

Plant Response to Mechanical Stress

Zeinolabedin jouyban

Young Researchers Club, Borujerd Branch, Islamic Azad University, Borujerd, Iran

Corresponding author Email: abed_jouyban88@yahoo.com

ABSTRACT: Mechanical stress vectors of nature include wind, rain, hail, and animal movements. Production agriculture and landscape practices provide further physical insults to plants in the form of pruning, pinching, tying, guying, and trimming. Urban high-rise buildings create air turbulence and downdrafts that permanently entrain trees and shrubs to growth habits reminiscent of natural plants inhabiting seacoasts and mountain slopes. Appreciation for wind per se as a powerful factor limiting plant development has been slow to develop. It is easy to overlook the mechanical aspect of wind and precipitation on plant form and growth habit because they are not always present and because many environmental stress factors coexist with wind in the outdoor environment. The influences of other environmental stress factors on plants often mask or negate the influence of mechanical stress. Confounding natural factors include airborne sea salt, desiccation, and evaporative chilling, all of which accompany wind. Only if controlled mechanical stresses (e.g., shaking, handling, flexing) are applied to plants growing in the wind-protected confines of a greenhouse or growth chamber is it possible to separate effects of mechanical stress per se from those of other environmental stresses, such as heat, cold, drought, flooding, and/or mineral deficiencies. It is surprising how sensitive plant growth can be to brief episodes of mechanical stress, especially if the plants are grown otherwise undisturbed in a stress-free environment.

Keywords: Mechanical stress, Environmental stress, Confounding natural, Plant growth

INTRODUCTION

Deviations from the physiological normal type are regarded as reactions to suboptimal or damaging quantities or intensities of environmental factors, i.e. situations for which we use the term stress. Thus stress and reactions caused by it (stress reactions) can be used as a measure of the strength of the stress on a scale of intensity, ranging from deficiency to excessive supply. Environmental factors deviating from the optimal intensity or quantity for the plant are called stress factors. The optimal quantity can, in fact, be zero, e.g. with xenobiotics. Stress factors which could potentially influence the plant are listed in Figure 1.

Several studies have shown that low-amplitude mechanical vibration in the frequency range of 50 to 60 Hz actually stimulates rather than inhibits cumulative plant growth (Takahashi et al., 1991). Such vibration for 30 min each hour for 7 days stimulated growth in size and mass of tomato seedlings 10% to 15% after 10 days of treatment (Akers and Mitchell, 1980). Mild growth stimulation occurred in various horticultural and agronomic crops after vibrating or slowly shaking them almost continuously. Japanese growers apply vibration, and even music,

below benches and position speakers in contact with components of commercial hydroponic culture systems. The vibroacoustic frequencies are claimed to stimulate photosynthesis, crop growth, and yield.

