Impact of mechanical stimulation on the life cycle of horticultural plant

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ABSTRACT

Mechanical stimulation technology is critical in agricultural crop production because it is constantly regarded as a developing green technology to regulate plants to meet people's need for green and healthy agricultural products. Various environmental mechanical stimulation impacts seed germination, seedling growth, flowering date, fruit quantity, and fruit quality throughout the life cycle of a horticultural plant. This study first outlines the basic characteristics of six types of common mechanical stimulation in nature: precipitation, wind, gravity, touch, sound, and vibration. The effects of various mechanical stimulation types on the seed, seedling, flowering, and fruit of horticultural plants throughout their whole life cycle are then presented, as reviewed in the recent 100 years of existing literature. Finally, potential future study directions are discussed. The main challenge in mechanical stimulation technology is to uncover its potential capabilities for regulating and controlling plant development and fruit quality in green agriculture instead of agricultural chemicals.

Keywords: Mechanical stimulation; Plant; Seed; Seedling; Flowering; Fruit

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1. Introduction

Horticultural plants contained numerous health-promoting substances such as vitamins, essential minerals, phytosterols, flavonoids, carotenoids, phenolic compounds, and fiber (Shahbandeh, 2021). In 2019, the global production of fresh fruit amounted to 883.42 million metric tons, increasing from 576.65 million metric tons in 2000 (https://www.statista.com/topics/1621/fruit-production/). With the fast growth of the global population, rapid urbanization, and improvement of people's living standards, the market demand for high-quality fruit is expanding dramatically (Han et al., 2022). Fruit is an important economic organ of horticultural plants. However, excessive development of the plant's branches and leaves may make it difficult to produce high-quality fruits effectively. Obviously, there is always a mutual restricting link between distinct stages of a horticultural plant's life cycle (Genard et al., 2008).

Many pesticides and chemicals are often used to control the growth and development of horticultural plants to produce high-quality fruits efficiently. For example, Gibberellin (GA3), Ethylene, and Brassinosteroids promote seed germination. Mepiquat chloride, Chlormequat (Cycocel), and Ancymidol (A-Rest) are used to inhibit the excessive growth of seedlings; 2, 4-D (2, 4-Dichlorophenoxyacetic Acid), IAA (Indole-3-acetic acid), and GA3 are used to prevent flowers and pre-harvest fruits from dropping. The use of chemicals causes farmland and environmental pollution and fruit contamination. Currently, world agriculture is transitioning from traditional chemical agriculture to green ecological agriculture, and the new developing concept is to boost the production and quality of fruit crops without polluting the environment or agro-products (Carlisle et al., 2019). As a result, modern agro-physics technologies, which consist of fundamental physical methods for regulating the life cycle of plants, have emerged as an essential means of achieving green ecological agriculture. In recent years, mechanical stimulation is one of the most promising green modern agro-physics technologies. It involves the application of a specific intensity and frequency of mechanical energy to a fruit tree organ such as branches, seeds, seedlings, and fruit to promote the growth and development of horticultural plants at a specific life cycle stage (Cai, 2013). Although mechanical stimulation technology in fruit production could significantly reduce chemical pollution and meet people's demand for green and healthy agricultural products, there is a knowledge gap in the physiological response mechanism of horticultural plants to these stimulations throughout their entire life cycle. Therefore, this paper aims to review the literature on the effects of mechanical stimulation on the life cycle of horticultural plants and suggest future research directions. This can provide fundamental data for evaluating mechanical stimulation as a tool for green and chemical-free agriculture and open up a new channel for regulating plant development and fruit quality.

2. Types of mechanical stimulation

Horticultural plants are susceptible to various abiotic stressors (e.g., rain, snow, wind, sound, vibration, gravity, and touch) during their whole life cycle (Fig. 1). These external natural environmental stress factors are called mechanical stimulation (Lamers et al., 2020). According to biological evolution theory, plants may adapt to the dynamic environment by changing their physiological structure and growth processes.

2.1. *Wind stimulation*

The natural movement of air or other gases relative to the surface of a planet is referred to as wind (Ikelle, 2020). Wind occurs on various scales, from thunderstorm flows to local breezes formed by heating land surfaces to global wind caused by differences in solar energy absorption between Earth's climate zones. Wind characteristics in nature, such as wind speed, wind direction, and duration, are mainly affected by the roughness of the surface, the stability of the atmosphere, and the terrain (Karmaoui, 2019). On the one hand, wind affects plants through the force acting on them, which is composed of viscous resistance and pressure. When the wind speed is low, the viscous resistance is dominant (Reynolds number $< 10^3$), but as the wind speed increases, pressure resistance becomes dominant, which is usually around three times that of the plant canopy (Li et al., 2018b). Wind can also affect plants' evapotranspiration and organ temperature. The shape, size, and biomechanical properties of plant roots, stems, leaves, and their constituent cells tend to adjust in response to wind load to adapt to the multiple coupling effects of wind. In detail, when some plants are constantly exposed to wind, their leaf area and stem height decrease, while their branch diameter, coarse/fine root ratio, and root/bud ratio increase, improving their ability to withstand wind load. In addition, the wind increases the cellulose microfiber angle of constituent plant cells but reduces the elastic modulus of cell walls. Similarly, the cuticle of plant leaves thickens to reduce the rapid loss of water caused by the wind (Gardiner et al., 2016).

2.2. *Touch stimulation*

Most plants in nature are rooted to the ground and cannot escape all forms of stress and stimulation. When objects interact with plant leaves and branches, contact stimulation occurs. The reactions of various plants or organs to contact stimulation vary substantially (Jaffe et al., 2002). Some plants, such as the venus flytrap (*Dionaea muscipula*), have highly specialized touch-response machinery and highly conspicuous thigmotropic or thigmonastic behaviors. This touch response turns plants into aggressors against animals, trapping and devouring them. Higher plants gradually undergo morphological changes after touch stimulation, such as repetitive touch stimulation leading to a delay in flowering and an inhibition of inflorescence elongation in thale cress (*Arabidopsis*). Because these touch-induced morphological changes occur slowly over time, they are not usually easily observed (Chehab et al., 2009). Most plants are sensitive to touch stimulation and even seemingly harmless, random touch stimulation can elicit different responses at the organ and cellular levels. An organ response manifests in morphological and structural changes such as plant height, diameter, leaf area, and petiole on a macro scale (Markovic et al., 2014). For example, stimulation causes leaves to close and flowers to bloom to ensure cross-pollination, and it causes branches to ascend to the height of the sunlight. The cellular response is manifested in the changes of many genes encoding calcium-binding, cell wall modification, defense, transcription factors, and kinase proteins at the microscale (Braam, 2005). Indeed, stimulation will make organelles move directionally in cells (Sato et al., 1999). These cellular responses may be significant for fundamental processes such as turgor regulation, cellular expansion, and morphogenesis. However, the mechanism of plant perception and intercellular and intracellular signal transduction after contact stimulation is unclear.

