

## Thigmomorphogenesis: the effect of mechanical perturbation on plants

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### Abstract

Thigmomorphogenetic responses occur in many environmental settings. The most pronounced effects are found under conditions of extremely high rates of turbulent wind or water flow. However, it is an ubiquitous phenomenon, since mechanical perturbations are to be encountered under all but the most stringent laboratory conditions. Our present understanding of these phenomena is the result of studies at the ecological, anatomical, physiological, biochemical, biophysical and molecular biological levels.

### Introduction

Thigmomorphogenesis is the physiological and morphological adaptation by a plant to environmental mechanical influences, and has been recognized at least since Theophrastus [78]. A plant cannot quickly move away from its external environment, as an animal can, so it must have means of adapting to environmental changes in order to survive. Among these environmental stresses and perturbations are those that are mechanical in nature. They include wind (Fig. 1), rubbing by animals and plants (Fig. 2A and B), constricting of woody plants by coiling vines (Fig. 2C), and visitation of flowers by pollinators. Mechanical Perturbations (MP) act as external mechanical stimuli, creating changes in plants. As a result, plants have developed both sensory and growth mechanisms with which to detect and respond to changes in MP such as the wind [54, 22], vibrations [73], rain or other types of water spray [84], trampling by people or other animals [16], wind shade caused by other plants [36] and reactions to gravity acting on leaning plants [23]. Another important cause of thigmomorphogenesis is the rubbing of one plant

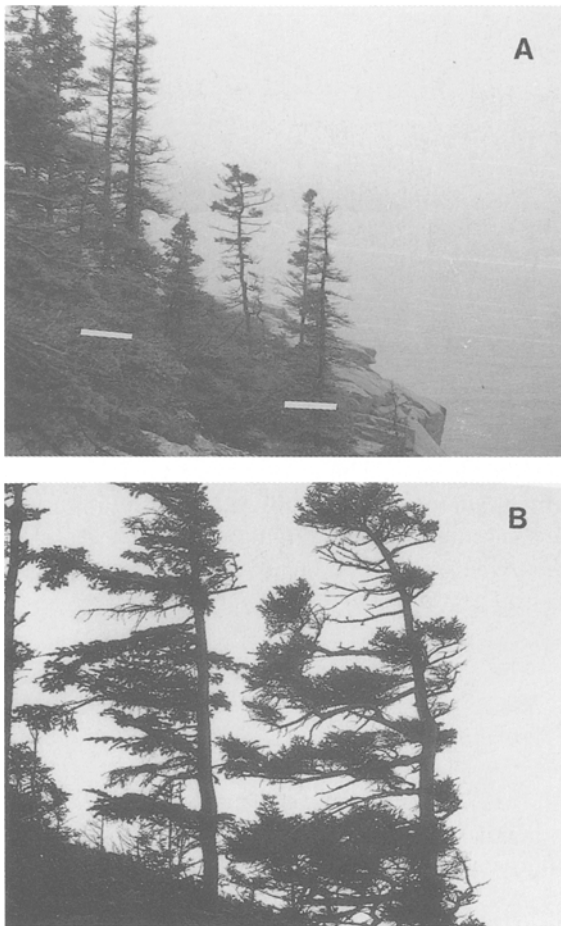
or plant part against another (Fig. 2A and B). These thigmomorphogenetic changes can include decreases in elongation [43, 76] (Fig. 1 and 3), increases in lateral enlargement [44, 76] (Fig. 2 and 3), increased senescence [25] and decreased susceptibility to various stresses [50]. The growth responses to MP come under the general rubric of thigmomorphogenesis, and are associated with decreases in photosynthesis coupled to increases in respiration [3, 27].

Probably the most primitive response to MP is found in single celled motile organisms, which reverse their direction when they bump into something [58]. It has been postulated that stretch activated ion channels in the plasma membrane of such organisms are the sensory mechanism [64]. In any event, responses to fluid flow have been reported for aquatic plants [81] and these responses (e.g., ruffled laminate margins which permit undulation, or high degree of dissection of foliage) may be the precursor of thigmomorphogenesis in terrestrial plants. This review will consider the ecological effects of wind and other mechanical perturbations on the aerial parts of terrestrial plants.