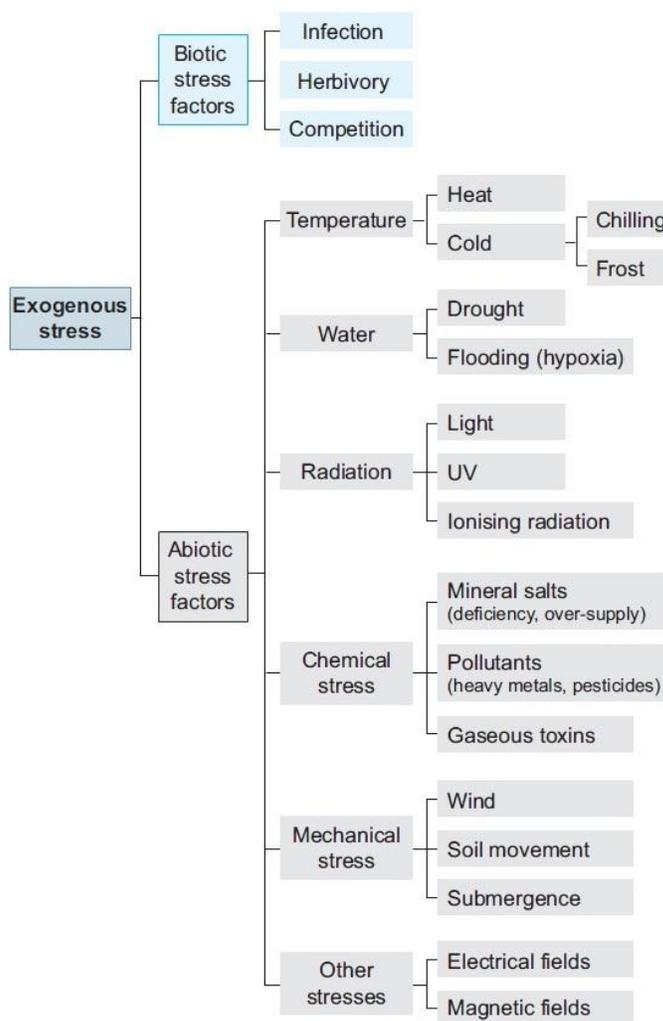


Figure 1. Biotic and abiotic environmental factors creating stress for plants

EFFECTS ON PHOTOSYNTHETIC PRODUCTIVITY

Less frequent episodes of seismic stress are much more effective for inhibiting photosynthetic productivity than is continuous stimulation (Pappas and Mitchell, 1985a). Soybean plants shaken for only a few seconds once or twice daily became proportionately dwarfed copies of undisturbed controls. A mild reduction in net assimilation rate (NAR) by shaken soybean plants was not quite offset by a compensatory increase in leaf area ratio (LAR). The resulting modest reduction in relative growth rate (RGR) according to the relationship $RGR = NAR \times LAR$ caused a lag in cumulative growth of seismostressed plants that was compounded each day stress was applied.

These decrements of lagging growth quickly added up to retarded growth in biomass, photosynthetic surface, and plant size. To determine what contributes to the stress-induced decrease in NAR, net photosynthesis was measured within a whole-plant, gas-exchange cuvette while the entire cuvette and its plant contents were shaken (Pappas and Mitchell, 1985b). Net carbon assimilation dropped within minutes of the onset of a brief shaking episode, and it took at least 40 min for photosynthesis to recover to the rate of nonstressed controls.

Leaf resistance analysis indicated that stomatal resistance for H₂O vapor and CO₂ diffusion increased 20 min after a brief shaking episode, especially on lower leaf surfaces. In contrast, mesophyll resistance was unaffected by

shaking. Thus, the combination of retarded expansion of new leaves plus the temporary reduction in stomatal aperture for expanded leaves contributed to the lighter mass of shaken soybean plants over time.

EVIDENCE FOR HORMONAL INVOLVEMENT

Observations that mechanical stress responses of plants are dose dependent (Jaffe, 1976), that the responses are saturable (Beyl and Mitchell, 1977), and that one or more morphogenetic stimuli are transmissible from physically disturbed plant parts to nondisturbed parts (Erner et al., 1980) have been taken as evidence for hormonal mediation. Furthermore, many symptoms of seismo- and thigmomorphogenesis can be either mimicked or antagonized by chemical agents, including exogenous hormones (Biro and Jaffe, 1984; Boyer et al., 1983; Erner and Jaffe, 1982).

Ethylene

Ethylene (C₂H₄), the so-called "stress hormone," has received the most attention of all the phytohormones with respect to mechanical stress growth regulation. Inhibition of stem elongation, stem swelling, loss of gravitropic sensitivity (Goeschl et al., 1966), and leaf epinasty (Jaffe, 1973) all are reported actions of C₂H₄ or mechanical stress.

Furthermore, mechanically stressed plants release C₂H₄ at an elevated rate following a 1-h lag (Biro and Jaffe, 1984). However, increased activity of the enzyme 1-aminocyclopropane-1-carboxylic acid (ACC) synthase, which catalyzes production of the immediate precursor of C₂H₄, begins within 30 min of a stress episode. Treatments known to inhibit C₂H₄ synthesis or action also prevent certain plant responses to mechanical stress. For example, cobalt blocks the conversion of ACC to C₂H₄ (Boyer et al., 1986). Lithium, a suppressor of cell-wall-bound peroxidases, negates mechanically induced stem dwarfing of *Bryonia dioica* L. (Boyer et al., 1983), but aminoethoxyvinylglycine inhibits only the lateral swelling component of thigmomorphogenesis (Biro and Jaffe, 1984), suggesting that something besides C₂H₄ mediates the complex of overall plant responses. Hypobaric pressures also negate some plant responses to mechanical stress (Jaffe, 1980), presumably by removing C₂H₄ from plant tissues.

Auxin

The evidence for auxin involvement is that supraoptimal auxin mimics mechanical stress effects (Erner and Jaffe, 1982), presumably by stimulating ACC oxidase and subsequent production of C₂H₄. Thigmic stress of dark-grown pea (*Pisum sativum* L.) seedlings reduces elongation of subsequently cut pea stem sections floated on auxin-containing solutions, provided that sufficient minimum time elapses between rubbing the plumule and cutting internode sections (Mitchell, 1977). Because polar auxin transport is inhibited substantially by mechanical stress or C₂H₄, it is likely that endogenous auxin cannot move below the point of mechanical stress application in an unhardened pea stem. Auxin accumulates above the point of thigmic stress but depletes below that point. Irritation of stem tissue by rubbing also activates membrane-associated peroxidases that destroy natural auxin like an IAA oxidase (Hofinger et al., 1979). Depending on the point of mechanical stress application, elongating cells in the growth zone are inhibited because the growth hormone auxin is either depleted or supraoptimal within those cells.

