was reasoned that the lignin accumulation observed with mechanical stimulation may function as a plant growth inhibitor. The authors also showed that the response of tomato plant to mechanical stress by the inhibition of internode elongation was related to the induction of CAD activity and peroxidase isoforms [62]. Further, a reduction in indole-3-acetic acid (IAA) content was also detected in the rubbed internode and the upper internode. These results also suggested that a decrease in rubbed internode length is a consequence of IAA oxidation leading to increase in enzyme activities (PAL, CAD and POD) [62]. Further, it was also shown that MS treatment through rubbing increased stem resistance to tensile forces. The mean tensile strength resulted in a significant increase of 113% in rubbed plants, when compared to plants that were not treated [63]. It was also shown that calcium induced changes brought about by rubbing was thought to elicit downstream changes in gene expression and that, the Ca^{++} effect is modulated by calmodulin [64].

Apart from these methods, mechanical impedance is a well applied method in plant mechanical conditioning to control excessive stem elongation. In a study conducted, tomato plants grown in green house was used to compare between mechanical impedance and brushing treatments. Mechanical impedance procedure was applied by means of a 5-mm thick acrylic sheet (Plexiglass) with a mean pressure of 66 N/m^2. On the other hand, brushing experiments were done using a Styrofoam by stroking 20 times. Results from these studies showed that physical impedance method was equally suited for stem reduction in tomato plants just, as the brushing method. In this study, the authors noted that both the treatments (impedance as well as brushing) reduced stem length by 3–4 cm. This reduction in stem length corresponded to a 40% reduction rate in elongation during 7–10 days of plant treatment. Impedance resulted in shorter and thicker stems, and also caused more horizontally oriented leaves [65]. It was also shown from these green-house experiments that, physical application by mechanical impedance below 66 N/m^2 was not effective in decreasing plant height. Physical impedance was also shown to result in increased stem diameter and adventitious root formation at the base of the stem. But, this method of application is more laborious than brushing experiments and requires more equipment to regulate stem height control [65]. There are also other studies that compared the two treatments (Brushing and Mechanical impedance). In another study, mechanical conditioning treatments were begun when the seedlings were 6 cm tall and 17 d old. The brushing treatment was applied with an unpainted, 25-mm-diameter hardwood dowel pulled gently 20 times, back and forth, across the canopy each day for 15 d. The impedance treatment was applied by suspending an acrylic sheet (4 mm thick) just below canopy height overnight. Mechanically conditioned transplants of processing tomatoes resumed growth after transplant shock as quickly as did untreated plants, and subsequent canopy development was also equal. In 4 years of field trials, yield was not reduced by mechanical conditioning. In this study, neither earliness nor defects in the fruits of the first cluster were affected by mechanical conditioning. Early and total yields were equal in both years that fresh-market crops were tested. Thus, there were no adverse effects on the field performance of either processed or fresh-market tomatoes as a result of reducing stem elongation by mechanical conditioning before transplanting [65].

In other studies, wind treatments were performed using a 20-inch fan blade, that were suspended 28 inches above tomato transplant seedlings. Wind speed was provided at the average speed of 30 km/hr. From this study, it was shown that tomato seedlings showed a 19% reduction in stem elongation with wind treatment in comparison to control seedlings. Interestingly, all day or all night or all day/night reduced the internode length compared to control tomato seedlings. In contrast, other times of the day/night cycle, for instance (early, mid or late day/night) wind treatments did not cause any alteration in internode length when compared to control tomato seedlings. The authors concluded that the impact of wind treatments vary greatly diurnally [66]. Further, Sparke et al. demonstrated the usefulness of an automated, directed air-stream application to control plant height in tomato and other ornamental plants. The air stream applied to the plants was generated by a stationary compressor with downstream connected pressure regulator. The automated air-stream application on a metal frame suspended on a longitudinal guide rail and was equipped with an electric motor to facilitate forward and backward movements across the entire greenhouse. The authors observed that directed air-jets applied either as laminar air stream or turbulent free air streams resulted in 26–36% reduction in tomato plant height [67].

