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Thigmomorphogenesis – Control of plant growth by mechanical stimulation

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ABSTRACT

Controlled regulation of plant growth is a general prerequisite for the production of marketable ornamental plants. Consumers as well as retailers prefer stronger, more compact plants with greener leaves as these not only better meet a certain desired visual quality but also allow for a maximization of production per unit area as well as facilitation of packaging and transport. The same applies for the production of young vegetable plants. Special attention is paid to solid, compact and resilient plants that survive transport and planting without any problems. During the last decades plant growth control has mainly been achieved through the application of chemical plant growth regulators that generally interfere with the function of growth regulating hormones. However, there is an increasing demand to replace chemical treatments by other means such as the modulation of growth conditions, including temperature, light and fertilization. Alternatively, the application of mechanical stimulation has been shown to induce plant responses that yield some of the commercially relevant phenotypes including increased compactness, higher girth, darker leaves and a delay in flowering. The ability of plants to sense and respond to mechanical stimuli is an adaptive trait associated with increased fitness in many environmental settings. Mechanical stimulation in nature occurs e.g. through wind, rain, neighboring plants or predatory animals and induces a range of morphogenic responses that have been summarized under the term thigmomorphogenesis. We are only just about to begin to understand the molecular mechanisms underlying mechanosensing and the associated morphogenic changes in plants. However, a number of examples suggest that mechanical stimulation applied in a greenhouse setting can be used to alter plant growth in order to produce marketable plants. In this review will briefly summarize the current knowledge concerning the biological principles of thigmomorphogenesis and discuss the potential of mechanical growth regulation in commercial plant production especially with respect to organic horticulture.

1. Introduction

The quality of a newly produced ornamental and vegetable plant determines its marketability and eventually the profitability for the grower. Quality characteristics of young plants relevant to the consumer or grower are linked to their potential to withstand biotic and abiotic stresses, their developmental and yield potential, and their visual appearance, the latter determining their aesthetics (Heuvelink et al., 2004). In general, this means that plants are rather compact without too long internodes, have dark green leaves, and many flowers. In addition, the grower needs to accommodate as many plants as possible on a given greenhouse area to make transplant production economically viable, which also benefits from a compact plant architecture. Furthermore, such plants have a long salable period after they reached market size and shorter or compact plants may be beneficial for efficient marketing and transportation as they require less space and will be less prone to damage during handling. Therefore, there is a commercial need for treatments which reduce plant growth and produce a more compact and uniform product.

Over the past decades, treatments with chemical plant growth regulators (PGRs) that produce some of the desired quality characteristics have been widely used in floriculture (Rademacher, 2015). The aim of PGR application is to reduce plant size in a controlled way, without extending production time or being phytotoxic. The general mode of action of PGRs currently in use to reduce plant growth is the inhibition of gibberellic acid (GA) biosynthesis. GA is a phytohormone that positively controls many aspects of plant growth and development (Sun, 2008). Thus, GA treatment has been used to achieve accelerated growth and development in certain vegetable production settings. For example, GA application to artichokes during flowering time allows for an earlier harvest to take advantage of the favourable winter market prices (Schrader, 1994) Despite their ease of application and the moderate

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cost of PGRs, their use contradicts the global trend toward sustainable farming with fewer chemicals. Consumers might also be concerned when the plants they bring to their home were subjected to chemical treatments and regulatory issues restrict the use of PGRs in vegetable production. Thus, novel approaches to control growth of greenhouses cultivated plants which do not require the use of chemicals are urgently needed. Besides breeding for more compact cultivars, which is a long term endeavor, crop cultivation practices influencing plant growth behavior have been suggested as alternative methods. These include the tight control of growth conditions in terms of temperature, light quantity as well as quality, and availability of mineral nutrients (for a recent review see Bergstrand (2017).

It has been recognized at least since the ancient Greeks that mechanical stimulation (MS), such as touching, bending and shaking, affects the growth and development plants, including crops (Darwin and Darwin, 1881; Jaffe, 1973; Jaffe and Galston, 1968; Jaffe et al., 2002; Mitchell, 1996; Telewski, 2006). Thus, application of MS has been proposed as an alternative means to control plant growth in agricultural and horticultural settings (Garner et al., 1997). Indeed, Japanese farmers have historically used the application of MS by treading, trampling, or stamping of wheat and barley seedlings in a process called mugifumi (Iida, 2014). The treatment of autumn-sown seedling by mugifumi was known to prevent spindly growth, strengthened the roots, shortened plant height, and eventually improved yield (Iida, 2014). However, in order to make growth regulation by MS widely applicable in horticulture, a thorough understanding of the physiological consequence of the treatment is required as well adoption of the technique to make it, flexible, easy to use and cost effective for a variety of different ornamental and vegetable plants.

In this review we will briefly summarize the current knowledge about the physiological and molecular basis of plant responses to MS and then discuss the possibilities and perspectives to use mechanical growth regulation in horticulture.

