

2 Neurobiological View of Plants and Their Body Plan

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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 hydrotodes, 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 crossroads. 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. 2005). 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. 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. Moreover, our preliminary data suggest that, in addition, root apices are specialized for neuronal-like activities based on plant synapses (Baluška et al. 2004b, 2005). Interestingly in this respect, roots enter into symbiotic interactions with bacteria (Denison and Toby Kiers 2004) and mycorrhizal fungi (Vandenkoornhuysen 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

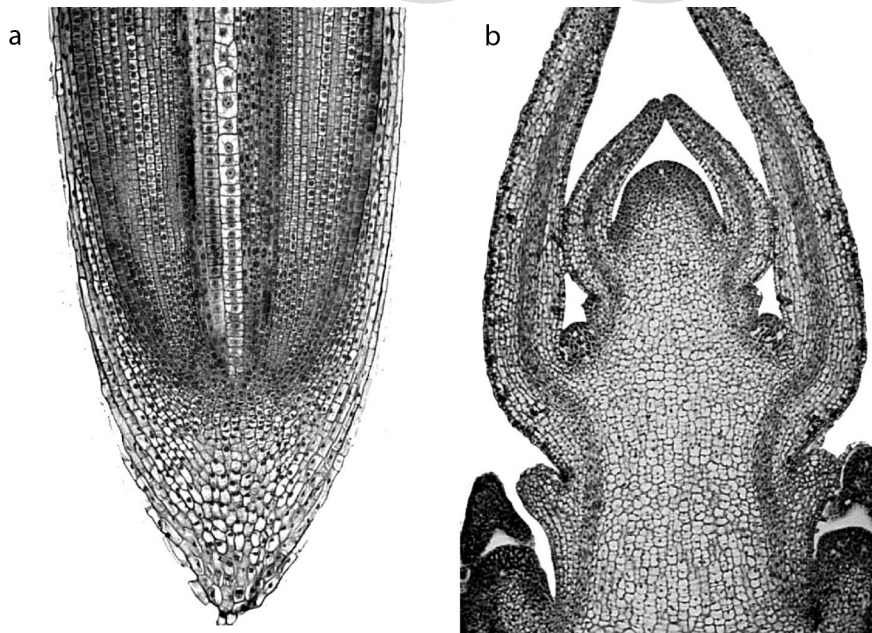


Fig. 2.1. Anatomical basis of root and shoot apices. Anatomical organization of root (a) and shoot (b) apices. Note very regular cell files, with cross-walls representing plant synapses, in root apices. On the other hand, cells in shoot apices are irregularly shaped and fail to arrange into regular cell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

2.4 Auxin as a Plant Neurotransmitter

Auxin is the most important morphogenic agent shaping the whole plant body in accordance with two physical parameters – light and gravity (Friml 2003; Sachs 2004). Recently, we proposed that auxin represents a plant-specific neurotransmitter which is transported, in a light- and gravity-dependent manner, along the anterior–posterior axis of the plant body (Baluška et al. 2003a, b, 2004b, 2005; Barlow et al. 2004). Importantly in this respect, auxin induces the formation of both vascular strands (plant nerves) as well as new root apices harbouring the command centre of the plant body (Baluška et al. 2004b). Root apices represent the major sink for polar auxin transport, and they also show extreme sensitivity to externally applied auxin (Jiang and Feldman 2002, 2005). Moreover, lateral root formation is induced by external auxin: initiation of root primordia is an endogenous process that recapitulates early embryogenesis (Jiang and Feldman 2002). In contrast, new shoots and leaves are formed exogenously from superficial cells.

2.5 Cellular End-Poles as Plant Synapses

Plant synapses are stable actin-supported adhesive domains, assembled at cellular end-poles (cross-walls) between adjacent plant cells of the same cell file, across which auxin and other chemical signals are transported from cell to cell via F-actin-driven and brefeldin A sensitive vesicular trafficking pathways (Baluška et al. 2003a, b, 2004b, 2005; Barlow et al. 2004). Besides these constitutive plant synapses, plants are also capable of forming facultative cell-to-cell junctions with cells of other organisms (plants, fungi, bacteria). These correspond to ‘immunological synapses’ (Baluška et al. 2005) – specialized cell-to-cell adhesion domains that involve the plasma membranes of the two organisms that are opposing each other. Such adhesive domains are also sites of active cell-to-cell transport of molecules and metabolites. Auxin-transporting plant synapses have been observed only in root apices where they are responsible for ordering of cells into very regular cell files (Baluška et al. 1997, 2000, 2003a, b, 2005; see also Fig. 2.1a). In contrast, shoot apex cells do not align into such regular files (Fig. 2.1b) and resemble rather anatomically aberrant root apices of diverse mutants (Baluška et al. 2001a, 2003b) or after exposure of growing root apices F-actin drugs such as latrunculin B (Baluška et al. 2001b).

