

Preface

Plants are unique as their development and morphogenesis are plastic throughout their lives. They continuously monitor diverse biotic and abiotic parameters of their environment and these sensory perceptions shape their organs and bodies. Although genes are critical, the final form and architecture of above-ground organs, and especially of root systems, are determined by their sensory activities associated with motoric responses (Friml 2003; Hodge 2009). Sensory plant biology and plant electrophysiology were two lively disciplines until the late 1970s (Bünning 1959; Haupt and Feinleib 1979) but then, for somewhat obscure reasons, they showed no further development. In the last few years, however, there have been numerous advances in plant sciences. These necessitate not just a revival of plant electrophysiology and sensory biology, but also the introduction of plant neurobiology, which includes also plant sensory ecology (Baluška et al. 2006a; Brenner et al. 2006). First of all, and contrary to all “mechanistic” predictions based on the high turgor pressure of plant cells, endocytosis has been found to be an essential process of plant cells which impinges upon almost all aspects of plant life (Šamaj et al. 2005, 2006). Moreover, recent advances in plant molecular biology have identified, besides classic neurotransmitters, also several proteins typical of animal neuronal systems, such as acetylcholine esterases, glutamate receptors, GABA receptors, and endocannabinoid signaling components, as well as indicating signaling roles for ATP, NO, and reactive oxygen species (Baluška et al. 2006b). Plant action potentials have turned out to influence processes such as osmotic-force-based cell shapes, actin-cytoskeleton-based cytoplasmic streaming, organ movements, wound responses, respiration and photosynthesis, as well as flowering (Dziubinska et al. 2003; Felle and Zimmermann 2007; Davies 2004; Fromm and Lautner 2007). Last, but not least, there have been significant advances in ecological studies on plant–plant and plant–insect communications, as well as in behavioral studies on memory, planning, and learning phenomena in plants (Trewavas 2005; Gális et al. 2009; Ripoll et al. 2009). Discovery of complex plant behavior (Baluška et al. 2006a; Hodge 2009; Karban 2008; Scott 2008) implicates signal perception, processing, the integration of ambient signals (Brenner et al. 2006), and even cognition (Calvo Garzon 2007).

Recent advances in plant cell biology, molecular biology and ecology have resulted in the accumulation of a critical mass of data, which are not “digestible” within the framework of these, now classical, disciplines of plant sciences (Baluška

et al. 2006a, b; Brenner et al. 2006, 2007; Baluška and Mancuso 2009; Hodge 2009). New approaches are required, characterized by systemlike analysis of information acquisition, storage, processing, and the making of decisions.

Plants retrieve properties of their environment via sensory perceptions which are critical for their survival. Especially light and gravity, two physical factors pervading the universe, are essential in this respect. Plants actively experience the environment and can both store and retrieve memories (Gális et al. 2009; Ripoll et al. 2009 to drive an active life-style (for roots see Baluška et al. 2004; Hodge 2009). Intriguingly, the translation of these physical forces into plant activities - typically differential growth responses - is based on the transcellular transport of auxin, which helps to bring about the final shape of the plant body (Friml 2003; Baluška et al. 2006b; Brenner et al. 2006).

Although the history of auxin can be traced back to the Darwin's early experiments with phototropism of coleoptiles, we still know almost nothing about its peculiar features. Let us examine the mystery of this unique molecule. Whereas auxin can probably be synthesized in each plant cell, it is tediously transported from cell to cell throughout the plant body (Friml 2003). Similarly puzzling is the well-known phenomenon that although the auxin molecule is sufficiently small to pass easily through plasmodesmatal channels, plant cells somehow manage to prevent this direct cell-to-cell means of auxin transport (Mancuso et al. 2006). Rather, plants maintain an energetically costly system based on vesicle trafficking, closely resembling neuronal and immunological cell-cell communication, to drive transcellular auxin transport (Baluška et al. 2003, 2005; Friml and Wiśniewska 2005). At least in the root apex, auxin is secreted via a synaptic neurotransmitter-like mode supported by phospholipase D ζ 2 (Mancuso et al. 2007; Baluška et al. 2008). Thus, this unique information-bearing molecule is central to our understanding of sensory and communicative plants.

The next peculiarity is that when extracellular auxin hits the outside leaflet of the plasma membrane, it induces electric responses based on the ABP1 auxin-binding protein (Felle et al. 1991; Steffens et al. 2001; Baluška et al. 2004). All this suggests that auxin, besides hormone- and morphogen-like (Dubrovsky et al. 2008) properties, possesses neurotransmitter-like faculties too. Since the cell-to-cell transport of auxin translates sensory perception into adaptive motoric responses, being central for organ tropisms to light and gravity gradients, a plant neurobiology approach is needed to explain this great mystery of plants (Baluška et al. 2005, 2006b, 2008; Baluška and Mancuso 2008).

Despite having a relatively simple body organization, plants need sophisticated sets of coordinative processes. Besides their root-shoot coordination, there is also need for coordination amongst radial tissues, especially within and between the cortex and stele. Action potentials run preferentially in the axial direction and they presumably integrate activities of root and shoot apices. Plants show modular and apparently decentralized organization of their bodies. Nevertheless, there are several critical situations requiring "centralized" decisions, such as the onset of flowering and the onset or breakage of dormancy. Although these decisions are based on information retrieved via numerous distant organs, they imply some central

“processor” which would reliably control the whole plant body. Importantly, any wrong decision would have detrimental consequences for the whole plant. Future studies focusing on these new aspects of plants will allow us to understand plants and their unexpected sensory, communicative, and social aspects.

