

Communication in Plants

Neuronal Aspects of Plant Life

Bearbeitet von
Frantisek Baluska, Stefano Mancuso, Dieter Volkmann

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2 Neurobiological View of Plants and Their Body Plan

František Baluška, Dieter Volkmann, Andrej Hlavacka,
Stefano Mancuso, Peter W. Barlow

Abstract All principal metabolic biochemical pathways are conserved in animal and plant cells. Besides this, plants have been shown to be identical to animals from several other rather unexpected perspectives. For their reproduction, plants use identical sexual processes based on fusing sperm cells and oocytes. Next, plants attacked by pathogens develop immunity using processes and mechanisms corresponding to those operating in animals. Last, but not least, both animals and plants use the same molecules and pathways to drive their circadian rhythms. Currently, owing to the critical mass of new data which has accumulated, plant science has reached a crossroads culminating in the emergence of plant neurobiology as the most recent area of plant sciences. Plants perform complex information processing and use not only action potentials but also synaptic modes of cell–cell communication. Thus, the term ‘plant neurobiology’ appears to be justified. In fact, the word neuron was taken by animal neurobiologists from Greek, where the original meaning of this word is ‘vegetal fibre’. Several surprises emerge when applying a ‘neurobiological’ perspective to illustrate how the plant tissues and the plant body are organized. Firstly, root apices are specialized not only for the uptake of nutrients but they also seem to support neuronal-like activities based on plant synapses. These synapses transport auxin via synaptic processes, suggesting that auxin is a plant-specific neurotransmitter. Altogether, root apices emerge as command centres and represent the anterior pole of the plant body. In accordance with this perspective, shoot apices act as the posterior pole. They are specialized for sexual reproduction and the excretion of metabolic products via hydathodes, trichomes, and stomata. Next, vascular elements allow the rapid spread of hydraulic signals and classical action potentials resembling nerves. As plants are capable of learning and they take decisions about their future activities according to the actual environmental conditions, it is obvious that they possess a complex apparatus for the storage and processing of information.

Life has always seemed to me like a plant that lives on its rhizome. Its true life is invisible, hidden in the rhizome. The part that appears above ground lasts only a single summer. Then it withers away – an ephemeral apparition. When we think of the unending growth and decay of life and civilisations, we cannot escape the impression of absolute nullity. Yet I have never lost a sense of something that lives and endures underneath the eternal flux. What we see is the blossom, which passes. The rhizome remains.

Carl Gustav Jung: *Memories, dreams, reflections*, Collins and Routledge & Kegan Paul, London, 1963. Translated from German into English by Richard and Clare Winston.

2.1

Introduction

It was Aristotle and his students who made the first philosophical attempts to understand plants in their complexity. At this ancient time, the main interest for plants was limited to their usefulness in medicine. Much later, in the sixteenth century, the first attempts were made to understand the basic principles of structure and function of plants. At first, these studies were largely devoted to plant distribution, taxonomy, and morphology. Later, because of the technological advances resulting in the invention of the microscope and inspired by the earlier work on medicine, anatomy and cytology were added to the plant sciences curriculum. In fact, the cellular nature of animals and plants was elaborated first in plants (Hooke 1665, reviewed by Baluška et al. 2004a).

By the end of nineteenth century, it was realized that plants were even more similar to animals than had been thought hitherto. In fact, Huxley (1853) went so far as to say that “The plant is, then, an animal confined in a wooden case...”. Advances in physiology helped confirm this, especially with regard to some of the basic physiological processes, such as respiration, digestion, and cell growth, where plants often provided the material of choice for experimental studies. In such circumstances, plant physiology was born; and it now dominates work in the plant sciences. Furthermore, a big surprise is that plants have been shown to be identical to animals from several rather unexpected perspectives. For their reproduction, plants use identical sexual processes based on the fusion between sperm cells and oocytes (Smyth 2005). Next, plants attacked by pathogens develop immunity using the same processes and mechanisms that operate in animals (Nürnberg et al. 2004). Last, but not least, animals and plants use the same molecules and pathways to drive their circadian rhythms (Cashmore 2003). Currently, plant science has reached another crossroad. A critical mass of new data has been accumulated which has culminated in the establishment of plant neurobiology as the most recent discipline of plant sciences.