2. Thigmomorphogenesis – ecological and physiological considerations

Due to their sessile life style plants are persistently challenged by a wide range of environmental stresses from which they cannot escape simply by relocation. Thus, they have evolved particular complex signaling response networks that allow withstanding adverse conditions to a large degree by dynamically adjusting their physiological and developmental state. These environmental stresses and perturbations include those of mechanical nature. Among the main sources of external mechanical stress (MS) for plants are wind, rain, physical barriers and predation. Plants perceive and respond to MS on short term, illustrated by the rapid leaf folding of *Mimosa pudica* upon touch, as well as over longer time scales. Long term responses to MS include developmental alterations such as a reduction in plant growth coupled to an increase in radial expansion, a delay in flowering levels and accelerated senescence (Braam, 2005; Braam and Davis, 1990; Jaffe and Forbes, 1993). Other responses include alterations in chlorophyll content and hormone levels, increased stress resistance and reduced transpiration rates (Biddington, 1986; Chehab et al., 2009; Jaffe and Forbes, 1993). Jaffe (1973) coined the term thigmomorphogenesis to describe the physiological and morphological changes of a plant upon perception of MS. Meanwhile, this phenomenon was documented in all types of plants, shrubs, trees, grasses, and dicot herbs, indicating its wide conservation (Jaffe and Forbes, 1993). Thigmomorphogenesis can be considered as an adaptive response allowing individual plants to mitigate the different levels of MS that occur in their natural environment. The advantage of this is that shorter and stronger plants are less easily damaged by natural mechanical stresses (especially wind) than their taller, more slender counterparts.

Although thigmomorphogenic responses to MS are generally perceived as long term changes to recurring stress conditions, several short time scale studies indicate that transient cessation of growth can occur very rapidly upon a mechanical stimulus. Rubbing of the first true internode of young bean plants for five times results in a complete cessation of growth three to six minutes after the stimulus has been applied with growth resuming after 15 min (Jaffe, 1976a). The elongation growth of maize seedlings completely stopped for 38 min only six minutes after a rubbing stimulus (Jaffe et al., 1985). Transient controlled stem bending of tomato plants led to a complete stop in elongation growth for 60 min only a few minutes after the bending was applied. Thereafter it took 120–1000 min to recover a rate of elongation similar to the unbend control (Coutand et al., 2000).

While these short term studies demonstrate that the first effect of MS perception is a rapid and transient cessation of growth, isolated MS exposure does not seem to affect plant growth and biomass accumulation on the long term. However, continued stem flexing of tomato plants over a period of 6 weeks for one minute per day led to an increase in root/shoot dry weight ratios compared to unflexed control plants, but flexed plants and controls did not differ significantly in total leaf area, root length, or total biomass (Garner and Björkman, 1999). This indicates that MS can lead to a change in carbon partitioning from the shoot towards the roots. Arabidopsis plants whose rosette leaves were gently moved back and forth repeatedly over the course of their development had shorter petioles, began to bolt later, and developed shorter bolts than untreated plants (Braam and Davis, 1990). Applying vibrations to plants of *Capsella bursa-pastoris* for 60 s every day during the course of growth to maturity shifts the allocation of biomass to the root system, again indicative for a change in carbon allocation (Niklas, 1998).

Beyond the macroscopically visible morphogenic changes of plants, MS also affects plant composition. Rubbing the internodes of tomato plants led to an increased activity of enzymes involved in the lignin synthesis pathway and which was described to correlate with an enhancement in lignification (Saidi et al., 2009). A response that likely serves to increase stem stiffness to better withstand MS. Stress lignins synthesized in response to MS displayed a distinct structure relative to constitutive lignins with a substantial enrichment in syringyl units (Saidi et al., 2009). A rapid response that has been observed after rubbing internodes of *Phaseolus vulgaris* was the deposition of callose within the phloem sieve tube plates (Jaffe et al., 1985). Callose deposition exhibited a major peak 6 h after rubbing and then gradually disappeared over a period of three days. Mechanical stimulation of papaya seedlings almost completely blocked the accumulation of anthocyanins (Porter et al., 2009). The biosynthesis, accumulation and transport of anthocyanins are dependent on multiple enzymes and substrates of the phenylpropanoid pathway some of which are also shared with lignin biosynthesis. The authors proposed that touch-driven lignin production compete for the same substrates and sharply decreases anthocyanin biosynthesis (Porter et al., 2009).

A recent study by Benikhlef et al. (2013) showed that soft mechanical stimulation of Arabidopsis plants without detectable signs of tissue damage led to a strong resistance towards the broad host range fungal pathogen *Botrytis cinerea*. This was accompanied by rapid changes in intracellular calcium concentrations and a release of reactive oxygen species. In addition, changes in cuticle permeability led to the release of biologically active diffusates from the leaf surface capable of inducing resistance to B. cinerea in untreated control leaves. Thus, the authors conclude that Arabidopsis can detect and convert gentle forms of mechanical stimulation into a strong resistance response towards pathogens.

3. Cellular signaling in MS perception

In order to adequately respond to changes in their environment, plants must be able to receive and process signals at the cellular level. As in all other living systems, this requires a signaling cascade consisting of a receptor to perceive the stimulus and which upon activation