2.3. Gravity stimulation

All plants on the earth are in a gravitational environment. Different gravity environments will impact plants' macromorphological development, microstructure distribution, and physiological and biochemical processes. When plants grow in a weightless environment, sensible and latent heat exchange between leaves and ambient air is delayed, leaf temperature rises (Kitaya et al., 2001), and stem and leaf growth is prone to red light (Kiss, 2014). In addition, a microgravity environment will also increase the number of plant flowers and seed quality (Karahara et al., 2020). When plants grow in an overweight environment, heat exchange between leaves and air increases, leaf temperature decreases (Kitaya et al., 2001), and leaf transpiration rate increases (Hirai and Kitaya, 2009). At present, the mechanism of plant response to gravity has been relatively more studied. The gravity response mechanism of plants can be divided into four stages: gravity perception, signal formation in the gravity perceptive cell, intracellular and intercellular signal transduction, and asymmetric distribution of auxin (Philosoph-Hadas et al., 2005). Two hypotheses have been proposed to explain how plants perceive the direction of gravity: the gravitational-pressure model and the starch-statolith hypothesis. Different experimental approaches in various plant species have strongly supported the latter. This hypothesis holds that the amyloplasts in plant cells play the role of dynamic balance stone, and the gravity signal is sensed by balance cells. These cells have special structure and are rich in starch particles with relative density greater than that of cytoplasm. These starch particles are called balance stones (Philosoph-Hadas et al., 2005). Mesocolumnar cells and endothelial cells perceive the change of gravity through the sedimentation of starch granules. When starch granules perceive a new gravity signal, they contact and destroy the actin microfilament network and then transmit the signal to the endoplasmic reticulum (ER) to promote the release of Ca^{2+} stored in the endoplasmic reticulum (Yoder et al., 2001). The increase in cytoplasmic Ca^{2+} concentration and the decrease in proton concentration lead to the differential distribution of auxin in the direction of gravity (Morita et al., 2004, Radin et al., 2021). This differential distribution of auxin leads to the growth of plants in the direction of the new gravity vector.

2.4. Sound stimulation

In agricultural applications, sound is a type of vibration produced by speakers and transmitted through gas as a pressure wave. Generally, according to the human hearing range, sounds with frequencies less than 20 Hz are referred to as infrasound waves, whereas sounds with frequencies more than 20 000 Hz are referred to as ultrasonic waves. Both infrasound waves and ultrasonic waves are outside the human hearing range, and they can interact with biological tissues through thermal and mechanical processes (Ghosh et al., 2016). Although plants lack organs to recognize air vibration, they can still use unknown organs to sense sounds (Jung et al., 2018). At present, sound waves have been applied to plants' growth and development stages, such as seed germination and seedling growth. They have a certain impact on the biochemical processes, such as plant endogenous hormone synthesis and partial gene transcription. Plant disease resistance can be improved using sound stimulation, reducing the need for chemical fertilizers and fungicides. In addition, plants can spontaneously produce low-frequency sound waves of 50-120 Hz and can also absorb specific external sound frequencies, thus changing the cell cycle (Hassanien et al., 2014).

2.5. Vibration stimulation

Vibration ranged from the universe to subatomic particles (Au-Yeung et al., 2019). All physical phenomena involve vibrations, including sound, light, and heat. As a source of stimulation, mechanical vibration usually refers to the plant's vibration, which is caused by the direct action of external forces on the plant itself. It can be defined using two fundamental parameters: frequency and amplitude. Vibration stimulation will make the high-density starch in plant cells produce a changing acceleration, so amyloplast may also be the vibration receptor of plants. Although the vibration has no fixed amplitude and frequency, some data show that after stimulation, plant stems become thicker and shorter, roots become longer and stronger, flowering is delayed, and the mature main inflorescence is shorter (Wang et al. 2008b; Far et al. 2019). In addition, vibration stimulation with artificially fixed frequency and amplitude could be beneficial to the growth and development of plants. Uchida and Yamamoto (2002) found that the mechanical vibration with the frequency of 70 - 100 Hz and 0.33 - 0.42 mm amplitude can promote the germination rate of *Arabidopsis* seeds. However, vibration stimulation exceeding a certain acceleration threshold cannot improve the seed germination rate (Uchida and Yamamoto, 2002). Hassanpour et al. (2017) found that 50 Hz sinusoidal vibration promoted the growth rate of henbane (*Hyoscyamus kurdicus*), increased the content of protein and proline and increased the activities of superoxide dismutase (SOD), ascorbic acid peroxidase (APX) and peroxidase (POX), while decreasing the level of total carbohydrate, H_2O_2 and CAT activity (Hassanpour et al., 2017). Ghalkhani et al. (2020) found that the vibration with 100 Hz increased the growth, branch length, chlorophyll content, and relative water content of pennyroyal mint (*Mentha pulegium*).

2.6. Precipitation stimulation

Precipitation is a significant natural environmental component, and its most common forms include fog, rain, sleet, snow, and hail. Precipitation modifies the natural microenvironment of plant development, such as the temperature and humidity of the atmosphere and soil. Additionally, precipitation provides the necessary water for plant survival. The physical falling process of precipitation would induce mechanical stimulation on the plant aboveground parts such as leaves, flowers, fruits, stems, etc. Early researchers considered the precipitation as a kind of mechanical stimulation, but it is not sure whether the water droplets significantly affect the plant morphology. Jaffe and Galston (1968) found that the touch sensitivity of tendrils shares a selective sophistication with that of sundew. Application of water droplets causes no coiling response; therefore, tendrils avoid nonproductive coiling in rainstorms. Darwin (1893) found that the mechano-sensitivity of sundew tentacles reached 1 mig, but they did not respond to the force of water droplets or even heavy rain. More researchers found that water droplets during precipitation will impact plant microstructure in recent years. Moerkercke et al. (2019) showed that the pressure of water droplets on the leaf surface triggers stress hormones such as jasmonic acid. These cellular changes quickly become apparent, allowing plants to resist disease and drought better. Matsumura et al. (2022) found that hair-like structures on plant epidermis directly sense external mechanical forces, including raindrops, to predict pathogen infection in *Arabidopsis*. Bhosale et al. (2020) demonstrated that the complex response of a superhydrophobic Katsura leaf upon raindrop impact could be decomposed into simple single degree-of-freedom linear modes of bending and torsion. This study provides a certain reference and basis for studying the influence of raindrops on leaves. Furthermore, when it rains heavily, the rainfall may wash away the roots of the subsurface organs, particularly certain exposed parts. Huang (2011) revealed that when rainwater scouring periods were reduced, the chlorophyll content of seedling leaves increased initially, then dropped, but root activity continued to increase. This is due to the simultaneous impact of washing and mechanical stimulation on the roots. Natural precipitation is uncontrollable in terms of time-space distribution, frequency, and intensity, and hence no rule can govern the mechanical stimulation of plants by precipitation. In addition, the irrigation combined with mechanical stress for precipitation makes the interpretation of the physiological effects difficult.