Traditionally, plants are considered to be passive creatures mostly because, relative to the perception of man, they hardly move and make no noise. However, recent advances in plant sciences clearly reveal that plants are “intelligent” organisms capable of learning and taking decisions in relation to their environmental situation (Trewavas 2001, 2003). Plants are not just passive victims of circumstance but, rather, are active organisms which can identify their herbivores and actively recruit enemies of these herbivorous predators (Dicke and Sabelis 1988; van der Putten et al. 2001). For instance, maize roots attacked by larvae of *Diabrotica* beetle induce volatile compounds which recruit entomopathogenic nematodes which in turn kill this rootworm (Rasman et al. 2005). Moreover, plants use a battery

of volatile compounds not only for plant–insect, but also for plant–plant, communication. Some of these serve as chemical warning signals by being sensed by other plants in the vicinity of the area attacked (Dicke and Sabelis 1988; van der Putten et al. 2001; Bais et al. 2004; Weir et al. 2004).

It is obvious that the immobility of plants imposes different and, perhaps, greater pressures on them if they are to survive. Smart plants can memorize stressful environmental experiences, and can call upon this information to take decisions about their future activities (Goh et al. 2003). Moreover, not only have neuronal molecules been found in plants (reviewed by Baluška et al. 2004b), but plant synapses are also present which use the same vesicular recycling processes for cell–cell communication as neuronal synapses (Baluška et al. 2005a). Roots respond sensitively, via increases of cytoplasmic calcium, to glutamate, while other amino acids do not show this feature (Filleur et al. 2005). Root systems can identify self and non-self roots (Gruntman and Novoplansky 2004). Recent new views about consciousness and self-awareness, when considered as biological phenomena inseparable from adaptation and learning processes (Searle 1997, 2004; Koch 2004a, b), are compatible with the new neurobiologically oriented view of plants.

2.2

Root Apex as the Anterior Pole of the Plant Body

Classically, the plant body is considered to have an apical–basal axis of polarity settled during embryogenesis, with the shoot tip representing the apical pole, and the root tip the basal pole of the plant body (Jürgens 2001). But there are several anatomical and physiological aspects which are incompatible with this view of the plant body axis. Originally, this terminology was derived from plant embryology where roots are considered to develop at the so-called basal end of the embryo (Baluška et al. 2005a). Nevertheless, this apical–basal terminology does not have any justification as plant embryos do not align along the gravity vector as is the case of postembryonic plant bodies. With reference to gravity, a positive gravity response, with downward movement of root apices, could be regarded as an apical or anterior feature. On the other hand, a negative response could be a basal or posterior feature. Such a neurobiological view of the plant body offers a possibility to unify plants with other multicellular organisms by defining the anterior–posterior axis of the postembryonic plant body. This would be logical as postembryonic plant bodies are clearly polarized into the root apices specialized for movements and uptake of nutrients, which are characteristics of the anterior pole. This is opposed by the shoot apices specialized for determinate growth and subsequent transformation into sexual organs, which are characteristics of the posterior pole.

Although plants cannot physically move, active root growth allows exploration of soil niches for nutrition. This implies that root apices are not only sites of nutrient uptake but also sites of forward movement, both of which are attributes of anterior poles of multicellular organisms (Douglas et al. 2005; Barlow, this volume). Moreover, our preliminary data suggest that, in addition, root apices are specialized for neuronal-like activities based on plant synapses (Baluška et al. 2004b, 2005a). Interestingly in this respect, roots enter into symbiotic interactions with bacteria (Denison and Toby Kiers 2004) and mycorrhizal fungi (Vandenkoornhuyse et al. 2002). In fact, most free-living roots are part of a root-fungus commune (Brundrett 2002). Moreover, roots are special also with respect to nematode parasitism when these hijack both auxin transport and signalling pathways to transform root stele cells into giant feeding cells (Hutangura et al. 1999; Bird and Kaloshian 2003). All this suggests that the underground roots are more engaged in social activities that require self-awareness than the aboveground shoots.