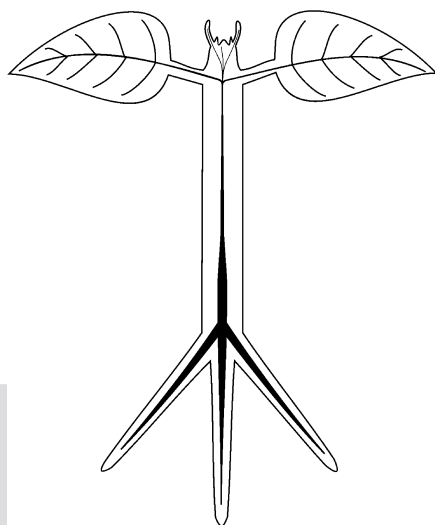


Fig. 2.2. Vascular bundles throughout the plant body. Thin strands of vascular tissue form networks in leaves, join into bundles in shoots, and transform into a large central cylinder of roots which is encircled by pericycle and endodermis

2.6 Vascular Strands as Plant Neurons

Vascular strands represent not only plant ‘nerves’ but also supply the plants with an endoskeleton. Along the plant body axis, there is a gradient of increasing portion of vascular/stelar tissues (Fig. 2.2). Leaves contain single thin strands which join together to form the vascular bundles. The latter extend along the stem up to roots to form the vascular cylinder of the root (Sachs 2000). In roots, a large portion (up to 50% of the root diameter) of the organ is the vascular tissue, and its strands are supported by numerous ‘nursery’ cells forming the vascular cylinder (Sachs 2000). Moreover, stelar tissues in roots are completely enclosed by meristematic pericycle and protective endodermis. The latter tissue is ontogenetically related to the quiescent centre, while both endodermis and pericycle, similarly like all vascular cells, are very active in transcellular auxin transport and pericycle cells initiate lateral root formation in a process very closely resembling early zygotic events during embryo formation.

Phloem can be viewed as a supracellular axon-like ‘channel’ which connects the shoot and root apices. Phloem is specialized for transmission of action-potential-driven electric signals (Mancuso 1999). Axon-like means that it is specialized for the rapid transfer of RNA molecules (Lucas et al. 2001) but it does not accomplish ribosome assembly and messenger