3. Impact of mechanical stimulation on the seed

Seed is vital for rebuilding crop production capacity, maintaining germplasm resources, and improving species diversity. On the one hand, seed germination is the key period of plant establishment. If plants can germinate and establish rapidly, seedlings can better withstand environmental stresses (Nazari and Eteghadipour, 2017). To break seed dormancy and promote seed germination, hormone treatment is often used, leading to health and environmental issues due to residues from this treatment.

3.1. Impact of mechanical stimulation on the seed germination

In recent years, mechanical stimulation has attracted the attention of researchers as a safe, simple, and time-saving technology to break seed dormancy (Table 1). The most common types of mechanical stimulation of seeds are sound waves (including sound waves and ultrasonic waves) and vibration, which are usually described by intensity and frequency. Different studies used various intensity parameters, such as power (W) and decibel (DB), alongside frequency (Hz), to measure the effects of different intensity, frequency, or combined mechanical stimulation on seeds at different times, including seed germination (germination rate, germination index, germination potential, etc.).

At present, the frequency that can promote seed germination is relatively wide and can be divided into low-frequency (5-1000 Hz) and medium-frequency (1000-4000 Hz) mechanical stimulation (Abhijith et al., 2018). For example, Yang et al. (2011) used 40kHz ultrasound to increase the seed germination rate of tomato and pepper by 15% and 10% and the germination potential by 14% and 18%, respectively. Chen et al. (2020)applied the same method to increase the germination rates of Impatiens balsamina seeds by 11.03% and that of Chinese pink seeds by 3.77%. Sharififar et al. (2015) investigated the effect of higher frequency ultrasound (42 kHz) on *Ariplex Lentiformis* and *Zygophylllum* seeds and found that and found that treatments with 5- and 7-minute exposures produced the highest rate of seed germination, while the 9-minute exposure had a negative effect on germination when compared to the other treatments. Similarly, several authors reported a significant increase in main crop seeds germination after acoustic wave treatment These include corn (*Zea mays L.*) at 300 Hz (Vicient et al.,2017), wheat (*Triticum aestivum L.*) at 70 Hz (Delone et al.,2010), broad bean (*Vicia faba L.*) at 42 kHz (Lahijanian and Nazari ,2017) and rice (*Oryza sativa L.*) seeds at 25 kHz (Zhao et al.,2011).

Furthermore, the intensity of mechanical stimulation has a serious impact on seeds. The intensity of mechanical stimulation in most studies is between 50 - 500 W (power). For example, Yang et al. (2011) and Chen et al. (2020) used ultrasonic waves with 50W and 500W to promote the germination rate of vegetables (pepper and tomato) and flowers (Impatiens balsamina and Chinese pink), respectively. However, the sound wave intensity that promotes the germination of agricultural crop seeds such as rice, maize mung bean is generally between 80-110 dB (Wang et al., 2003a; Vicient et al., 2017; Cai et al., 2014).

The duration of mechanical stimulation has a significant influence on seed germination. It is now recognize that too short or too longsound wave treatment time could have no effect or negative impact seed germination rate This phenomenon has been verified in vegetables and flowers, such as pepper, tomato, *Impatiens balsamina*, Chinese pink, *Echinacea*, etc (Yang et al., 2011; Chen et al., 2020). Indeed the seed germination rate increase with the sound wave treatment time until a critical time atfter which any further exposure results in aa negative outcomes. Therefore, there is an optimal treatment time for specific varieties of seeds when they are treated with sound waves of specific frequency and intensity. The above literature seems to suggest that that the optimal time for ultrasonic treatment is generally within 60 minutes.

3.2. Mechanical stimulation mechanism affecting the seed germination

The basic principles of the seed germination promoted by mechanical stimulation methods like ultrasound, sound waves, and vibration may be different. There are many studies on the effects of ultrasound on different seed germination. Most people believe that ultrasound with appropriate intensity and frequency can promote seed germination by enhancing fundamental seed germination conditions such as water absorption and oxygen availability. When the cavitation effect generated by ultrasonic wave in water occurs in the liquid near a rigid surface such as the seed boundary, bubbles collapse with a high-speed liquid jet that impacts the seed surface and form pores on its surface. If the shell breaks, water and oxygen will enter the seed more freely (Vicient, 2017; Zhao et al., 2011). The additional absorbed water would react freely and rapidly with the cell embryo, accelerating the metabolic processes such as gibberellin release and enzyme activation, which explained the shorter average germination time, as well as the improved germination rate and yield (Lahijanian and Nazari, 2017; Yaldagard et al., 2008). However, when the intensity or frequency of ultrasound is too large, the local pressure and temperature change rapidly, resulting in shear damage, strong cavitation, cell membrane thinning, local heating, and the production of free radicals. These consequently lead to physical and chemical damage that could be fatal to cells and thus unfavorable to seed germination (Liu et al., 2016).

Low and medium frequency sound waves or vibrations have significantly less energy than ultrasonic waves, which have just one billionth of the energy necessary for chemical bond fracture and are insufficient to generate water cavitation. A resonance effect occurs when the inherent frequency of the organelle in the cell matches the frequency of the applied sound wave or vibration. In this situation, the impacts of a single continuous sound wave or vibration will be cumulative and may cause higher vibration of organelles, thereby affecting cell biochemical or biophysical processes related to germination and growth (Weinberger and Measures, 1968).

4. Impact of mechanical stimulation on the seedling

The seedling stage is when plants begin to grow on their own. Without the wrapping and protection of seed coat and soil, plants in the seedling stage begin to experience different types of mechanical stimulation in nature, such as wind, vibration, touch, etc. Plants have developed the capacity to sense and respond to these stimulations (Table 2), changing the morphological structure, physiology, and biochemistry to increase their resistance to these external stresses.

4.1. Impact of mechanical stimulation on the seedling stem

In addition to conveying water and inorganic salts and storing starch and sugars, stems support the weight and pressure of branches, leaves, flowers, and fruits to withstand or resist wind, rain, snow, and hail damage. Certain stems are also capable of reproduction. As a result, many papers concentrate on the effects of mechanical stimulation on seedling stems. Firstly, gravity, provides important external conditions for determining the direction of plant growth. Gravity is especially important during the early stages of seedling growth. It stimulates the negative gravity response of the main stem and directs it toward the light source, which promotes photosynthesis and organic matter production (Strohm et al., 2013).