### Ecological aspects of MP

Responses to MP can be seen in single leaves, stems

\* This contribution is dedicated to Art Galston, who gave me (M.J.) the freedom to begin my exploration of thigmophysiology.



*Fig. 1.* The appearance of coniferous trees on Atlantic coastal cliffs (Maine) (A) and near the peak of Roan Mountain in North Carolina (B). In both cases, the prevailing wind is from the right. In "A", thigmomorphogenesis can be seen as a shortening of the stems, as indicated by their length observed from their bases (white lines). In "B" the flagging is formed during the summer by the bending backward, toward the leeward side of the tree, of extremely plastic, young branches [76].

and petioles, as well as on the level of the whole plant. On a larger scale, plant responses to MP such as wind can affect the ecological aspects of a community such as vegetation zonation at the mountains and on coastal regions (Fig. 1 and 3). For various reasons, it has become important to know the impacts of weather including wind, on vegetation. Although experiments under controlled conditions are valuable, it will always be important to complement the controlled studies with field observations. The ecological aspects of MP such as

wind involve such elements as vegetative zonation at the mountains and at the sea coast. In mountainous areas, the vegetation occurs in zones in relation to altitude [19]. Measurements of yield of individual crops in upland areas show a diminishing performance with increasing altitudes [38]. Furthermore, the vitality of individual members of a species frequently decreases along an altitudinal cline. Many species of plants only occur on mountains where they have adapted specific means to deal with their environment. Plants such as heather are affected by the wind, but they can withstand wide variations in windspeed due to evolutionary adaptations [6]. Vegetation in relation to altitude cannot be due to a single factor; soil factors, as well as the weather play roles. Hence, it is difficult to dissect the effects of wind from the effects of cold, dehydration, etc. In general, the plants at or just below the tree line exhibit some form of Krumholz sculpturing (i.e., wind-induced deformation) (Fig. 1). This ranges from brushing or slight flagging to severely wind-clipped and/or carpeted plants [28]. We can conclude that the wind plays an important part in this sculpting because, comparable effects can be found in Elfin tropical rain forests [55]. These forests are characterized by a dense growth of short, thick stemmed, gnarled trees, whose crowns are tightly packed into a single layer of canopy. Plants that have undergone moderate to severe thigmomorphogenesis are also found on the sea coast, where the air pressure is higher than on mountain tops and the temperature is temperate or even tropical.

Vegetation in coastal situations is often wind-clipped and dwarfed, showing similarities to mountain zonation. In a sea level situation, the impact of salt-laden air may be severe on the plants, whereas at the mountain tree line the late autumn high winds may contain ice crystals which "machine gun" the plants. Wind velocity affects the quantity of salt from ocean water, that could be trapped in the onshore wind. The velocity of this wind will decrease with the distance from the shore, and the salt it contains will affect plant growth [10]. Salt can be toxic to plants and cause symptoms resembling "scorched" vegetation [31]. The results of these studies suggest that the wind-blown salt, as well as the wind itself is an important factor in a coastal environment. Cuticular abrasion by the wind, as well as wind blown sand can also increase the