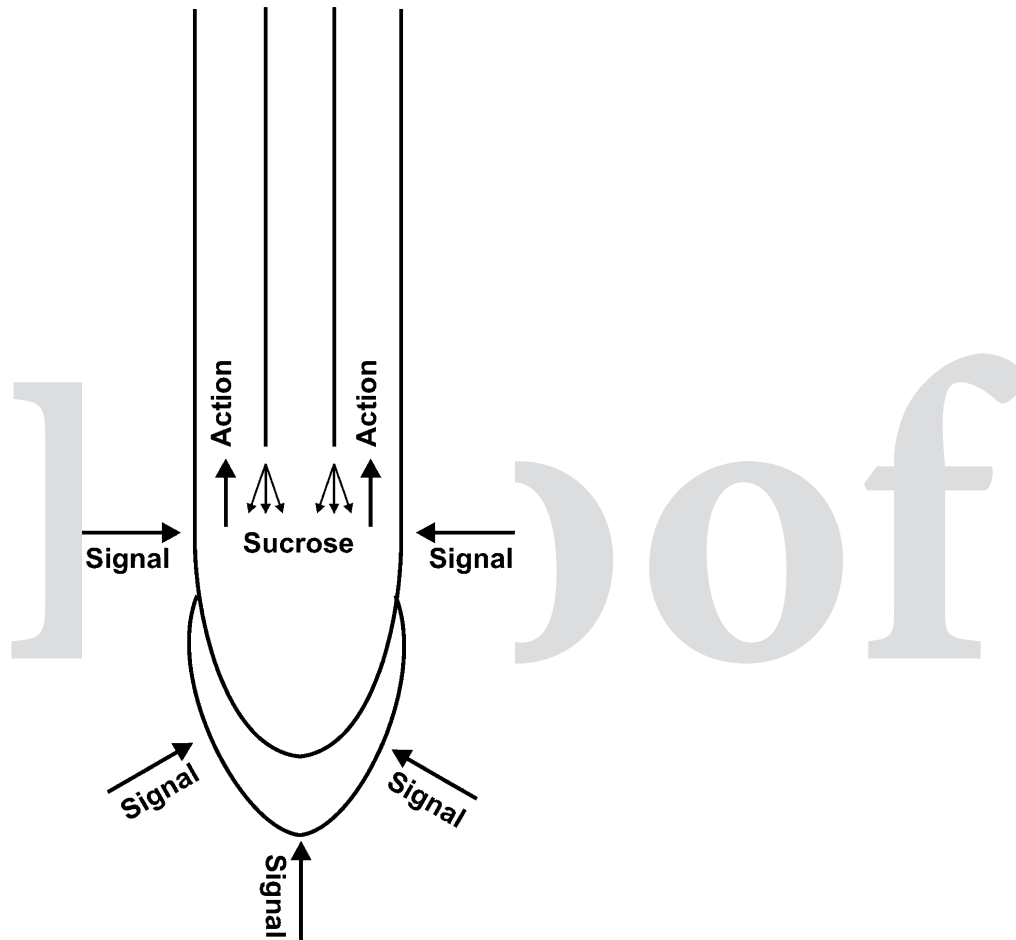


Fig. 2.3. Sensory zones in the root apex. There are two clearly defined sensory zones in the root apex: the root cap covering the meristem and the transition zone interpolated between the meristem and elongation region. Both these sensory zones receive diverse signals and the output is differential switch-like onset of rapid cell elongation, resulting in either straight growth (when all postmitotic cells start their rapid cell elongation simultaneously) or rapid turnings of the root apex. The transition zone is flooded with sucrose, which allows energy-demanding 'brain-like' information processing in cells of the transition zone

RNA translation (van Bel 2003). Mature xylem elements represent non-living and water-filled tubes surrounded by metabolically active cells of xylem parenchyma (de Boer and Volkov 2003; Gilliam and Tester 2005). Xylem tubes are specialized for transmission of hydraulic signals, which are self-transmitting waves induced and driven by changes in hydrostatic pressure (Mancuso 1999).

2.7

Root Apices as 'Brain-Like' Command Centres

Root apices show distinct cell files throughout their apices, a feature which is especially prominent in root apices with closed meristems, such as maize and *Arabidopsis*. The cell files are distinct because the end-poles of adjacent cells within cell files are tightly adhered, forming actin-based plant synapses transporting auxin (Baluška et al. 2003a, b, 2004b, 2005). In contrast, the shoot apices do not show distinct cell files and also fail to show a DR5-signalled auxin maximum (Aloni et al. 2003) which is characteristic for root apices (Sabatini et al. 1999). Besides having synapses, root apices also exhibit clear zonation whereby the apical meristem joins to a so-called transition zone which has sensory capabilities and where root curvatures are initiated (Baluška et al. 2001c). As cells of the transition zone are not engaged in any demanding activities, such as mitotic divisions or rapid cell elongation, they are free to focus all their resources on the acquisition, processing, and storing of information. As they are close to the phloem unloading sites (Fig. 2.3), they are also flooded with sucrose (Stadler et al. 2005), which allows them to perform ATP-dependent processes such as robust ion channel activities, rapid vesicle recycling, and continuous cytoskeleton rearrangements. Interestingly, the transition zone phloem elements are of ancient type as there are lacking companion cells (van Bel 2003).