Furthermore, mechanical stimulation with appropriate intensity would limit seedling growth rate and height, increase plant diameter, and make plants more compact. For example, Sparke et al. (2021, 2022a, 2022b) found that the height of tomato seedlings after wind disturbance treatment was 26~36% lower than that of the control group. Similarly, Li et al. (2018a, 2020) reported a reduction in the height of tomato seedlings by wind blowing. Far et al. (2019) revealed that treating coleus (*Coleus blumei*) with 12.5 Hz vibration frequency every day for 10 minutes could reduce the plant height by 31%. In addition, similar findings have been found in other plants such as tobacco (*Nicotiana tabacum L.*) (Anten et al., 2005), brushing ryegrass (*Lolium perenne L.*) (Wang et al., 2010) and slender false brome grass (*Brachypodium distachyon*) (Gladala-Kostarz et al., 2020). Ethylene and abscisic acid have long been thought to play an important role in morphogenesis. Plants may respond to mechanical stimulation by producing more ethylene or abscisic acid (Mitchell, 1996). Both hormones are growth inhibitors, which may lead to longer stomatal closure, reduced carbon dioxide absorption, and decreased total plant biomass. Furthermore, mechanical stimulation caused cavitation of the water column in the xylem, destroying the transport pathway (Wang et al., 2008b). It could also be transmitted to the roots of underground parts, resulting in water stress in the rooting area, which continually causes fracturing of root hairs at the end and restricts water absorption. As a result, greater ABA (Abscisic acid) concentration and transfer from roots to aboveground sections may occur. The reduction in total biomass will ultimately reduce the size of numerous tissues and organs (Reubens et al., 2009). This dwarfing strategy limits bending moments, reduces the risk of different mechanical strains, plastic deformation, uprooting, rod buckling, and failure, and could be regarded as a plant adaptive approach (Gladala-Kostarz et al., 2020).

Mechanical stimulation impacts the elastic modulus, bending, and stiffness of seedling stems. On the other hand, plants respond differently, and their mechanical characteristics improve, allowing the plant to be more resilient to increasing mechanical stimulation. For example, according to Patterson et al. (1992), bending the sunflower (*Helianthus annuus*) for 60 s at a frequency of 2 Hz every day raises the elasticity and bending stiffness of the stem. From the microscopic point of view, it may be due to the varied effects of mechanical stimulation on the cell wall. The plant cell wall is generally made up of four major polymers: cellulose, hemicellulose, pectin, and lignin. The lignin content of the stem cell wall rose dramatically (by 27%-40%) after mechanical stimulation, particularly in the interfascicular tissue and cortex. These findings suggest a correlation between the increase in lignin and the increase in Young's modulus of the internodes. Lignin-related structural reinforcement may increase tensile strength (Barros et al., 2015) and lodging resistance (Li et al., 2018a). On the contrary, the mechanical properties of some plants have shown a downward trend after receiving external mechanical stimulation. For example, Li et al. (2020) observed that a wind treatment of $0.6\ m \cdot s^{-1}$ every 30 min for 5 min reduced tomato seedlings' hardness and elastic modulus by about 25% and 24%, respectively, in summer. In contrast, in winter, the hardness was reduced by 29%, while no significant effect was observed for the elastic modulus. Far et al. (2019) found that treating coleus (*Coleus blumei*) for 5-10 min every day with a 12.5 Hz vibration frequency reduced the elastic modulus and bending stress. Additionally, increasing the acoustic frequency from 7.5 Hz to 12.5 Hz reduced the elastic modulus and bending stress. The reduction of these mechanical properties can make the plant become softer. Under the same intensity of external stimulation, the plant can adjust its posture to minimize the stress area, thus indirectly increasing its resistance to external mechanical stimulation. Therefore, to resist greater mechanical stimulation, plants typically enhance their flexibility or stiffness, or seek a trade-off between these two characteristics (Wang et al., 2008b).

4.2. *Impact of mechanical stimulation on the seedling leaf*

The leaf is crucial in plant development and adaptation processes such as photosynthesis, transpiration, nutrient absorption, and secretion release and may occasionally withstand insects and harsh environments. Many studies, have discovered that brushing or vibration, bending, contact, and other stimulation can reduce the number of leaves or leaf area while having distinct impacts on their chlorophyll content. For example, Biddington and Dearman (1985b) found that the leaf areas of cauliflower (*Brassica oleracea* L.), lettuce (*Lactuca sativa* Linn.), and celery (*Apium graveolens* L.) decreased by 17%-21%, 15%-25% and 25%-34% respectively after brushing 40 times per min for 1.5 min every day for 6, 4 and 14 days, respectively. Hong et al. (2021) revealed that using 4.0 m · s^{-1} wind every day for 18 weeks reduced the chlorophyll content and the angle between leaves of beef-wood (*Australian pine*). However, the difference was not statistically significant. According to Wang et al. (2008b), shaking astragalus root (*Hedysarum*) leaves less than 45° twice per second for 1 min will reduce the number of *Hedysarum* leaves by 10% - 23%. Also, mechanical stimulation could increase the activities of enzymes in leaves, promote the secretion of lignin and phytoalexin, and improve plant resistance to a variety of diseases and pests. For example, Wang et al. (2006) stimulated the first true leaf of cucumber with 980 Pa pressure for 120 min. The results revealed that PAL activity began to increase after stimulation, while POD associated with cell wall thickening rose dramatically after stimulation. Mechanical stimulation could also induce lignin deposition, and the content increases with time. Through the same method, Zhao et al. (2008) found that mechanical stimulation significantly increased phytoalexin content, while the infection index decreased by 85%. Zhao et al. (2005) found that after 1000 Pa pressure stimulation on cucumber leaves for 120 min, PAL activity increased by nearly 50%, but there was no difference with the control group when treatment duration was prolonged (120 h). Also, POD activity increased by about 10% and did not change with time. Stress-induced lignin synthesis may provide a physical barrier against pathogens (Zhao et al., 2005).

4.3. Impact of mechanical stimulation on the seedling root system

The root system is responsible for conveying water and nutrients, storing nutrients, synthesizing several vital amino acids and alkaloids, as well as fixing and maintaining aboveground parts. Hence, the effect of mechanical stimulation on the root system will indirectly affect the healthy growth of the entire plant. Many research showed that mechanical stimulation on the aboveground part of horticultural plants will often increase the root length, quantity, and weight. For example, Jia et al. (2003) found that the fresh weight, root length, and root vigor of chrysanthemum (*Dendranthema morifolium*) roots increased significantly by 21.4%, 30.3%, and 44.4%, respectively, after being stimulated by sound waves with an intensity of 100 dB and frequency of 1000 Hz for 3, 6, 9, 12 and 15 days for 60 min a day. Li et al. (2020) reported that 0.6 m · s^{-1} wind treatment for 5 min every 30 min improved the dry mass of tomato roots by about 34.63 %.

On the other hand, mechanical stimulation may also enhance the mechanicalproperties horticultural plant rootsthough more research focused on agricultural crops. For example, Goodman and Ennos (2001) found that mechanical stimulation increased the stiffness of the root of the primary node of the fourth node by 41%, the strength by 44%, and the hardness of the material, constituting them by 42%. The stiffness of the primary root of the fifth section increased by 75%, the bending strength increased by 60%, and the bending modulus of the bending root increased by 70%. The mechanically stimulated root is harder and stronger than the non-stimulated root, which may be explained by secondary thickening of the cell wall. Gravity is critical to plant growth and survival, especially after underground seed germination. Gravity is the only clue to guide the growth of roots and buds (Petra et al., 2015). Most roots respond to gravity by producing a positive gravity response in primary roots, allowing them to grow deeper into the soil, where water and nutrients can be used for plant growth and development (Chen and Guan, 2002).