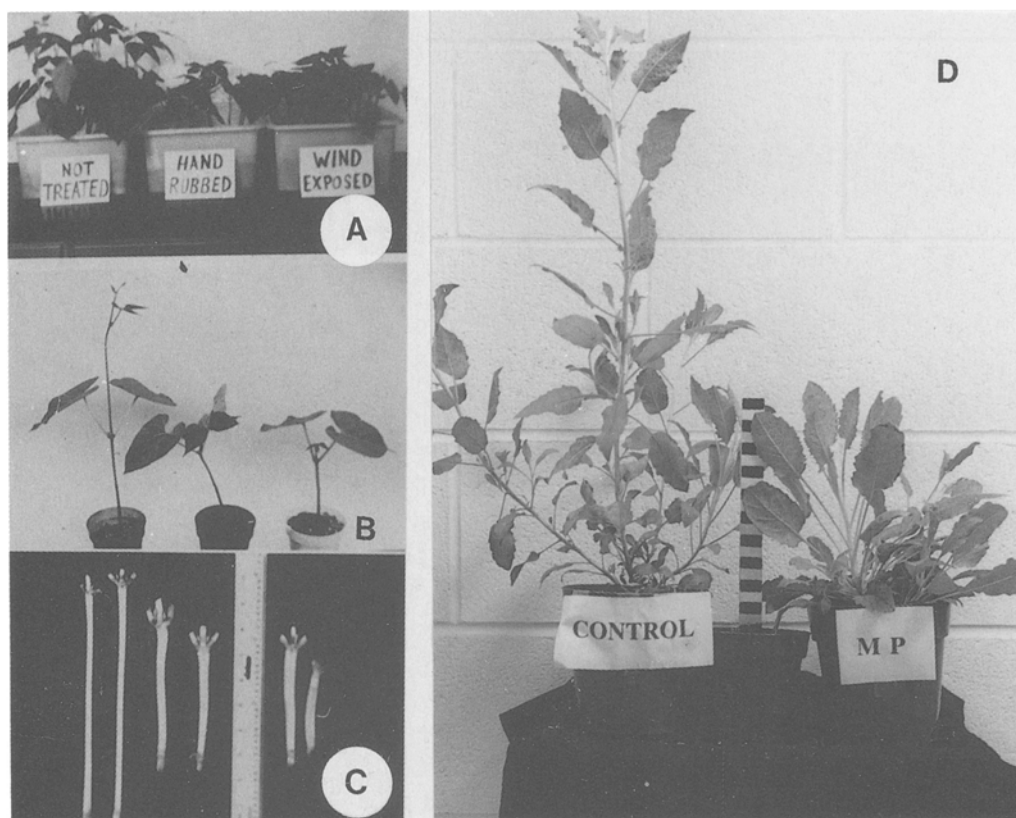
Fig. 2. Different examples of thigmomorphogenesis in woody plants. (A) Self-grafting of two stems of the same tree due to rubbing caused by wind sway. (B) The horizontal branch of the cherry tree rubbed back and forth against the stem of the oak, causing thickening of the branch (between the white pointers). (C) Swelling of a tree stem due to constriction by a twining liana. The narrower, normal thickness of the stem can be seen above the constricted region.

susceptibility of the plant to this salt toxicity. On cliffs overlooking the ocean, however, where the salt may not be a problem, there is still considerable flagging of trees and carpeting of vegetation. Thus, we may conclude that the wind is an important, if not the most important factor in the sculpturing of Krumholz vegetation. An account of species zonation in a coastal area of North Carolina is given by Boyce [10]. The immediate coastal vegetation is treeless, while an herbaceous and shrubby zone occupies the positions next to the sea. A shrub, *Ilex vomitoria* shows considerable wind shaping which Boyce [10] related to the degree of exposure to oceanic winds. Coastal areas exposed to the prevailing sea wind experience very high

wind speeds and a rapid increase in wind speed with distance above the ground [28]. This is due to the lack of surface roughness, and therefore turbulence, over the ocean.

#### **MP as a hardening agent against mechanical injury and other stresses**

When plants are exposed to less than severe winds, they become hardened to very strong winds [22]. The obverse of this is that when plants are sheltered from winds, they become more susceptible to rupture by strong winds. Thus, when saplings of *Liquidamber styraciflua* [59] or *Pinus taeda* [17] were prevented from swaying by guy wires, they



