Bio-communication of Plants

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Abstract

Plants communicate with a great variety of symbiotic partners, above and below ground. Constant monitoring of signals of biotic origin as well as abiotic environmental influences allows plants to generate appropriate response behavior. These communication processes are primarily sign-mediated interactions and not simply an exchange of information. They involve active coordination and active organization of a great variety of different behavioural patterns – mediated by signs.

Keywords: multilevel plant-communication, sign-mediated interactions, context-dependency

1. Introduction

Biosemiotics of plant communication investigates both communication processes within and among cells, tissues, organs of plants as sign-mediated interactions which follow (1) *combinatorial* (syntactic), (2) *context*-sensitive (pragmatic) and (3) *content*-specific (semantic) levels of rules. As can be seen in most cases the context of interactions in which a plant organism is interwoven determines content arrangement of response behaviour. As outlined at the example of Auxin this means that this chemical molecule with its identical chemical structure may function for transport of different meanings (semantics) that are determined by the different contexts (pragmatics) in which this sign is used.

2. Sign-mediated interactions within and among plants

Plants have been viewed and treated as growth automatons. Today, however, it is recognized that the coordination of growth and development in plants is possible only by using signs rather than pure mechanics. Understanding the use of signs in communication processes requires a differentiated perspective: chemical molecules are used as signs. They function as signals, messenger substances, information carriers and memory medium in either solid, liquid or gaseous form, in order to guarantee coordination and organization processes.

Plants are sessile, highly sensitive organisms that actively compete for environmental resources both above and below the ground. They assess their surroundings, estimate how much energy they need for particular goals, and then realize the optimum variant. They take measures to control certain environmental resources. They perceive themselves and can distinguish between self and non-self. This capability allows them to protect their territory. They process and evaluate information and then modify their behaviour accordingly (Trewavas 2003, Baluska and Mancuso 2007).

To understand these highly diverse competences it may be noted that this is possible due to parallel communication processes within the plant body (*intraorganismic*), between the same and different plant species *(interorganismic)* and between plants and non-plant organisms (*trans-specific*). Successful communication processes allow plants to prosper; unsuccessful ones have negative, potentially lethal repercussions. Intraorganismic communication involves sign-mediated interactions in cells (intracellular) and between cells (intercellular).

Intercellular communication processes are crucial in coordinating growth and development, shape and dynamics. Such communication must function on both the local level and between widely separated plant parts.

2.2. Chemical molecules serve as vocabulary

The chemical communication in and between plants is complex. More than 20 different groups of molecules with communicatory function have currently been identified. For instance, up to 100,000 different substances, known as secondary metabolites, are actively used in the root zone. This diversity is necessary considering the high abundance of microbes, insects and related or non-related plant roots in this zone (Bais et al. 2003). Here, I summarize the important role of auxin, being *only* one example of the molecular vocabulary in plant communication beneath the great variety of others, such as hormones, RNAs and multiple reusable elements, which I have outlined in another article and will not refer to in this contribution (Witzany 2007).

2.2.1. Auxin as neurotransmitter, hormone, morphogenic sign

Plant roots and plant shoots detect environmental signals as well as development levels and communicate over long-distance pathways. The decentralized nervous system of plants is advantageous for decentral growth and development under constantly changing environmental conditions (Baluska et al. 2004, 2006).