5. Impact of mechanical stimulation on the flowering

Flowers are the sexual reproductive organ of most plants. They are also a significant indicator of a plant's transition from vegetative to reproductive growth. This transformation necessitates a change in the overall characteristics of the shoot tip meristem, as well as the vegetative bud apical meristem (SAM) exhibiting the characteristics of the inflorescence meristem (IM) (Huijser and Schmid, 2011). Given the biological significance of this transformation and the horticultural community's interest in understanding and controlling flowering time, the events leading to flowering have been intensely studied (Kim, 2020). Long-term studies have found that flowering time is affected by various environmental factors, such as photoperiod, temperature, water and nutrients in the soil, exogenous compounds, microorganisms, and pollinators (Huijser and Schmid, 2011). The influence of mechanical stimulation on flowering has attracted widespread attention (Table 3).

5.1. Effects of mechanical stimulation on the flowering date and number

Appropriate mechanical stimulation can delay flowering and reduce the number of flowers, which plays a role in adjusting the flowering date and thinning flowers and fruits. For example, Jędrzejuk et al. (2020) stroked the top part of the seedling 40, 60, or 80 times each day. Three weeks after stimulation, the number of morning glory (*Pharbifis nil*) dropped from 36 to 21. Onguso et al. (2006) showed that the flowering number of 5-year-old peach (*Amygdalus persica* L.) trees after vibration every 2 h for 15 min was slightly lower than that of the control. Because these mechanical treatments create no evident damage to the plant, the delay in plant growth and loss in flower quantity are clearly the outcome of internal resource allocation trade-offs (Cipollini and Schultz, 1999). For example, with the increase in mechanical disturbance exposure, the relative increase of aboveground stem resource input is negatively correlated with plant development and flowering. Proteins known to have significantly enhanced structural functions in mechanically disturbed plants include annexin, extensin, xylan endoglycosidase, lipoxygenase and peroxidase (Cipollini, 1998). Increasing the distribution of such mechanical strength-enhancing proteins and/or their substrates, such as phenolic monomers of lignin, may be part of the reasons for the delayed or reduced flowering of mechanically disturbed plants. The change in flowering time is caused by either a regulatory change in the number of leaves prompting the transition or a change in leaf formation rate. Therefore, mechanical stimulation delays flowering because leaf production is hindered, and JA (Jasmonate) is likely to slow down the emergence of leaves (Chehab et al., 2012).

Mechanical stimulation may even increase the number of flowers for other plants. Jędrzejuk et al. (2020) stroked the top part of the seedling 40-80 times a day. Three weeks after the stimulation, the number of Petunia 'Dark Red' flowers increased, and had no effect on the flowering time (Jędrzejuk et al., 2020). Takahashi and Suge (1980) applied friction stress twice a day for 30 s for 20 days, increased the average number of female flowers of monoecious cucumber. Vernier et al. (2002) used brushing (four times a day, once every three hours), shaking (220 $r \cdot min^{-1}$, four times a day, once every three hours) and impulse (night) to mechanically stimulate a bunch of red leaves until flowering. The results showed that these mechanical stimulations did not affect the flowering date and flower size of a bunch of red leaves. The study also found that mechanical stimulation can also inhibit the growth and development of flower-related tissue structures such as inflorescence and rosette.

5.2. Effects of mechanical stimulation on the flower structure

Mechanical stimulation not only has a significant impact on the flowering date and the number of flowers, but also has an impact on some structures of flowers. *Scrophularia* (the traditional boundary), especially in *Taxaceae*, *Leguminosae*, *Martiniaceae*, and *Scrophulariaceae* have sensitive stigmas. The common characteristics of plant species with sensitive stigmas are hermaphroditic flowers, tubular corolla, and two-leaf stigma (Milet-Pinheiro et al., 2009). Generally, the behavior of sensitive stigmas includes three consecutive events: temporary closure, reopening, and permanent closure (Jin et al., 2017). After a certain mechanical stimulation, such as pollen falling, the stigma will be closed temporarily and reopened after touching. When a sufficient amount of pollen is deposited on the stigma, it may become permanently closed (Yang et al., 2004). Among them, different forces will significantly impact the reaction time and duration of the temporary closure of stigma (Jin et al., 2017; Milet-Pinheiro et al., 2009). These sensitive stigmas ensure reproduction, avoid selfing and promote outcrossing. In addition, it may also play a role in the selection of pollination media because only the appropriate pollination media can trigger this mechanism (Jin et al., 2017).

6. Impact of mechanical stimulation on the fruit

Fruit can protect seeds and aid in the propagation of seeds to new and distant locations. Furthermore, the fruits of many plants provide essential nutrients for seed germination. There are generally two fruit growth and development laws, namely single S-type curve and double S-type curve, as shown in Fig. 2 (Li et al., 2017). Many factors in nature, such as light and temperature, will significantly impact fruit growth and development. However, research on the influence of mechanical stimulation on fruit texture, nutrition, and the mechanism is still in its early stages.

6.1. Changes in fruit cell features under the stress stimulation

The cell is the basic component of the whole plant, and its physical characteristics can determine the physical properties of fruits and plants. The environmental stimulation-induced variation plays a significant role in cell growth and evolution. For cells, environmental mechanical stimulation includes common external mechanical stimulation, such as touch, bending, etc., and intrinsic mechanical stimulation. The intrinsic mechanical stimulation in plants comes from pressure stress (shape-derived stress), with cells and tissues modeled as pressure vessels and growth-derived stress, with the balance between turgor pressure and wall tension at the cell level scaling to the tissue level. It is worth mentioning that because the turgor pressure is the driving force behind growth, differential growth and the mechanical conflicts that occur will ultimately be caused by the turgor pressure. To accommodate the internal turgor pressure, microtubule (MT) arrays are reorganized to align in the direction of maximal tensile stress, presumably reinforcing the local cell wall by guiding the synthesis of cellulose (Yang et al., 2021). Yang et al. (2021) and Lin et al. (2022) found that the FER-pectin complex senses and/or transduces mechanical forces to regulate MT organization through activating the ROP6 signaling pathway. Furthermore, the epidermis of plant aerial organs is under tension while the inside tissues are compressed and that the epidermis serves as a load-bearing structure in plant growth (Savaldi-Goldstein et al., 2007). However, it is unclear to what extent both external and intrinsic mechanical stresses can work synergistically in favor of plant and fruit quality and resilience to mechanical damage during harvest and postharvest.