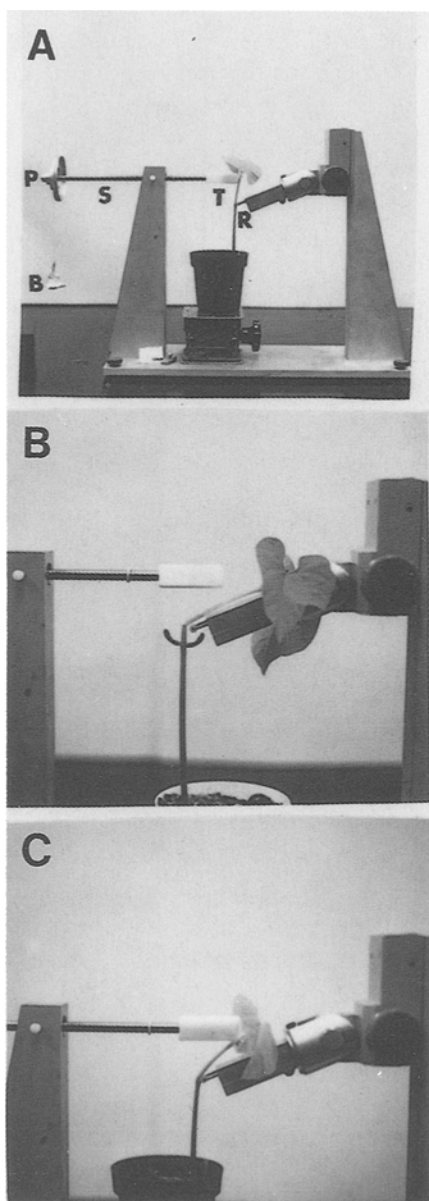
**Fig. 3.** Thigmomorphogenesis in herbaceous plants. (A) Appearance of bean plants whose first internodes were not rubbed or rubbed once daily for 10 days, and which were grown just near the glass wall of the greenhouse. These plants can be contrasted or compared, respectively, to plants grown just on the other side of the glass, exposed to wind (B and C). Bean plants (B) and their first internodes (C) of, from left to right, control plants, not mechanically perturbed; plants given MP by gently rubbing the first internode once a day for 5 days; plants treated with one 50  $\mu$ L drop of ethrel solution on the first internode, once a day for 5 days. Note the decrease in elongation and increase in thickness due to both MP and ethrel. (D) Control and rubbed plants of the Golden Aster (*Chrysopsis gossypina* M. (Michaux). This plant grows in the front of and behind sand dunes fronting the Atlantic Ocean on the North Carolina coast. These plants were grown and treated in the laboratory, but mimic the appearance of wild plants growing behind (and sheltered by) the sand dune (left) and the plants growing in front of the sand dune (and exposed to the offshore wind) (right).

broke more easily when exposed to wind than did wind-hardened controls. Jacobs [39] showed that when trees are supported over a number of years, so that no MP such as swaying occurs, they were no longer stable when the props were removed. These trees that were kept from moving, developed trunks that were taller and thinner than those exposed to the wind. In nature, the trees at the edge of a stand become hardened by winds. When they are removed, the weaker, slender trees that had been sheltered by them are quite easily knocked over by strong winds (i.e., a windfall) [54].

Laboratory studies have been performed to elucidate this response. Bean plants which have been given MP by flexing, rubbing or being wind-

blown, bend but do not break, whereas the controls are much more brittle, and rupture [51] (Fig. 4). MP-treated pine, *Bryonia* and tomato seedlings are able to resist rupture not because they become more flexible, but because they become much stiffer than controls [77, 42, 33]. Thus, at least two types of biomechanical properties can be affected by MP to cause greater resistance to mechanical rupture: elastic resilience and flexural stiffness. These changes are correlated with comparable increases in lignified xylem [42, 77] as well as cell wall polymers [47].

Other important changes occur in trees due to the MP effect of wind. The sculpturing of the canopy of trees in a prevailing wind, produces a



*Fig. 4.* A experiment demonstrating the mechanical hardening effect of MP. The photograph in (A) shows how the bottom of the first internode was pressed against point "R" by applying a force from the left at point "T". In (B) a control internode has snapped with the application of about 1 N of force. In (C), an internode which had been rubbed 10 times, once each day for 5 days bends but does not break under the same force load as the plant in (B).

streamlined airfoil, which presents minimal resistance to the force loading of the wind [76]. In addition to thickening of the trunk in line with the direction of the wind, a "plywood" effect also is produced in the trunk, by inducing the grain helix angle to run in different directions in consecutive years. This also serves to strengthen the trunk against rupture [76].

Wind also plays a role in the formation of reaction wood which develops when the trunks of some species are displaced from the vertical position. Wind-induced swaying of the stem may stimulate the cambium and cause compression wood to form in gymnosperms [83]. In a study of conifers, Bannan and Bindra [4] found that on the side of the tree facing the prevailing wind the tree rings were narrower than on the side in the lee of the wind. Trees seem to adapt to the prevailing winds so that they can remain stable [28].

Another interesting phenomenon that has been observed, is the ability of MP to harden plants to injury by stresses other than mechanical. Thus, bean plants given MP are more resistant to drought and frost stress than controls [70, 50] and MP-treated pine saplings are more resistant to frost injury than controls [50]. One possible reason for these responses involves similar changes in membrane lipids caused by MP [21] or other stresses [88, 65, 89, 60].