Bonn, October 2008
Florence, October 2008

František Baluška
Stefano Mancuso

References

- Baluška F, Mancuso S (2009) Plant neurobiology: from sensory biology, via plant communication, to social plant behaviour. *Cognit Process* (in press)
- Baluška F, Šamaj J, Menzel D (2003) Polar transport of auxin: carrier-mediated flux across the plasma membrane or neurotransmitter-like secretion? *Trends Cell Biol* 13:282–285
- Baluška F, Mancuso S, Volkmann D, Barlow PW (2004) Root apices as plant command centres: the unique ‘brain-like’ status of the root apex transition zone. *Biologia* 59:9–17
- Baluška F, Volkmann D, Menzel D (2005) Plant synapses: actin-based domains for cell–cell communication. *Trends Plant Sci* 10:106–111
- Baluška F, Mancuso S, Volkmann D (2006a) Communication in plants: neuronal aspects of plant life. Springer, Berlin
- Baluška F, Hlavacka A, Mancuso S, Barlow PW (2006b) Neurobiological view of plants and their body plan. In: Baluška F, Mancuso S, Volkmann D (eds) *Communication in plants: neuronal aspects of plant life*. Springer, Berlin, pp 19–35
- Baluška F, Schlicht M, Volkmann D, Mancuso S (2008) Vesicular secretion of auxin: evidences and implications. *Plant Signal Behav* 3:254–256
- Brenner ED, Stahlberg R, Mancuso S, Vivanco J, Baluška F, Van Volkenburgh E (2006) Plant neurobiology: an integrated view of plant signaling. *Trends Plant Sci* 11:413–419
- Bünning E (1959) Physiology of movements. Part 1. Movements due to mechanical and electrical stimuli and to radiations. In: Ruhland W (ed) *Encyclopedia of plant physiology*. Springer, Berlin
- Calvo Garzon F (2007) The quest for cognition in plant neurobiology. *Plant Signal Behav* 2:208–211
- Davies E (2004) New functions for electric signals in plants. *New Phytol* 161:607–610
- Dubrovsky JG, Sauer M, Napsucialy-Mendivil S, Ivanchenko MG, Friml J, Shishkova S, Celenza J, Benková E (2008) Auxin acts as a local morphogenetic trigger to specify lateral root founder cells. *Proc Natl Acad Sci U S A* 105:8790–8794
- Dziubinska H, Filek M, Koscielniak J, Trebacz K (2003) Variation and action potentials evoked by thermal stimuli accompany enhancement of ethylene emission in distant non-stimulated leaves of *Vicia faba* minor seedlings. *J Plant Physiol* 160:1203–1210
- Felle HH, Zimmermann MR (2007) Systemic signalling in barley through action potentials. *Planta* 226:203–214
- Felle H, Peters W, Palme K (1991) The electrical response of maize to auxins. *Biochim Biophys Acta* 1064:199–204
- Friml J (2003) Auxin transport – shaping the plant. *Curr Opin Plant Biol* 6:7–12
- Friml J, Wiśniewska J (2005) Auxin as intercellular signal. In: Fleming AJ (ed) *Intercellular communication in plants*. Blackwell, Oxford, pp 1–26
- Fromm J, Lautner S (2007) Electrical signals and their physiological significance in plants. *Plant Cell Environ* 30:249–257
- Gális I, Gaquerel E, Pandey SP, Baldwin IT (2009) Molecular mechanisms underlying plant memory in JA-mediated defence responses. *Plant Cell Environ* (in press)

- Haupt W, Feinleib ME (1979) Physiology of movements. In: Encyclopedia of plant physiology, vol. 7. Springer, Berlin
- Hodge A (2009) Root decisions. *Plant Cell Environ* (in press)
- Karban R (2008) Plant behaviour and communication. *Ecol Lett* 11:727–739
- Mancuso S, Barlow PW, Volkmann D, Baluška F (2006) Actin turnover-mediated gravity response in maize root apices: gravitropism of decapped roots implicates gravisensing outside of the root cap. *Plant Signal Behav* 1:52–58
- Mancuso S, Marras AM, Mugnai S, Schlicht M, Zarsky V, Li G, Song L, Hue HW, Baluška F (2007) Phospholipase D ζ 2 drives vesicular secretion of auxin for its polar cell-cell transport in the transition zone of the root apex. *Plant Signal Behav* 2:240–244
- Ripoll C, Le Sceller L, Verdus MC, Norris V, Tafforeau M, Thellier M (2009) Memorization of abiotic stimuli in plants. A complex role for calcium. In: Baluška F (ed) *Plant–environment interactions: behavioral perspective*. Springer, Berlin (in press)
- Šamaj J, Read ND, Volkmann D, Menzel D, Baluška F (2005) Endocytic network in plants. *Trends Cell Biol* 15:425–433
- Šamaj J, Baluška F, Menzel D (2006) *Plant endocytosis*. Springer, Berlin
- Scott P (2008) *Physiology and behaviour of plants*. John Wiley & Sons Ltd
- Steffens B, Feckler C, Palme K, Christian M, Böttger M, Lüthen H (2001) The auxin signal for protoplast swelling is perceived by extracellular ABP1. *Plant J* 27:591–599
- Trewavas A (2005) Green plants as intelligent organisms. *Trends Plant Sci* 10:413–419

Signaling in Plants

Baluška, F.; Mancuso, S. (Eds.)

2009, XII, 308 p. 22 illus., 2 illus. in color., Hardcover

ISBN: 978-3-540-89227-4