The majority of research on the impact of mechanical stress on plant cells focuses on biochemical reactions, cell morphology, and mechanical properties (Table 4). The biochemical effect of stress stimulation on plant cells is essentially related to the activity, content, and distribution of various macromolecules in the cells. Zhao et al. (2005) found that mechanical stimulation can increase the deposition of lignin in the cell wall, thicken the plant cell wall and improve the mechanical properties of cells of cucumber seeding. Wang et al. (2006) found that appropriate mechanical stimulation of cucumber seedlings can significantly improve plant resistance and induce lignin synthesis. Saidi et al. (2009) found that rubbing the internodes of tomato plants led to cell wall hardening, which is associated with the induction of lignification processes.

Limited research has been conducted on plant cells' mechanical properties when subjected to mechanical stimulation. Similar investigations have mostly focused on the plasma membrane and cell wall plasma membrane adhesion. Wang et al. (2003b) discovered that when the stimulation frequency increases, the membrane elastic modulus and viscosity coefficient rise, indicating that the membrane deformability decreases. Zhou et al. (2007) found that chrysanthemum cells grew preferentially perpendicular to the principal stress vector. In addition, cellulose staining showed that mechanical force could enhance the cell wall structure. However, cell wall mechanical support is limited because the interaction between the rigidity of the wall and the internal hydrostatic pressure (turgor) of cell contents, as well as cell arrangement and packing within the tissue, determine the mechanical strength of fruits and, to some extent, their resistance to mechanical damage.

Fruit comprises numerous cells of various sizes and shapes that are grouped in a certain way via the cell wall, which contains three complex permeable macromolecular networks: cellulose hemicellulose, pectin, and structural protein (Devaux et al., 2005). The mechanical properties of microscopic cells and the macrotexture of the fruit are inextricably linked (Zhao et al., 2016; Zaharan et al., 2020). As a result, changes in cell wall composition and structure and changes in internal cell pressure generated by various mechanical stimulations could impact the texture of the fruit.

6.2. Changes in fruit nutrition components under the stress stimulation

Fruit are a major source of antioxidants, anticarcinogenic phytochemicals, and complex carbohydrates, essential for human health and well-being. Kowalczyk et al. (2012) found that supplemental light increased the total sugar content of Komeett F1 varieties tomato by 39.4%. In contrast, the nitrate content of tomato fruits was lower when exposed to HPS sodium discharge lamps and LED lamps (Kowalczyk et al., 2012). Although most of the studies focused on postharvest stress stimulation, Table 5 presents some highlights of research on the influence of mechanical stress on plant development and fruit quality, which support the postharvest data. When tomato plants were treated with a sound wave of 90 dB at different frequencies in the first, second, and the third week of growth, the fruit quality characteristics increased with the increasing sound frequency. Moreover, the total phenol, lycopene, and ascorbic acid content of the tomato plants increased at the rate of 70%, 20%, and 14%, respectively (Altuntas and Ozkurt, 2019). The effect of sound waves on plants was reported to be more effective than that of fertilizers, with the combination of the two technologies, known as agri-wave technology, yielding the best results (Hou and Mooneyham, 1999). In a 17-hectare field trial, the same authors proved that agri-wave technology stimulated the growth rate and yield of spinach (*Spinacia oleracea Linn*.). The study showed a 22% increase in yield, a 37.5% increase in sugar content while vitamin A, C, and B content increased by 35.63%, 41.67%, and 40.00%, respectively, compared to the control group. Additionally, the control group was infected with rot disease, but the treated group had no disease, implying that the technology could be employed for chemical pesticide-free agriculture. In a comparative study with tomato plants, agri-wave technology treatment increased output by 14%, doubled tomato storage time, increased the sugar by 26%, and increased vitamin A and niacin content by 55% and 92%, respectively (Hou and Mooneyham, 1999). Although specific minerals, such as vitamin C and vitamin E, were reduced, the overall results demonstrated that agri-wave technology could promote plant growth, increase yield, and improve fruit quality.

To adequately respond to changes in the environment, plants must be able to receive and process signals at the cellular level. At the same time, each cell can be assumed to have the molecular configuration to sense mechanical stimulation and process it into a cellular response (Monshausen et al., 2013). Three families of mechanosensitive ion channels implicated in mechanoperception at the plasma membrane have been identified in plants: The MscS-like (MSL), Mid1-complementing activity (MCA), and TPK channels (Yoshimura et al., 2021). Members of thmmm vary widely in structure and function, localized to different cell compartments, and conduct a variety of ions. Another class of proteins implicated in mechanoperception at the plasma membrane are receptor-like kinases

(RLKs). These proteins consist of an extracellular ligand-binding domain, a transmembrane domain, and a cytosolic protein kinase domain and thus can relay extracellular ligand binding into a phosphorylation signal within the cytosol (Börnke et al., 2018). The most promising candidate RLKs possibly involved in mechanoperception include the wall-associated kinases (WAKs) and the Catharanthus roseus RLK family (crRLKs) (Nissen et al., 2016). At present, the physiological and molecular basis of plant response to mechanical stimulation has been studied such as Börnke et al. (2018) and Chehab et al. (2009).

To summarize, most research indicate that mechanically induced stress could lead to improved fruit nutritional and health-promoting qualities, mainly through the production of reactive oxygen species and secondary metabolite biosynthesis to counteract oxidative stress. The same process also helps defend the plant against infections, indicating a possible approach for green agriculture. However, more systematic research is needed to gain a better understanding of the mechanism and to confirm the influence of mechanical stimulation on overall fruit quality.

7. Future research directions

One of the most critical issues of the twenty-first century is to increase agricultural productivity to meet the needs of a growing population while reducing the negative environmental effect of intensive agriculture. As a result, we reviewed the different responses of plants to mechanical stimulation. This method can regulate the growth and development of fruiting crops. For example, appropriate mechanical stimulation can improve seed germination, seedling development, flowering date and quantity, fruit texture and nutritional content, and overall fruit quality. However, research on the effects of mechanical stimulation on horticultural plants is sparse. As a consequence, based on the study content presented here, we propose numerous potential future research areas.

(1) While ultrasonic stimulation can be used to break dormancy in seeds, excessive stimulation can be harmful. As a result, numerous research found vastly disparate optimal treatment time, intensity, and frequency, partly due to differences in the kind of studied seeds. It is expected that an appropriate mathematical model can be established, and the best treatment parameters can be predicted based on seed characteristics if the mechanism by which mechanical stimulation affects seeds is adequately understood, as well as the relationship between seed mechanical properties (hardness), geometric properties (seed coat thickness, hydrophobicity, density, etc.) and the most important treatment parameters that promote seed germination.

(2) The responses (such as germination rate, flowering number, and so on) of the same plant type to the main parameters of various mechanical stimulation such as intensity, frequency, and treatment time can be used in conjunction with a comprehensive index of these three parameters such as the total energy applied to the plant over the entire treatment time. Furthermore, determining if there is a time, intensity, or frequency threshold in the response of plants to various degrees of mechanical stimulation is an essential research direction.

