14 Electrophysiology in Mechanosensing and Wounding Response

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14.1 Mechanosensing

14.1.1 Responses of plants to mechanical stimulus

Touch induces rapid leaf movement in "sensitive" plants such as *Mimosa pudica*. This characteristic response indicates the recognition of mechanical stimuli, and it is termed thigmonasty or seismonasty. On the other hand, "insensitive" plants move passively in response to touch. The passive movement is believed to indicate a lack of recognition. However, this is not the case. After daily touching, the plants become shorter and thicker. Increased thickness reinforces the physical strength of the plant, therefore reducing the impact of mechanical stress on the plants. According to Jaffe and Forbes (1993), this phenomenon is termed thigmomophogenesis. Aequorin-expressing, transgenic plants undergo increases in cytoplasmic free Ca^{2+}, a second messenger (Knight et al. 1992). Thus, it is clear that even insensitive plants can sense mechanical stimuli.

In the plasma membrane, ionic processes are believed to play important roles in stimulus-perception and signal processing. Electrophysiological techniques are useful when monitoring the rapid ionic processes in the mechanosensing of plants.

14.1.2 Receptor potential in higher plants

Since the perception of the stimuli can easily be visualized, action plants are frequently utilized in mechanosensing analysis. *M. pudica* is the most common plant used in this type of investigation (Fig. 14.1). The leaves are equipped with three types of motile structures: main pulvinus (primary pulvinus), sub-pulvinus (secondary pulvinus) and pulvinule (tertiary pulvinus). These structures are responsible for movement of the petiole, pinna, and leaflet, respectively. The mechanosensitive leaf movement of *M. pudica* has been extensively studied. In the first step of mechanoperception, mechanical

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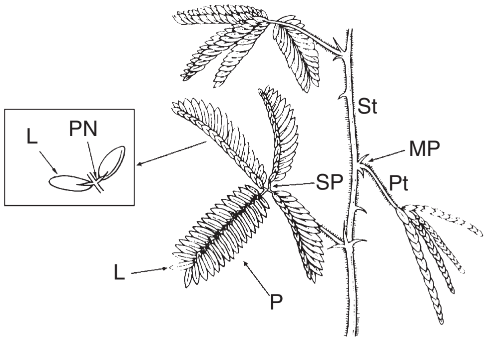

Fig. 14.1. Leaf movement of *Mimosa pudia*. Leaf is equipped with three kinds of motile structures, main pulvinus (*MP*), sub-pulvinus (*SP*) and pulvinule (*PN*), and responsible for movement of petiole (*Pt*), pinna (*P*) and leaflet (*L*), respectively. *St* stem. *Left leaves*: before stimulation. *Right leaf*: after stimulation. (Modified from Ishikawa 2003)

stimuli must be transformed into electrical signals or receptor potentials. Sibaoka (personal communication) suggested that pulvini are mechanosensitive organs. However, the sensory cell has not been identified in this material.

Receptor cells have been identified in action plants such as the terrestrial *Dionaea muscipula* and aquatic *Aldrovanda vesiculosa*. Although their habitats are different, both plants are carnivorous. The leaves are modified as traps for prey, and each trap is composed of paired lobes containing sensory hairs. The lobes are connected by the motile midrib (Fig. 14.2). When the sensory hairs are bent by the prey, the trap quickly closes to catch the prey.

In case of *A. vesiculosa*, each lobe has 20 sensory hairs. Individual hairs have four small sensory cells. Using sophisticated techniques, Iijima and Sibaoka analyzed the receptor potentials and action potentials (Sibaoka 1991) (Fig. 14.3). One microelectrode was inserted into a sensory cell and other into an epidermal cell of a lobe. When a stimulus was applied by bending the hair, the receptor cell showed depolarization. The amplitude of the depolarization increased as the bending force increased, indicating that the response is a receptor potential. When depolarization reaches its threshold level, an action potential is recorded in a cell of a lobe. This action potential is transmitted to the midrib of the trap, inducing closure. The receptor potentials and action potentials were generated upon mechanical stimulation. Voltage-sensitive and mechanosensitive ion channels should be involved, respectively.

14.1.3 Analysis of receptor potential in Characean cells

Internodal cells of Characeae have been useful materials for the study of plant electrophysiology for the following reasons: (1) due to the simple morphology, the electrical responses of a target cell can be easily measured, (2) since