Many plants undergo autolysis of their pith either as part of their normal development, or in response to stress. This hollow-stemmed condition is called "pithiness". The development of pithiness seems to be associated with rapid growth [48, 49]. An interesting effect of MP is to inhibit the development of pithiness, probably via the production of ethylene [62].

### Morphogenetic effects

Most plants have evolved morphogenetic responses to MP. For example, wind affects the growth rate of various species [85, 86, 87]. However, there are many different types of adaptive changes illustrated by different species. Venning [80] studied the effect of wind on the development of collenchyma in celery. He found that the wind motion stimulates the development of collenchyma within the bundles, resulting in larger areas of collenchyma. In an

experiment by Whitehead [85], plants were grown at windspeeds of 0.45, 4.02, 8.49, or 14.75 m s<sup>-1</sup> for 30 days. The higher wind speeds caused a retardation of growth of the whole plant, although the roots were inhibited less than the shoots. This resulted in a larger relative root system, which provided greater anchorage as well as greater water uptake. The decrease in photosynthesis that resulted was due to development of smaller leaf areas, and not to a reduction of photosynthetic rate per unit area.

From a physical point of view, turbulent wind will cause more flapping of the leaves (and therefore more MP) than will laminar wind flow. Even when prevailing wind (i.e., moving straight in one direction) impacts a leaf, what might have been laminar flow is often converted to turbulent flow by the flapping of the leaf, caused by its morphology [82].

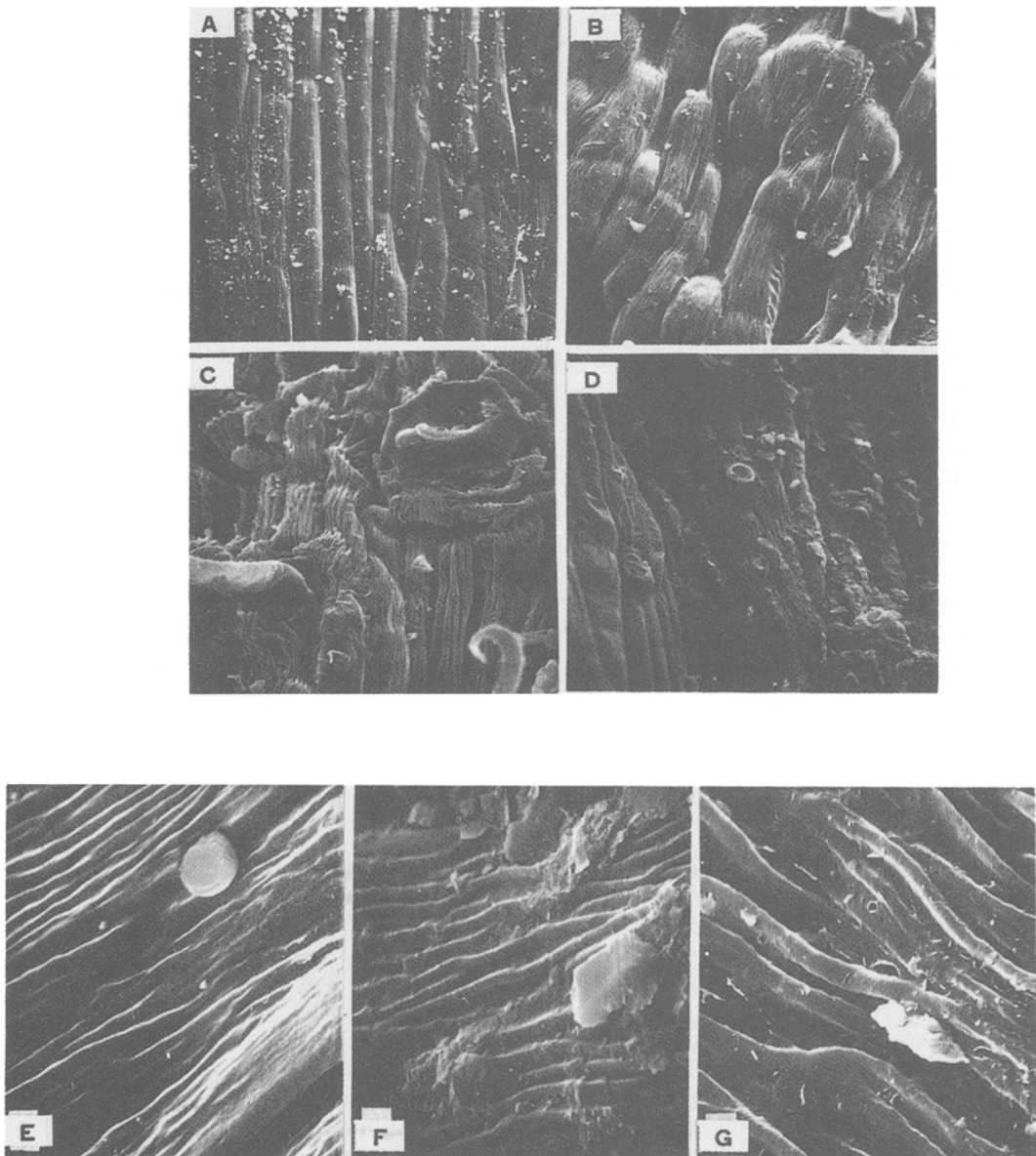
Increasing wind speed caused a decrease in the rate of transpiration. The leaves which developed at higher wind speeds lost less water per unit area than those developed under lower wind speeds. These changes were due to structural changes that therefore seem to be adaptive. The results of this experiment suggest that the morphological and anatomical changes of the leaves due to wind can be considered advantageous with respect to their water economy. Observations which follow the transpiration rate over a long period of time are more valuable than those which are short term. This is because the purely physical response to an increase in wind speed will be seen as soon as the leaf's heat balance has adapted to a new equilibrium [28]. The temporal effect resulting from a physiological response, rather than a purely physical reaction can be seen in an experiment by Hiron and Wright [35]. They directed warm air from a hair drier onto bean seedlings. At first, the plants lost water rather rather quickly and began to wilt. However, after 40 min., they started to recover, and completely regained their turgor by 90 min. This was due to closure of the stomata, which occurred with an increase in abscisic acid in the tissues. This increase in abscisic acid content is known to result from MP [52]. The reduction of the size of the plant is probably due to the shaking of the plant. Wind or other kinds of MP can alter the surface of leaves or stems, breaking hairs and changing the waxy cuticle [74, 46]. Rubbing or flexing bean stems