Auxin is used in hormonal, morphogenic and transmitter pathways. Because the pragmatic context of use can be very complex and highly diverse, identifying the momentary usage is extremely difficult for researchers (Baluska et al. 2005). In the specific context of synaptic neuronal-like cell–cell communication, plants use neurotransmitter-like auxin (Schlicht et al. 2006, Brenner et al. 2006) and, presumably, neurotransmitters such as glutamate, glycine, histamine, acetylcholine, dopamine – all of which they also produce (Baluska et al. 2004). Auxin is detected as an *extracellular* signal at the plant synapse (Baluska et al. 2005) in order to react to light and gravity. However, in another specific context it also serves as an extracellular messenger substance to send electrical signals and functions as a synchronization signal for cell division (Campagnoni et al. 2003). In contrast to this, in the context of *intracellular* signalling, auxin serves in organogenesis, cell development and differentiation. In the organogenesis of roots, for example, auxin enables cells to determine their position and their identity (Casson and Lindsey 2003). The cell wall and the organelles it contains help regulate the signal molecules. Auxin is – as the name suggests – a growth hormone. Intracellularly, it mediates in cell division and cell elongation. At the intercellular, whole plant level, it supports cell division in the cambium, and at the tissue level it promotes the maturation of vascular tissue during embryonic development, organ growth as well as tropic responses and apical dominance (Friml and Wisniewska 2005). Dependent on the different pragmatic contexts in which the plant organism is interwoven, auxin is used for different purposes. This allows transportation of different messages (by the same chemical molecule) which trigger different response behaviours.

3. Interpretation of mechanical influences

As can be seen in the chapter on coordination of plants in defence behaviour plants are able to distinguish biotic and abiotic influences clearly. Mechanical contact has an influence on the overall organism and on the cell level. Mechanical contact can cause plants to react aggressively, for example toward the animals that want to eat them, (B) to discard their pollen and (C) can cause the plant stem to grow into the sunlight (Braam 2005). The entire

configuration of a plant (morphogenesis) is partially determined by abiotic mechanical inputs, for example wind and gravity (Morita and Tasaka 2004).

The detection of nutrition resources and their *periodic, cyclic availability* plays a key role in plant memory, planning, growth and development. When, for example, young trees obtain water only once a year, they learn to adjust to this over the following years and concentrate their entire growth and development precisely in the expected period (Hellmeier et al. 1997).

Interpretation processes in the plant body are highly sensitive. In taller-growing plants, for example, the *water balance* places enormous demands on cell wall development and cell wall structures, which must adapt to the (often extreme) pressures involved in storage and pressure distribution (Baluska et al. 2007). A sophisticated and multilevelled feedback- and feed-forward system guarantees a plant-compatible water balance even under extreme environmental conditions (Zimmermann et al. 2004, Buckley 2005).

Plants are especially sensitive to *light* and have various receptors for UV, blue, green, red and far-red light (Trewavas 2005). The angle of the light, combined with the sensation of the growth of adjoining plants, is decisive in enabling plants to coordinate their growth with respect to the optimal light angle and shade avoidance (Ballare 1999). The adaptive response of the plant, i.e. altered growth, depends on the seconds-, minutes- and hours-long dominating wavelength of the incoming light, and on the combination of wavelengths across the whole day. These abiotic influences trigger behavioural patterns which must be communicated within the plant body; the roots receive constant signals from the above ground parts of the plant for specific growth orientations (Baluska et al. 2006).

4. Plant communication with non-plant organisms

Sign-mediated interactions with organisms belonging to other species, genera, families and organismic kingdoms are vital for plants and are coordinated and organized in parallel. They are almost always symbiotic or parasitic and range from mutually beneficial via neutral to damaging behaviours. The different forms of symbiotic communication represent different pragmatic contexts and require a great variety of different behaviours from the participating partners. This involves large numbers of complementary (i) direct and (ii) indirect defence, but also (iii) mutual beneficial behaviours. There are some indicators that especially plant-derived extracellular g-Aminobutyrate (GABA) serves for sign-mediated communications between plants and animals, fungi, bacteria, and even other plants (Shelp et al. 2006).

4.1. Coordination of defence

Chemical signal substances are the oldest form of signs and are used by any organism: microbes, fungi, animals and plants (Witzany 2007). They are transmitted via liquids in the environment and can be distributed and perceived through the atmosphere. Leaves always emit such volatiles in small doses, but in the specific context of pest infestation by parasitic insects they emit greater quantities. This allows them to attack the parasites either directly by producing substances that deter them, or indirectly by attracting other insects that are natural enemies of the parasites. These volatiles are also perceived by neighbouring plants, allowing them to initiate pre-emptive defensive responses (Pare and Tumlinson 1999).