(3) More study is needed to understand how plants detect sound fully. Because plants lack eardrums, it would be intriguing to learn how plants sense the intensity and wavelength of sound signals and incorporate this

information into plant cells. Despite the fact that plants can benefit from sound through their mechanosensory machinery and those plants emit ultrasound under natural field conditions, which is associated with high transient changes in xylem water tension, identifying an organ, specific protein, or ion that can recognize sound waves in plants will help us maximize the effect of sound processing in field experiments.

(4) Great strides have been achieved in the study of plant stress tolerance at the molecular level due to the advancement in molecular biology. Plant stress tolerance mechanisms, such as gene composition, expression regulation, and signal transduction, may be understood at the molecular level, and some essential genes from plant stress signal transduction have been cloned. These studies, however, are quite restricted in their understanding of the mechanisms of plant stress resistance. Hence, it is necessary to investigate the mechanisms of more plants responding to more stresses at the genetic level.

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Table 1 Response of seeds to various mechanical stimulation

Types of stimulation	Plant species	Plant responses	Reference
Sound	Okra and zucchini	Promoted germination	Creath and Schwartz, 2004
Sound	Compositae	Promoted germination rate	Duan et al., 2004b
Ultrasonic	Compositae	Increased the activities of α-Amylase, protease, and alcohol dehydrogenase, and the seed germination rate	Rasouli et al., 2020
Ultrasonic	Pepper	Increased the germination rate and germination potential of seeds by 10% and 18% respectively	Yang et al., 2011
Ultrasonic	Tomato	Increased the germination rate and germination potential of seeds by 15% and 14% respectively	Yang et al., 2011
Ultrasonic	Impatiens balsamina	Increase the germination rate	Chen et al., 2020
Ultrasonic	Chinese pink	Increase the germination rate	Chen et al., 2020
Ultrasonic	Ariplex. Lentiformis	Increase the germination rate	Sharififar et al., 2015
Ultrasonic	Zygophyllum. eurypterum	Increase the germination rate	Sharififar et al., 2015
Music	Alfalfa	Rock music reduced the germination of alfalfa seeds, while classical music, nature music, and waltz music promoted the germination rate	Youning and Howchiun, 2020

Table 2 Response of seeding to various mechanical stimulation

Types of stimulation	Plant species	Plant responses	Reference
Brushing	Tomato	Reduced the stem height of seedlings	Duman and Düzyaman, 2002
Brushing	Cucumber	Increased the accumulation of phytoalexin and induced resistance	Zhao et al., 2008
Brushing	Tomato	Improved the dry weight and compactness of stems and roots	Kim et al., 2018
Brushing	Tomato	Inhibited plant height	Jeong et al., 2020
Brushing	Lettuce	Increased the stomatal density on the leaf surface	Biddington and Dearman, 1985b
Brushing	Cauliflower, Lettuce, and Celery	Made the plant smaller and more compact; reduced the fresh weight, dry weight, leaf area, root length and branch number of the root system	Biddington and Dearman, 1985a
Wind	Tomato	Reduced the growth of plant height, leaf number, leaf area, chlorophyll fluorescence, and dry matter	Hwang et al., 2019
Wind	Tomato	Reduced the plant height of seedlings, improved the root stem mass, root shoot ratio, seedling quality index, as well as the mechanical indexes such as hardness and elasticity of seedling stems	Li et al., 2020
Pressure	Cucumber	Increased the activities of phenylalanine ammonia lyase (PAL) and peroxidase (POD) and induced lignin synthesis	Zhao et al., 2005
Touch	Rose	Increased the number of branchings from the most proximal metamers	Morel et al., 2012
Vibration	Spring Chrysanthemum	Increased relative water content, chlorophyll a, b, and protein content	Hassanpour and Niknam, 2019
Vibration	Coleus	Reduced plant height, increased stem elasticity, and resistance to fracture	Far et al., 2019
Sound	Chrysanthemum	Increased the activity and soluble protein content of roots	Jia et al., 2003
Shaking	Astragalus root	Reduced stem height and hardness, reduced leaf and biomass	Wang et al., 2008b

Table 3 Response of flowering to various mechanical stimulation

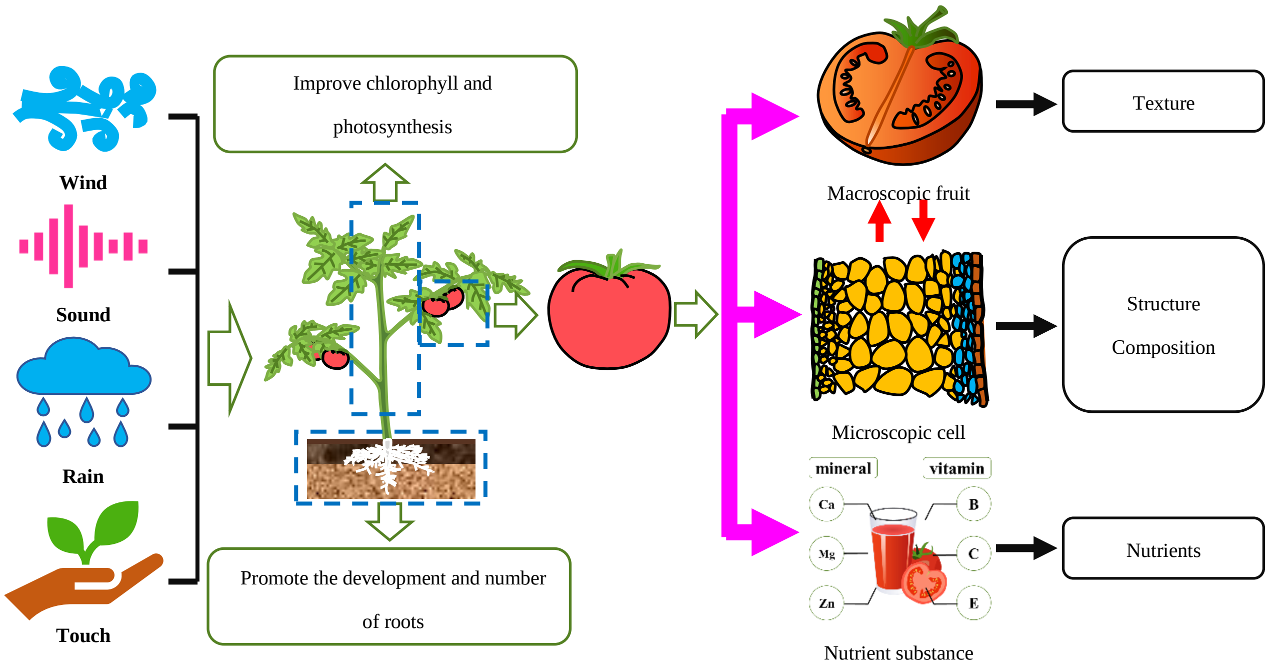
Types of stimulation	Plant species	Plant responses	Reference
Touch	Bignoniaceae	Promoted the closure of flower stigmas	Milet-Pinheiro et al., 2009
Touch	Phrymaceae	Temporarily closed the stigma of the flower	Jin et al., 2017
Wind	White mustard	Delayed flowering period	Retuerto and Woodward, 2001
Wind	Bellflower	No effect on the number of flowers	Sparke et al., 2021
Vibration	Peach	Reduced the number of flowers	Onguso et al., 2006
Brushing	Petunia hybrida	Reduced the number of flowers but flowering time was not affected	Jędrzejuk et al., 2020
Friction	Cucumber	Increased the number of female flowers of monoecious plants	Takahashi and Suge, 1980
Friction	Pepper	Reduced the number of flowers	Graham and Wheeler, 2017