causes a great increase in the thickness of the cuticle and in the shape of the waxy depositions (Fig. 5). Hallam [30] reports that waxes can be regenerated at a rapid rate only in rapidly expanding leaves, and that damaged epidermal cells or hairs do not become repaired or regenerated. These changes in the epidermis and cuticle will effect the rate of transpiration. In measuring the hydraulic conductivity in isolated epidermal strips, Meidner [57] found that an epidermal cell with a fractured outer wall can sometimes carry out a moderate rate of evaporation using water supplied by nearby epidermal cells. Todd et al. [79] suggested that ethylene production due to MP might mediate the morphological changes. As will be seen later on, this is no doubt the case.

Prolonged exposure to MP induces morphological and anatomical changes in plants [28, 43, 46, 8, 45]. Whitehead and Luti [87], in studying *Zea mays*, demonstrated that leaves developed in the wind were thicker with more stomata and smaller stomata than those of the controls. In the leaf margins of plants given MP by wind, rows of hyaline sclerenchymatous cells developed. This did not occur in the leaves of control plants. Furthermore, the cuticle of wind treated plant leaves was thicker than the cuticle of control leaves. This latter phenomenon was also found on the epidermal cells of rubbed bean stems [46]. Whitehead [86] argues that wind and soil moisture stress cause similar anatomical changes leading to the ability to restrict water loss. Grace and Russell [29] separated the effects of wind and leaf water loss by studying the anatomy and water relations of *Festuca arundinacea*. Growth in the wind caused adaptations which were sometimes similar to those resulting from drought. Some of these changes are of use in maintaining a positive leaf water balance, but others may be adaptations to withstand mechanical stress. For example, in the case of trees, strengthening anatomical responses to MP such as wind are pronounced in woody tissues.