Depending on the different interactional context – destruction, injury or parasitic infestation – the emitted scents clearly differ for both the insects and neighbouring plants (Pare and Tumlinson 1999). The plants coordinate complementary direct and indirect defence mechanisms in a step-wise manner and tailor them flexibly to the severity of the injury or the density of pest infestation (Kant et al. 2004, Engelberth et al. 2004).

When plants are attacked by pests, they develop immune substances that function in the same way as in animals (Nürnberger et al. 2004). Injured plants produce aromatic substances that warn other plants. These warned plants rapidly produce enzymes that make the leaves unpalatable for herbivorous insects. Rather than being passive prisoners of their surroundings, plants are active organisms (Peak et al. 2004) that identify their pests and actively promote the enemies of these pests (Van der Putten et al. 2001).

In lima beans, for example, various coordinated defence strategies against mite infestation have been discovered. First, they change their scent to make them unattractive to the mites. Then the plants emit scents that are perceived by other plants, which then do precisely the same thing to warn surrounding lima beans before the mites even reach them. Some of the emitted substances have the effect of attracting other mites that eat the attacking red mites (Mithöfer et al. 2005). Similar defence processes have been described in tomato plants (Kant et al. 2004, Pearce and Ryan 2003).

Plant roots have the capacity to produce a great variety of secondary metabolites, many with cytotoxic properties, in order to prevent the spread of microbes, insects and other plant roots (Bais et al. 2003, Walker et al. 2003). For example, plants have developed defensive strategies in which substances are emitted in the root zone such as signal mimics, signal blockers and/or signal-degrading enzymes to respond to bacterial quorum sensing (Walker et al. 2003). In the defensive position, they can disrupt the communication of parasitic microorganisms to the point that the internal coordination of the parasitic group behaviour collapses.

4.2. Coordination of symbioses

In contrast to the sign-mediated coordination of defence behaviour, the communicative coordination of symbioses is a completely different pragmatic context. A limited number of chemical messenger substances is available to maintain and simultaneously conduct the communication between (A) root cells of three different types, (B) root cells and microorganisms, (C) root cells and fungi and (D) root cells and insects (Bais et al. 2003, Walker et al. 2003, Callaway 2002, Dessaux 2004, Dunn and Handelsman 2002, Teplitski et al. 2000). The communication processes in the root zone require a high communicative competence in order to be successfully interactive on all three levels (trans-specific, inter- and intraorganismic) and to distinguish biotic messenger molecules from molecules not part of biotic messages (Federle and Bassler 2003, Hirsch et al. 2003, Sharma et al. 2003).

It has been postulated that the origin of root cells in plants, and therefore the basis for the youngest organismic kingdom on our planet, arose through the symbiogenesis of fungi and algae (Baluska et al. 2006, Jorgensen 1993, Zyalalov 2004). One hypothesis assumes that land plants are the symbiogenetic product of green algae and a tip-growing fungus-like organism that combined autotrophic and heterotrophic capabilities (Jorgensen 2004).

4.3. Parallel communication of plant roots with bacteria, fungi and insects

Plants use their plant-specific synapses (Baluska et al. 2005) to conduct neuronal-like activities and establish symbiotic relationships with bacteria (Denison and Kiers 2004). Similar mutually advantageous relationships are established with mycorrhizal fungi (Vandenkoornhuyse 2002). A special type of plant synapse resembles the immunological synapse of animal cells and allows plants to respond to pathogen and parasite attacks as well as to establish stable symbiotic interactions with rhizobia bacteria and fungal mycorrhiza (Baluska et al. 2006, Estabrook and Yoder 1998, Yoder 1999, Keyes et al. 2000, Kahmann and Basse 2001, Imaizumi-Anraku et al. 2005). Electrical signals can reinforce chemical signals or overcome short-distance responses of fungal mycelia that can be present on root

surfaces (Van West 2002). Interestingly, rhizobia bacteria are taken up into plant cells via phagocytosis during symbiotic interactions with roots of leguminous plants (Samaj et al. 2004).