A similar result was observed in the height of tomato seedlings by wind-blowing [68]. The authors also observed that the wind treatment of 0.6 m/s every 30 minute for 5-minute reduced tomato seedlings hardness and elastic modulus by about 25 and 24%, respectively. Similar improvement in plant growth characteristics have been shown using Bending/Flexure of plant and also, vibrations [1].

3.1 Mechanical conditioning and other plant responses

3.1.1 Seed germination

Mechanical stimulation has also been used as a simple, cost-effective technique to break seed dormancy and improve seed germination. The most popular techniques to improve seed germination are sound and ultrasonic waves and vibration. Vibration is described by two parameters of application, the frequency and amplitude. In *Arabidopsis thaliana*, the effect of sinusoidal vibration (40–120 Hz) on seed germination and amplitude equal to or smaller than 0.42 mm was studied. The authors observed that amplitude of 0.42 mm and frequencies higher than 70 Hz or amplitudes larger than 0.33 mm and frequencies of 100 Hz increased *Arabidopsis* seed germination rate. By employing ethylene in sensitive mutants, it was concluded by the authors that, mechanical stimulation by vibration increased the rate of seed germination most likely through the action of ethylene [69]. In another study, Yang et al. showed an increase in seed germination rate and potential by 15 and 14% respectively in tomato using 40 KHz ultrasound frequency [70].

3.1.2 Mechanical conditioning and cross tolerance to salinity

Plants exposed to various forms of mechanical stress conditions caused by wind, rain, herbivores, and pathogens induce responses in the plant that were shown to have an adaptive value. In earlier studies, mechanical stress associated with damage or wounding was shown to result in increased resistance to insects, pathogens. For instance, Capiati et al. showed that mechanical wounding performed by cutting with a dented forceps improves salt stress tolerance in tomato plants. Wounded tomato plants were shown to be more tolerant to salt stress conditions than un-wounded plants. Pre-wounding also resulted in increased relative water content in comparison to un-wounded leaves. The results further point to the role of Calmodulin like activity (LeCDPK1), a Ca^{2++}-dependent protein kinase from tomato in salinity cross-tolerance. It was concluded that pre-wounding of tomato increased salt stress tolerance through the mechanism involving the signaling peptide systemin and the subsequent synthesis of Jasmonic Acid, leading to increased expression of LeCDPK1 [71]. Further, it was also shown that artificial wounding experiments induce defense response in tomato by involving the crucial involvement of a signaling molecule, H_2O_2. A sudden surge in H_2O_2 levels was shown within the few hours of wounding stress performed on either the leaf mid-rib or lamina of tomato. Primed, wounded plants showed increased total phenol, total flavonoid content and antioxidative activity. Alleviation of salt stress was higher in mid rib cuts than in lamina was confirmed through the stabilization of relative water content and also, an increase in antioxidant scavenging activity. Therefore, the defense response was stronger in plants with plants with leaf midrib injury than in those with laminar injury [63]. However, these experiments were done by methods that lead to discernible injury in the plant. The question remains if the salinity stress cross tolerance can be initiated

SI No	Primary Stress	Plant	Cross Adaptation	Conditions	Reference
1.	Wounding	Tomato	Salt tolerance	Controlled	[71]
2.	Brushing	Tomato	Cold tolerance	Controlled	[73]
3.	Weight Loading/Pressing	Wheat	Cold tolerance	Semi-field	[74]
4.	Cylinder Roller	Wheat	Cold tolerance	Controlled	[75]
5.	Heat Shock	Maize	Heat, Chilling, Drought and Salt	Controlled	[76]
6.	Sound vibration	*Arabidopsis*	Drought	Controlled	[77]
7.	Sound vibration	*Mentha pulegium*	Salt stress	Controlled	[78]
8.	Rubbing/stroking	Bean	Drought	Controlled	[79]
9.	Salt	Tomato	Wound stress	Controlled	[80]
10.	Increasing rotational speed	Tobacco	Heat, chilling, salt	Controlled	[22]

Table 2.
Type of mechanical stress induced cross adaptation in plants.

by conditioning methods without causing explicit damage to the plant tissues. Results from other studies show that gentle sweeping of leaf surfaces leads also to strong resistance to *Botrytis cinerea*. The soft mechanical stress induced burst of calcium flux and ROS induce the expression of genes required for defense against the virulent fungus *B. cinerea* [72] (**Table 2**).