Postmitotic cells entering the transition zone reorganize actin filaments from a previously diffuse perinuclear network into robust bundles which extend from the nuclear surface towards non-growing end-poles (Baluška et al. 1997; Volkmann and Baluška 1999; Voigt et al. 2005). After reaching end-poles, the F-actin bundles anchor at these subcellular domains which are specialized for the synaptic vesicle recycling which drives transcellular auxin transport and which is also important for synaptic information processing and storing (Baluška et al. 2003b, 2004b, 2005). Another dramatic reorganization of the actin cytoskeleton is accomplished at the basal limit of the transition zone when conical actin bundles, organized around the centrally localized nucleus, become loosened, leave the nuclear surfaces, and extend longitudinally between the non-growing end-poles. This second reorganization of the actin cytoskeleton is essential for the onset of rapid cell elongation (Baluška et al. 1997; Volkmann and Baluška 1999; Baluška et al. 2000). In addition to the actin cytoskeleton, microtubules also undergo rearrangements in cells which traverse the transition zone in such a way that all cortical microtubules become transversely (with respect to the root axis) oriented. This allows polarization of cell expansion with rapidly extending side walls but non-growing end-poles (Baluška et al. 1992, 1993; Barlow and Baluška 2000).

Why does the transition zone exist? Why do root apices need a zone interpolated between the apical meristem and the elongation region which is almost the same size as the meristem? Root apices drive an exploratory mode of root growth in which the search is for oxygen, water, and ions to feed the whole plant body. This is not an easy task, and root apices have two zones which, in a coordinate fashion, allow them to perform rapid turnings. The first zone – transition zone – is close to the meristem and is the one most critical for the exploratory nature of root apices. Burst-like onset of rapid cell elongation, which can happen independently on the opposite root sides, allows instant turning of root apices (for graviresponse see Baluška et al. 1996). The second zone is the elongation region in which cell elongation can be slowed down differentially on the opposite root sides, thereby resulting in rapid turning of whole root apices (Massa and Gilroy 2003). In contrast, shoot apices lack clearly defined meristematic, transition, and elongation zones, and cannot perform such dynamic tropisms. Similarly, they lack regular cell files (Fig. 2.1) and presumably also very active synapses. Shoot apices cannot switch on differential rapid cell elongation, as root apices at the basal border of their transition zone, and the only mechanism is to change the growth rate of the cells. These so-called shade-avoidance shoot movements are much slower when compared with dynamic root behaviour.

Root apices are covered with a root cap (Barlow 2003) which protects the apex and also has numerous sensory abilities. It is a unique structure and is not present at the shoot apex. All this allows growing root apices to screen numerous environmental parameters, to process this information, and to change the growth direction accordingly. As a result, roots behave almost like more active animals, performing very efficient exploratory movements in their search for oxygen, water, and ions. Enclosed by the root cap is the quiescent centre, which represents the major catabolic sink for auxin (Jiang and Feldman 2002, 2005), and the apical portion of the root meristem, which is followed by the sensory transition zone (Baluška et al. 2001c). Furthermore, the distal portion of the transition zone represents the major sink both for exogenously applied auxin (Mancuso et al. 2005) and for oxygen while emitting large amounts of nitric oxide (Mancuso, Mugnai, Volkmann, Baluška, unpublished data). This anatomically distinct group of cells is unique in that it shows rhythmic patterns of ion fluxes and in this respect behaves as a brain-like organ (Baluška et al. 2004b).

Each root apex is proposed to harbour brain-like units of the nervous system of plants. The number of root apices in the plant body is high, and all 'brain units' are interconnected via vascular strands (plant neurons) with their polarly-transported auxin (plant neurotransmitter), to form a serial (parallel) neuronal system of plants. From observation of the plant body of maize, it is obvious that the number of root apices is extremely high,



Fig. 2.4. Body plan of maize (*Zea mays*). Note the very rich root system within which there are numerous indeterminately growing root apices which are involved in inorganic nutrition for the whole plant and processing of neurobiological information (the anterior pole of the plant body). On the other hand, there are only few shoot apices with determinate growth which eventually transform into plant sexual organs (the posterior pole of the plant body)

whereas there are only few shoot apices (Fig. 2.4). This feature makes the 'serial plant brain' extremely robust and the amount of processed information must be immense.