Table 4 Response of fruit cells to various mechanical stimulation

Treatment	Plant species	Characteristics of cells	Reference
Oscillatory or acoustic stimulation	Kiwifruit	Decreased permeability of Actinidia cell plasma membrane	Yang, 2002
Acoustic stimulation	Chrysanthemum	The plasma membrane became loose, the surface charge density and hydrophobicity decreased, and the membrane fluidity increased	Duan, 2004a
Compress by agarose gel	Chrysanthemum	Protoplasts tend to elongate at 60-90° in the main direction of the stress tensor, and there is a nonlinear dose-dependent relationship between them	Zhou, 2006
Compress by agarose gel	Chrysanthemum	The cell wall of the chrysanthemum was thickened by stress	Wang et al., 2008a
Compress by agarose gel	Chrysanthemum	Mechanical stress can enhance the structure of cell wall	Zhou et al., 2007
Compress by agarose gel	Chrysanthemum	The cells divided along the direction perpendicular to the principal stress, and the thickness of the cell wall increased	Wang et al., 2008a
Acoustic stimulation	Chrysanthemum	The elastic modulus and viscosity of the plasma membrane of the callus increased with the increase of stimulation frequency	Wang et al., 2003b

Table 5 Response of fruit nutrition components to various mechanical stimulation

Treatment	Plant species	Plant responses	Reference
Acoustic wave	Chrysanthemum	Sound stimulation could increase the content of soluble protein, the absorption rate of calcium, and the content of ATP in Chrysanthemum callus	Wang et al., 2003b
Acoustic wave	Tomato	Sound waves can increase the content of lycopene, vitamin C, total sugar, total acid, and total phenol	Altuntas and Ozkurt, 2019
Acoustic wave	Dendrobium candidum	Sound stimulation may increase the absorption and utilization of carbon dioxide, thus increasing the content of polysaccharides	Liu, 2004
Acoustic wave	Dendrobium candidum	The content of polysaccharide and free proline can be increased, and the content of malondialdehyde can be reduced by acoustic treatment of Dendrobium candidum	Li, 2007



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715 **Fig. 1. Schematic illustration showing the potential effect of some mechanical stimulation methods on a horticultural plant**

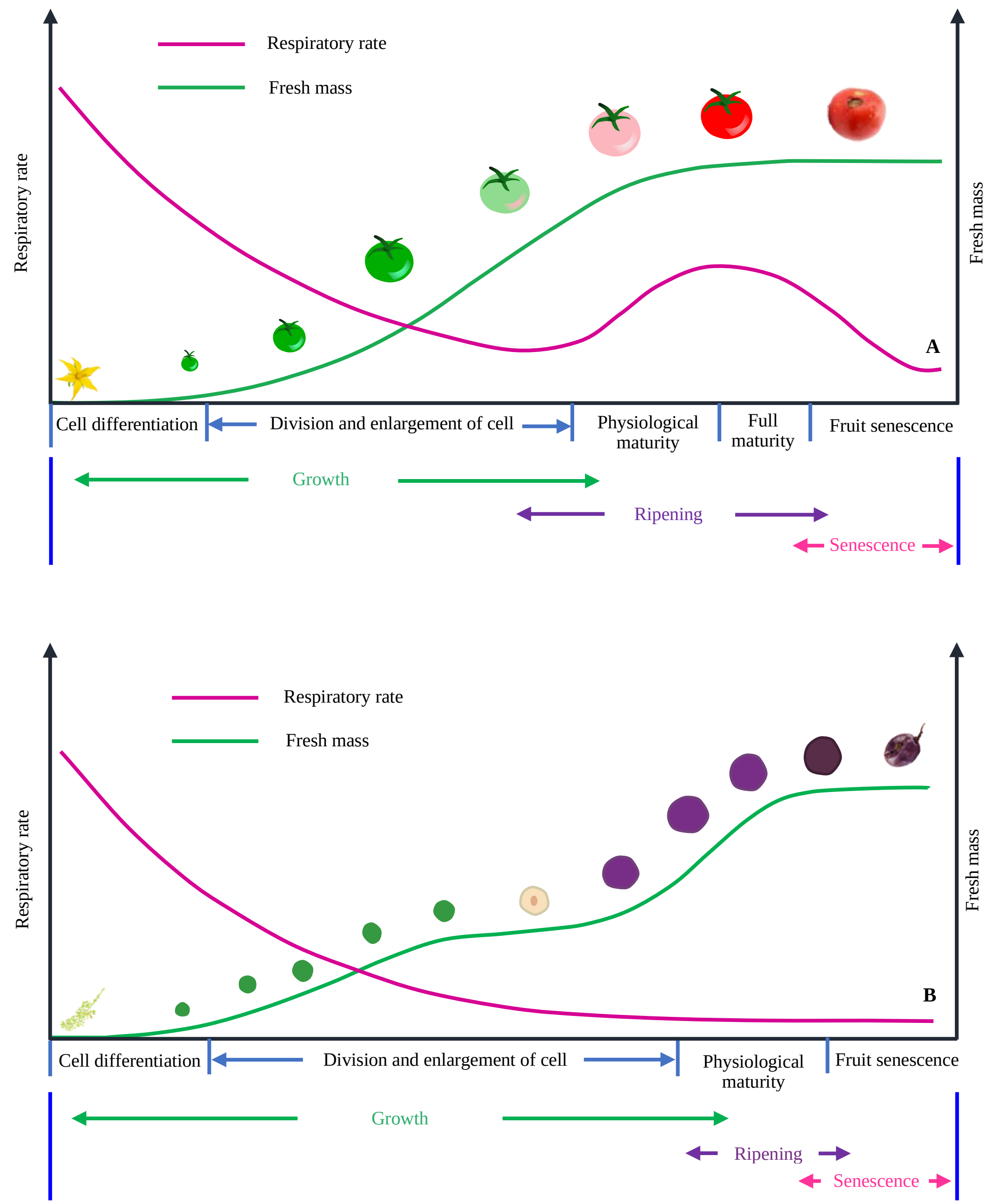

Fig. 2. Typical growth curves of tomato (A: single S-type curve) and grape (B: double S-type curve) (Ang et al., 2017)