3.1.3 Improvement in metabolites and nutritional quality

In a study conducted at an experimental station using floating hydroponics, vegetable Horti crops (lettuce and chicory) were given mechanical conditioning (MC) treatments. This was performed by brushing the vegetable crops with a burlap cloth either for 10 passes (MC10) or 20 (MC20) per day [81]. In this study, all the specialized metabolites (Ascorbate, Total Phenolic and Total flavonoid content) showed a marked increase in amount in MC20 treatments in comparison to control. In general, the highest mechanical conditioning treatments (20 passes) resulted in antioxidant enhancement in both lettuce and chicory. Mechanical conditioning treatments in this study therefore, resulted in major alterations in metabolic pathways (phenylpropanoid) leading to increase in specific activation of phenolic compounds (TPC and TFC), pigments (chlorophyll and carotenoids) and also antioxidants (Ascorbate), those, that are significant for defense response. It is well established that exposure to brushing or wounding in nature by herbivores, insects etc. cause major changes in the polyphenolic content [22]. The increase in the content is crucial for plants to recover from any damage to DNA and cell membrane from the rapid accumulation of ROS in plant cells. Antioxidants function as radical scavengers, chelators, quenchers and oxygen scavengers [82]. Most interestingly, the total chlorophyll content and carotenoids also increased with exposure to MIS in lettuce. This is a significant observation and therefore, it can be concluded that imposition of MS as a good practice in horticultural crops for production of plants with high nutritional rich phytochemical content [81]. There is a large body of scientific evidence that consumption of nutritionally enhanced food crops/vegetables could have a beneficial effect on human health [83].

4. Mechanical conditioning and mechanism of action

Plants are sessile and, in order to respond to mechanical stimuli in the environment, plants begin an intricate cascade of signaling events. The signaling cascade is stimulated with a receptor, that perceives the mechanical stimulus, resulting in a biochemical reaction, involving Ca^{++} and culminates in the thigmotropic response. Plants do not possess specialized cells for thigmotropic perception. Each of the individual cells is understood to have the ability to sense MS that gives rise to a cellular response. In *Arabidopsis thaliana*, trichomes and passage cells can sense mechanical stimuli [84]. In an elegant experiment carried out in *Arabidopsis thaliana*, it was demonstrated that plants sense such mechanical stimuli through changes in cytosolic $Ca^{++.}$ The authors showed that plants can sense pressure changes applied onto the leaves using micro-cantilever device that exert a compressive force [84]. The plant thigmotropic response is also shown to be dose dependent, saturable and also systemic, in that the response is shown to translocated from the mechanostimulated local tissue to unperturbed distal tissues [85]. This is now understood to be mediated by proteinaceous as well as diffusible signaling molecules [86].

4.1 Calcium and TCH genes

Calcium acts a universal signaling molecule essential for the response to adaptation to a changing environmental condition. The cell perceiving a stress stimulus leads to a rapid rise in cytosolic Ca^{2++} through the opening of calcium channels present in the plasma membrane and intracellular organellar membranes. This quick and transient rise in cytosolic calcium is a key factor in expression of stress-responsive genes and physiological responses of plant cells to stress conditions. In part, the morphophysiological response to mechanical stimuli is due to alterations in gene expression and synthesis of new proteins. This process of mechanoreception was elucidated by the identification of TCH genes (Touch) genes, induced within 10–30 minutes of exposure to perturbation by touch or wind [87]. Several genes have been identified TCH1, TCH2 and TCH3 that encode calmodulins or calmodulins like proteins. The TCH4 gene encodes a xyloglucan endotransglucosylase (XTH) involved in cell wall modification [88]. The discovery of calmodulins or calmodulins like proteins as universal calcium-dependent activators of enzymes and their activation with Mechanical stimulation suggests the involvement of Ca^{2++} in mechanosensing. Interestingly, transcriptomic studies have shown that mechanostimulation results in up-regulation of large number of *Arabidopsis* genes (including genes for calcium binding, disease resistance and cell-wall modifying proteins) [89]. This also suggest a central role of gene regulatory network in the thigmomorphogenetic response.