### Effects on reproduction

In general, the rubric of thigmomorphogenesis may include an increase in the number of pistillate cucumber flowers [72], a decrease in flower, fruit and seed production and a delay in anthesis of



*Fig. 5.* The effects of treatment with ethrel or MP (rubbing) on the epidermal cells of bean first internodes observed by scanning electron microscopy. Magnification: (A–D) 640 diameters, (E–G) 4000 diameters. (A) Control epidermal cells. (B) MP 10 times once each day for 5 days, or (C) for 10 days. (D) 50  $\mu$ L ethephon applied once daily to the terminal bud. (E) same as “A”, showing waxy cuticular ridges on epidermal cells. (F) same as “D” showing waxy cuticular ridges on epidermal cells. (G) same as “B”, showing waxy cuticular ridges on epidermal cells. Note the thickened, gnarled appearance of both the cells and the waxy cuticular ridges caused by the MP or ethrel. Adapted from Ref. 46.

several species [1, 2]. While this might seem to be of adaptive disadvantage, it better enables the plant to assure successful reproduction. Let us consider the extreme example of Krumholz vegetation at the tree line on a mountain top. At first glance, the

recumbent carpet dwarf forms of trees growing at the mountain tree line are barely able to survive. But the point to be made is, that hardened in this extreme way by the high winds to be found there (over 200 mph) [26], they do survive and produce

viable seed [28]. Without this survival, they could not reproduce at all. Hence the decreased yield of propagules and offspring should not be considered as a deficit for the plant and the species. Rather, the severe thigmomorphogenesis to be found in such habitats must be considered a necessary mechanism to insure the continuation of the species in that environment, and therefore, a beneficial adaptation.

### Photosynthetic and respiratory effects

Wind and other types of mechanical perturbation affects photosynthesis in leaves and other photosynthetic organs. The rate of photosynthesis was enhanced by winds of  $1.7 \text{ m s}^{-1}$  [28]. However, winds of higher velocities did not necessarily show a further increase in photosynthesis. In fact, anything more than a very gentle MP causes a retardation of overall photosynthesis. For example, Caldwell [18] exposed *Rhododendron ferrugineum* and *Pinus cembra* to wind-speeds of  $15 \text{ m s}^{-1}$ . Leaves of *R. ferrugineum* experienced a decreased rate of both photosynthesis and transpiration, whereas *P. cembra* leaves exhibited a decrease in photosynthesis, but transpiration was not affected.

In an experiment by Todd et al. [79] the effects of wind of different velocities on the respiration of plants in darkness was studied. The results demonstrate that the respiration rates of all of the species tested increased substantially when either shoots or intact plants were exposed to wind velocities of  $3.6 \text{ m s}^{-1}$  or above. The effect of wind may be primarily due to the shaking it causes. Todd et al. [79] tested this hypothesis by comparing the effects of wind on restrained and unrestrained magnolia leaves. Unrestrained leaves exposed to  $7.1 \text{ m s}^{-1}$  wind respired about 40% more than restrained leaves. This is further evidence that MP is the primary effector of respiration increase, rather than its being caused by a secondary stress such as drought.

Wind is not the only type of MP that can increase respiration. Audus [3] and Godwin [27] each demonstrated that rubbing or bending cherry laurel leaves or twigs could as much as triple the rate of respiration. A similar effect was found by giving MP to soft potato tissue [5]. As to long term effects, the effect of a prolonged wind period on respiration produces a gradual decline in respiration [79].

The increase in respiration and decrease in

photosynthesis caused by MP, must surely result in the production or retention of less biomass in MP-plants than in controls. This in turn is at least partially responsible for the "stunting" habit of thigmomorphogenesis. Where less carbon is available, the plant cannot grow as large as it can where there is more carbon.

### The role of plant growth regulators

Several endogenous plant growth regulators play a role in thigmomorphogenesis. In the wild cucurbit, *Bryonia doica*, indoleacetic acid (IAA) content decreases following MP, so that growth decreases [11, 37]. In some species, MP induces an increase in auxin, to the point where ethylene production occurs [20, 46, 9], probably through the mediation of an elicitor [71] and via the ACC pathway [41]. It is this MP-induced ethylene that mediates the increase in stem thickness, as well as playing a role in the MP-induced decrease in elongation [9, 12, 13, 34, 66, 67] (Fig. 3 and 5). Ethylene has also been demonstrated to play a major role in thigmomorphogenesis in pine saplings [56, 15, 77]. In a recent study, Telewski [75] showed that the stem diameter correlated positively and the wood density correlated negatively with MP-induced ethylene production. Thus, in different species, MP induces the same response, but uses different hormonal mechanisms. In addition to the effects of auxin and ethylene, the MP-induced decrease in gibberellin in beans and sunflower [69, 7] and increase in abscisic acid in rice, beans and sunflower [52, 20, 7], also contribute to the growth retardation caused by MP.