2.8 Ancient Fungal-Like Nature of Roots

The most characteristic feature of roots is their invasive behaviour and exploratory nature based on their ability to actively penetrate soil in the permanent search for water and ions. In this respect, roots resemble fungi. Green shoots are less exploratory owing to the omnipresent light and specialization for photosynthesis. In holoparasitic plants like *Rafflesia*, the green part of the plant is missing completely, the root system being replaced

by an invasive 'fungus-like' network which penetrates the host tissues in a search for organic nutrition. In this respect, roots might represent fungal vestiges of putative ancient mergings between fungi and algae to generate higher plants (Atsatt 1988; Zyalalov 2004). This would explain the inherent tendency of roots to fuse with mycorrhizal fungi and thus generate plant root-fungal networks (Brundrett 2002). Early land plants suffered from a dry environment and could survive only if buried in wet parts of soil. After inventing a cuticle that would prevent desiccation, plants could extend into the aboveground space. Hypothetical merging between fungal and algal organisms would be beneficial for survival during this very critical period. Relevant in this respect is that lichens are also formed by association of fungal and algal partners. But this took place in recent times and the individual partners are still clearly distinguishable and separable. Recent advances in studies on lichens reveal that this association enables both components to invade separately hostile terrestrial niches exposed to high irradiation and dramatic desiccation (Kranter et al. 2005). It might be that similar, but much more ancient, associations between fungi and algae, resulting in the establishment of root-fungus communal networks, allowed plants to colonize land. The fungal/animal-like nature of roots is also supported by holoparasitic plants which can rely solely on the plant host which is penetrated via fungal-like root-derived haustoria (Yoder 2001). Parasitic plants represent an extremely diverse group of organisms with regard to their taxonomy and they have profound effects on the ecosystems in which they live (Press and Phoenix 2004).

Roots resemble ancient plants in their intimate association with water which is taken up and distributed throughout the plant body (Zyalalov 2004). The root apoplast is freely accessible to the water which surrounds the root system. Despite the effective colonization of land, roots are still continuously bathed in aqueous soil solutions. Fungal features of roots are interesting also from the perspective of the inherent symbiotic interactions between roots and fungi (Vandenkoornhuyse et al. 2002). Whereas roots of most plant species are engaged in symbiotic interactions with fungi (Brundrett 2002; Karandashov and Bucher 2005), the aboveground organs do not share this feature and fungi are, by contrast, pathogens of shoots. The only cells of aboveground organs with a fungus-like characteristic are pollen tubes which are capable of an active lifestyle owing to their haustorium-like growth within female tissues (Palanivelu and Preuss 2000), resembling in this respect the root-derived haustoria of holoparasitic plants.

Another ancient root feature relates to their phloem elements. In root apices, protophloem lacks companion cells which are associated with all other phloem elements of angiosperm plants (van Bel 2003). In this respect, root protophloem resembles the conductive system of moss gametophytes.

2.9 Conclusions and Future Prospects

Our view of plants is changing dramatically, tending away from seeing them as passive entities subject to environmental forces and organisms that are designed solely for accumulation of photosynthetic products. The new view, by contrast, is that plants are dynamic and highly sensitive organisms, actively and competitively foraging for limited resources both above and below ground, and that they are also organisms which accurately compute their circumstances, use sophisticated cost-benefit analysis, and that take defined actions to mitigate and control diverse environmental insults. Moreover, plants are also capable of a refined recognition of self and non-self and this leads to territorial behaviour. This new view considers plants as information-processing organisms with complex communication throughout the individual plant. Plants are as sophisticated in behaviour as animals but their potential has been masked because it operates on time scales many orders of magnitude longer than that operating in animals.

Plants are sessile organisms. Owing to this lifestyle, the only long-term response to rapidly changing environments is an equally rapid adaptation; therefore, plants have developed a very robust signalling and information-processing apparatus. Signalling in plants encompasses chemical and physical communication pathways. Chemical communication is based either on vesicular trafficking pathways, as accomplished also across neuronal synapses in brains, or through direct cell-cell communication via plasmodesmata. Moreover, there are numerous signal molecules generated within cell walls and also as diffusible signals, such as NO, reactive oxygen species, jasmonates, and ethylene, which penetrate cells from the extracellular space. On the other hand, physical communication is based on electrical, hydraulic, and mechanical signals. Besides abundant interactions with the environment, plants interact with other communicative systems such as other plants, fungi, nematodes, bacteria, viruses, insects, and predatory animals. All this great variety of interactions and responses can be embraced within the recently introduced field of plant neurobiology.

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