4.2 Mechanosensing

Mechanosensing in plants is understood to involve a large class of mechanoreceptors, among which are the mechanosensitive ion-channels, a protein complex (MS channels). These ion channels span the membrane facilitating the regulated movement of ions upon mechanical stimulation. Among these, the mechanosensitive channel of small conductance like-MSL are understood to be involved in mechanosensitive properties in *Arabidopsis* [90, 91]. *Arabidopsis* has a minimum of 10 MSL proteins, differentially localized, some in the plasma membrane, plastid or mitochondria. Another major class of proteins involved in mechanosensing and mechanoperception are the Plasma membrane localized receptor like kinases (RLKs). Plant Receptor like kinases (RLKs) recognize the damage associated molecular patterns (DAMPs) that are produced by plants during pathogen attacks and induce a series of intracellular events such as MAPK cascade, ROS burst and Ca^{2++} spiking [92]. Ca^{2++} spiking immediately after mechanical stimulation is one of the upstream signaling events in the plant that triggers rapid protein phosphorylation through calcium-dependent protein kinases (CDPKs) and calcium binding proteins (CBPs). CDPKs and CBPs play important roles in converting Ca^{2++} signals into transcriptional responses [93].

5. Automation of MS treatment for potential benefits

One of the bottlenecks for field applications is the tangible nature of Mechanical Stimulation stress treatments. MIS *per se* is laborious and the manual nature of this technique due to deliberate human interventions can lead to varied results in the field scenario. Therefore, few attempts have been made to automate the method for field applications. One of the earliest applications was the use of low cost, manually operated brushing apparatus. This moveable system is mobile, set on castors and has a size of dimensions of about 6 × 5 feet with adjustable working height and width. Brushing of tomato seedlings were performed by pulling a four-bar apparatus across the tomato seedlings several times [94]. In yet another interesting case-study, various herbs (Basil, coriander, mint) were mechanically stimulated in production house style green-house with a machine using light clothes attached to an irrigation boom continuously for 108 times per day. Results from these experiments showed that the brushed plants significant reduction in elongation and more stability [95]. Several other production style methods have developed that include soft clothes [96], motion vibrators [97], roll-table system [98]. More recently, in a well-devised experimental design, the authors used two different robotic platforms for investigating the potential of automation in a MS study [99, 100]. In the first case, a seven-DoF Franka Emika robotic arm, equipped with a stroking end-effector consisting of a row of plastic strings, was placed in a greenhouse setting. In the second case, an autonomous cultivation bed (LOMAS^{++}) with a growing area of 1.2 m^2 and, capable of holding plants of 30–35 com was also equipped with fully automated three-DoF robotic manipulator with a stroking end effector. In the experiment 1, the objective was to study if the frequency of mechanical motions affects plant morphology and elemental composition in plants in a greenhouse setting using the method elaborated in Case 1. A total of 50 pots with 3–5 basil seedlings in each was assigned randomly to 6 groups designed to provide variations in motion type (stroking and dipping) or motion frequency (either 100 times a day or 2 times a day). Treatments were provided to the treatment plants for a total of 27 days. Plants assigned to controls were not provided these treatments. In the experiment 2, a total of 200 plants were randomly split to five groups (treatments vs. controls) that differed in the amount of time of total application for mechanical treatments. In the experiment 3, variation in experimental design were provided by using softer material for mechanical treatment and also sampling strategy. A clear difference was shown in plant height with mechanical treatments using robotic platforms in experiment 1 and 3. Though there were no differences between control group and treatments in which stroking was applied 2 times a day, plants that were stroked 100 times a day produced 31% shorter inter-node length and 50% shorter stem length. Dipping experiments also showed a significant shortening of stem length. Experiment 2 which studied the effect of time of total application of MS showed that with increase in time of application (4 weeks), MS treatment produced shorter stems. On the other hand, results from experiment 3 revealed that MS treatments affects only internode length that developed after treatments but not already developed internodes. Therefore, the authors concluded that difference in treatment frequency, total time of MS application and stage of development affect the plant overall response to MIS treatment. Most interestingly, results with elemental composition showed a statistical increase in Magnesium in treatments when compared to control groups. Further, MS treatments resulted in increased DHA (Dehydroascorbic acid) and GABA levels. The authors concluded that increases in these metabolites is linked to build up of ROS and changes in nitrogen metabolism and aminoacid accumulation with mechanical induced abiotic stress [99, 100]. In another interesting application, a model automated touch machine was designed for the purpose of studying the effect of touch response in *Arabidopsis thaliana* [101]. The model automated touch machine was equipped with a H -shaped metal rack, a robotic metal arm equipped with hair brushes and a controller. The design automation in this study resulted in significant difference in the plant phenotype when compared to control treatments. Further, automation was used in this case to offer labor-saving and uniform touch response in comparison to human interventions. They are also useful to study the mechanism of touch response. For instance, using this experimental set-up, two proteins, MKK1 and MKK2 were shown to be crucial for bolting delay in *Arabidopsis* but not for rosette shape and area [101].