In contrast to shoot apices, root apices assemble active synapses along distinctive cell files (Fig. 2.1), show a clear developmental zonation with a transition zone (discussed later), and execute complex patterns of polar

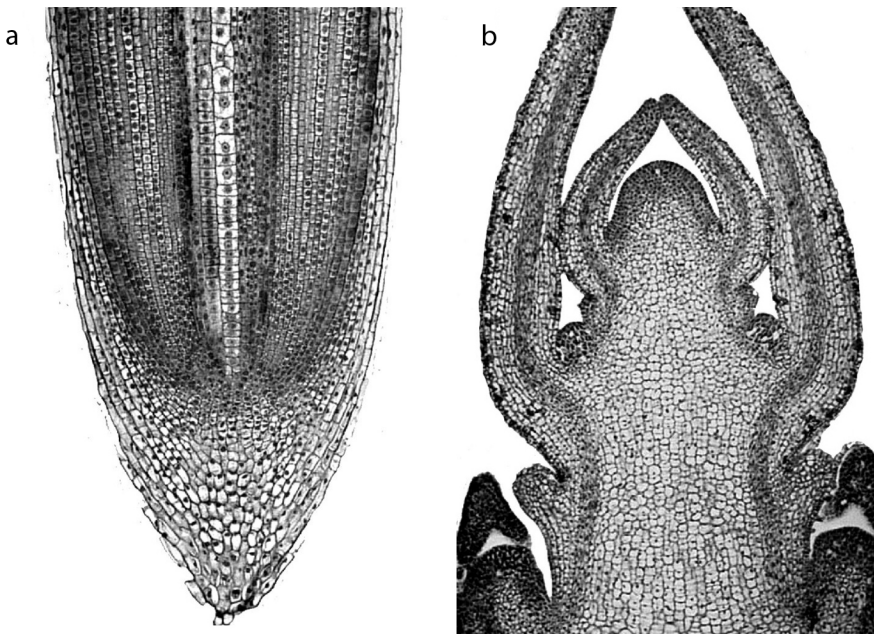


Fig. 2.1. Anatomical basis of root and shoot apices. Anatomical organization of root (a) and shoot (b) apices. Note very regular cell files, with cross-walls representing plant synapses, in root apices. On the other hand, cells in shoot apices are irregularly shaped and fail to arrange into regular cell files

auxin transport (Blilou et al. 2005; Kepinsky and Leyser 2005). On the other hand, shoots, bearing leaves and flowers, are more specialized to perform photosynthesis and sexual reproduction. Of course, flowers do entertain interactions with insects and even small birds (Raguso 2004), to allow effective spread of pollen, but flower cells do not interact directly with insect cells as is the case of root cells invaded by symbiotic bacteria and fungi. The latter act only as pathogens if they interact with shoots and leaves.

Parasitic plants provide very convincing evidence that roots represent the essential part of the plant, whereas shoots can be dispensable. If the plant nutrition is achieved by heterotrophic mechanisms then the plant is highly reduced to a haustorial system, derived from roots, specialized for organic nutrition. For instance, in holoparasitic plants, such as *Rafflesia*, the aboveground green part of the plant is completely missing (Brown 1822; Barkman et al. 2004). Nevertheless, haustoria of *Rafflesia* generate the largest flowers in the plant kingdom, which reveals that this unique organism really belongs to plants. Moreover, the primary role of roots in determining the nature of shoots is obvious also from grafting experiments which show that the rootstocks determine several shoot characteristics such as photosynthesis performance, shoot branching, leaf development, vein patterning, pathogen sensitivity, and stress tolerance (Jensen et al. 2003; Booker et al. 2004; Van Norman et al. 2004; Nelson 2004; Estan et al. 2005). Interestingly in this respect, non-pathogenic rhizobacteria interacting with roots can elicit induced systemic resistance in diverse plants against fungi, bacteria, and viruses (van Loon et al. 1998).

2.3

Shoot Apex as the Posterior Pole of the Plant Body

If the root apex is the anterior pole of the plant body then the shoot apex must represent the posterior pole. In all multicellular organisms, the posterior pole is specialized for excretion of metabolites and for sexual reproduction. Plants conform very well with this expectation. Their shoots harbour organs of excretion – the trichomes and hydathodes. Moreover, stomata perform gas exchange. Trichomes are unicellular or multicellular protuberances of shoot and leaf epidermis which allow removal of excess ions from the plant and can excrete toxic compounds via pores (striae) at their tips (Wagner et al. 2004; Kolb and Müller 2004). Trichomes also protect plants from herbivores, heat, and sunlight, and control leaf temperature and water loss, as well as regulating apoplasmic calcium (Fahn 2000; DeSilva et al. 2001; Jensen et al. 2003; Wagner et al. 2004; Kolb and Müller 2004). Interestingly, hydathodes seem to function analogously to the kidney (Pilot et al. 2004).