Gibberellins

One of the most dramatic correlations between mechanical stress and phytohormones involves the gibberellins. When only the shoot tips of sunflower (*Helianthus annuus* L.) plants were thigmo-stressed, all extractable gibberellin (GA)-like activity disappeared from those tissues compared to undisturbed controls, which contained substantial amounts of GA activity (Beyl and Mitchell, 1983). When sunflower plants were shaken, GA-like activity disappeared mainly from flapping leaves. The tissue that is physically disturbed the most seems to undergo the greatest loss of gibberellin. *Phaseolus vulgaris* seedlings lost virtually all GA activity when they were mechanically perturbed (Suge, 1978).

Exogenous GA₃ prevented the usual stunting of rubbed bean stems (Jaffe and Biro, 1979). The combination of GA₄₊₇ nullified the tendency for mechanically stressed cucumber (*Cucumis sativus* L.) plants to favor femaleness of monoecious flowers (Takahashi and Suge, 1980). The conclusion of these studies is that mechanical stress or C₂H₄ favors femaleness of cucurbit flowers, whereas GA favors maleness. Furthermore, many chemical growth retardants are GA biosynthesis inhibitors, and the effects of growth retardants often resemble effects of mechanical stress.

Other phytohormones

Reports of improved drought tolerance in beans (Moore, 1979) and prevention of drought-induced pithiness in tomato stems by mechanical stress suggest a possible role for ABA in mechanical stress action, similar to its known role in drought tolerance. ABA level rose 3-fold in bean stems that had been manipulated physically (Erner and Jaffe, 1982). Exogenous ABA can mimic effects of mechanical stress or C₂H₄ treatment in terms of retarded stem elongation, but unlike the other two treatments, ABA does not affect internode diameter (Jaffe, 1985). Mechanical stress increased cytokinin activity in xylem exudate from sunflower roots, but directly diminished it in leaves, suggesting that stressed plants adapt to ensure a continued supply of cytokinins for growth and development (Beyl and Mitchell, 1983).

Physical stimuli and ion gating

The most direct evidence for rapid increases in intracellular Ca²⁺ concentration in response to mechanical perturbation come from studies with tobacco (*Nicotiana tabacum* L.) plants genetically transformed to express aequorin, a Ca-sensitive, bioluminescent protein that occurs naturally in jellyfish [*Aequorea victoria* (Forakalea)] (Knight et al., 1991). This luminescent protein emits blue light in the presence of Ca and coelenterazine, a luminophore, and can be used to measure quantitative cytosolic Ca changes in transformed plant cells. These transformed cells can be differentiated into transformed plants that give off proportional pulses of blue light whenever cytosolic Ca content increases by a given increment.

Transformed tobacco seedlings placed within the cuvette of a luminometer gave off a pulse of blue light when exposed to puffs of air from a syringe (Knight et al., 1992). Luminous intensity was proportional to the force of air, or touch, applied to the seedlings. These results have been interpreted as an indirect, quantitative measure of the amount of Ca released suddenly into the cytoplasm in the presence of aequorin. The plasma membrane channel blocker lanthanum, and the stretch channel blocker gadolinium, failed to block the wind-induced increase in cytosolic Ca.

(hence, blue pulse detected), but they did block the same response for cold shock. However, ruthenium red, a blocker of organelle and endomembrane Ca channels, abolished the wind-induced cytosolic Ca increase but failed to block the same response for cold shock. Thus, wind-induced elevation of cytosolic Ca probably is of intracellular origin. According to current models, spectrin-like linkers connect various stretch-activated ion channels in membranes (Guharay and Sachs, 1984). Membranes become distorted when force is applied to them, and the inelastic linkers tug at their points of attachment to channel proteins. Tugging opens channels briefly and allows specific ions, like Ca²⁺, to flow from mitochondria, endoplasmic reticulum, or other internal membranes into the cytoplasm, where they activate calmodulin. However, since initial perception of mechanical stress occurs first outside the cell, that force must be transmitted through the extracellular matrix, across the plasma membrane, and signaled along to stretch-activated Ca²⁺ channels within the cytoskeleton. Proteins called "integrins" are physically connected to cell wall proteins on the outside of the plasma membrane and have domains extending into the cytosol where they can bind to actin-like filaments and other elements of the cytoskeleton to transmit physical stimuli outside the cell to stretch channels inside (Fleurat-Lessard et al., 1988).

Thus, the plant cell is emerging as a highly integrated structure for mechanoperception and transduction of physical signals into biophysical responses involving ion compartmentalization, water status, and subsequent molecular and physiological changes.

CONCLUSION

Plants are bound to places. They, therefore, have to be considerably more adaptable to stressful environments and must acquire greater tolerance to multiple stresses than animals and humans. This is shown very clearly by the limitations in the distribution of particular types of vegetation.

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