6. Farming practice, sustainable agriculture and conclusions

The most critical direction that practices of farming need to take is to incorporate strategies that combine agricultural sustainability by moderating the use of harmful chemicals and also, reducing the negative environmental effects of the farming practice. The strategies summarized in this chapter, both seed priming and mechanical conditioning of plants are cost-effective and are also easy to conduct. We can also conclude that under controlled conditions, both seed priming and mechanical conditioning have resulted in improvement in plant growth characteristics and stress cross – tolerance. Nonetheless, there are challenges that need to be overcome for wide-spread use under field conditions. The storage and short shelf life of the primed seeds are a limitation of the priming technique. The methods developed involve rapid re-drying of seeds for storage purposes at the end of treatment. However, seed drying can alter the beneficial effects of the priming agent, which are lost during storage [102]. The optimal seed priming treatment can vary depending on the plant species, variety and even, seed quality. This variability represents a major limitation of the priming method, as trials are required to determine the most appropriate strategy for each situation [103]. Mechanical conditioning applied on plants has similar disadvantages. The optimal results are dependent on species, growth stage, season and also, time-interval between treatments. Apart from these, mechanical conditioning treatments is also dependent on the intensity and frequency of treatments. Additionally, both these strategies need to be explored at the molecular level for better understanding of the complex mechanism. Nevertheless, both seed priming and mechanical conditioning can be considered as valuable strategy to improve plant establishment under adverse agroclimatic conditions without compromising on plant yield and under field conditions. An example of field-level utilization of one such strategy that is, employed in Japan is the practice of treading seedling using feet or even tractor equipped with a treading roller, leading to mechanical stimulation of Barley and Wheat, termed Mugifumi. Mugifumi is shown to increase tillers, and higher yields when compared to untreated plants. This is usually performed several times at the three-seedling stage and before internode start to appear. Results from experiments of treading performed in wheat seedlings showed 54% increase in grain weight per plant. The number of spikes and weight of whole plant also increased by 18 and 41%, respectively [104].

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Author contributions

JMN wrote the draft manuscript with inputs from VV and KN. VV conducted the experiment on hydropriming in tomato. TR contributed to the initial experiments on MS in tomato. All authors have agreed to the final draft. The authors have no conflicting or competing interests.

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