### Mechanosensing, transduction and integration

As mentioned above, mechanosensing by animal cells has been shown to involve the opening of stretch-sensitive ion channels [64]. Since calcium ions ( $\text{Ca}^{2+}$ ) at high concentration are toxic to cells, they might be expected to retard growth. Jones and Mitchell [53] have shown that exogenous  $\text{Ca}^{2+}$  applied at the extraordinarily high concentration of 10mM inhibited the growth of soybean plants when applied together with the ionophore A23187. In addition, inhibitors of calmodulin action blocked



MP-induced growth inhibition. These data suggest that thigmomorphogenesis is mediated by  $\text{Ca}^{2+}$  via calmodulin. That this is the case has been shown by the elegant experiments of Braam and Davis [14] with *Arabidopsis*. They demonstrated that various types of MP (i.e., wind, rain, touch) regulate the induction of at least four MP genes (called TCH for touch) within 10 to 30 minutes after MP. The TCH genes code for four different forms of calmodulin. This suggests that  $\text{Ca}^{2+}$  modulates thigmomorphogenesis by turning on several different processes following the MP. Such processes might include callose deposition [47], auxin-stimulated growth [63] and mitosis [32].

After the mechanical perturbation has been received, it must be transmitted throughout the plant. Three integrative mechanisms have been reported. 1) Hormonal activity has been described in the previous section. 2) When plants are mechanically perturbed phloem transport is inhibited. In an elegant experiment, Jaeger et al. [40] administered a continuous stream of  $^{11}\text{CO}_2$ -labeled air to a single cotton or bean leaf, while monitoring the basipetal movement of the  $^{11}\text{C}$  with gamma detectors. They found that gentle massage, shaking or vibration caused localized phloem blockages within 1-2 minutes of MP. The blockages lasted for up to 55 minutes, and up to 175 minutes were needed for complete recovery. The rapidity of the phloem blockage correlates very well with that of the decrease in growth and in electrical resistance of the stem tissue [44]. 3) A number of laboratories have described the transmission of MP-induced bioelectric signals [68, 61, 24]. It may be that all three of these integrative mechanisms mediate thigmomorphogenesis among plant species.

## Synthesis

The response to mechanostimulation is undoubtedly very ancient, probably having evolved from osmotic pressure transducers in cell membranes [64]. It is probable that the mechanisms further developed into responses to fluid flow, first in the chaotic turbulence of water at shorelines [81] and then in terrestrial windy environments, such as montane treelines, coastal situations or plains environments. In all of these situations, turbulent, or even laminar fluid flow creates mechanical perturbations that

produce thigmomorphogenesis. Thigmomorphogenesis is thus widespread in nature and serves important adaptive advantages in plants. It strengthens the plant to help it resist rupture due to strong winds, but also due to other types of stress such as frost and drought. Some plants become hardened in extremely inimical conditions, such as montane treelines, where winds can be in excess of 200 mph [26]. Even in such conditions, a thigmomorphogenetically hardened plant can survive and produce viable seed [28]. One of the problems involved in understanding the role of wind (or other MPs) is the contribution of other environmental stresses, such as salt spray, blown sand, low temperatures or desiccation. We see the same sort of syndrome produced in all of the biomes studied, so it is logical that since wind is the one constant in these environments, that MP is an important factor in producing the hardened plant. Desiccation can be the primary or secondary stress in several of these windy environments, but not in all of them. Furthermore, the wind does not have to be very strong in order to produce a hardened plant. Taken together, all the evidence strongly suggests that MP plays the central role in creating the thigmomorphogenetic syndrome.

Although other hormones may play roles in thigmomorphogenesis, the strongest evidence suggests that ethylene mediates MP-induced morphogenetic changes. One of the earliest thigmomorphogenetic events seem to involve membrane changes which allow  $\text{Ca}^{2+}$  to act as a second messenger, probably via the mediation of calmodulin. It will be interesting to see how these sensory and transductive events may be coupled to ethylene production and evolution.

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