The symbiotic relationship between legumes and rhizobial bacteria leads to the formation of nitrogen-binding nodules in the root zone. Nod factor signalling and thigmotrophic responses of root hairs overlap here as well. This once again shows context-dependency, i.e. how the same signalling pathways are used for different content transfer (Guerts et al. 2005).

Today, several hundred species of fungi colonize more than 100,000 different plant species. This type of cohabitation requires symbiotic signalling (Lammers 2004). Roots develop from rhizomes in order to provide better conditions for mycorrhizal fungi, which in turn supply plants with better nutrients (Brundrett 2002). For the fungus the relationship is either balanced or predatory. Endophytic fungi, however, live in plants without triggering disease symptoms (Brundrett 2002).

Plants, insects and microbes share a particular repertoire of signals. Interestingly, some are therefore also employed strategically. Thus, plants also use insect hormones (prostaglandins) for specific defence behaviour. Signal theft is common. Because plants can detect their own signals, they can presumably also detect similar signals that are used in communication between insects (Schultz and Appel 2004).

5. Plant communication with other plants

Plants can distinguish between self and non-self (McCubbin 2005). In the context of defence behaviour, defence activities are initiated against foreign roots in order to protect the plant's own root zone against intruders. The individual sphere of a root, along with its symbiotic partners, requires certain fundamental conditions in order to survive and thrive. When these prerequisites are threatened by the roots of other plants, substances are produced and released in the root zone that hinder this advance (Bais et al. 2003, Walker et al. 2003, Dessaux 2004, Dunn and Handelsman 2002). Such defence activities are also deployed as antimicrobial substances against the microflora in the root zone.

Research has shown that plants can distinguish between damage caused by insects and mechanical injuries. Mechanically injured plants emitted substances that are *ignored* by neighbouring plants, i.e. do not trigger any kind of response behaviour, whereas they all reacted *immediately* to communicated pest infestation.

Plant roots produce a wide range of chemical substances for different purposes: (A) some enable species-specific interactions; (B) many of these substances are released tens of centimetres into the surroundings; (C) these substances have strong but not necessarily negative effects on animals, bacteria, viruses and fungi; (D) released substances have a defensive function against other plants; (E) many substances have absorptive characteristics that reduce the negative effects of substances (Bais et al. 2003).

Plants use biotic signals to inform each other about the presence, absence and identity of neighbouring plants, growth space, growth disturbances and competition (Callaway 2002). Plants that are removed and planted elsewhere *remember* the identity of their former closest neighbours for several months (Turkington et al. 1991). Recognition patterns in neuronal-like networks are one possible explanation.

6. Bio-communication of plants within their body

In contrast to the central nervous system of animals, which controls metabolism and reactions centrally, the control in plants is decentral. This enables plants to start independent growth or developmental activities in certain regions of their body, for example on how a particular

branch should grow, depending on the wind, light angle and overall 'architecture' of the plant body (Trewavas 2005).

The cellular organization of the roots is determined during the plant's embryonic development and is controlled by intercellular communication. Bonke et al. (2005) provide a particularly good example of communicative control of 10 phases of embryogenesis.

6.1. Intercellular communication

Short-distance communication differs considerably from long-distance communication; as a rule, they complement each other. Intercellular communication in the root zone (in the soil) differs from that in the stem region above ground (Baluska et al. 2004, Bonke et al. 2005, Golz 2005). Both are necessarily coordinated with one another in order to enable life in these very different habitats. Intercellular communication informs other plant parts about events in specific organs or regions of the plant (especially in large plants), for example sugar production in leaves, the reproduction in flowers and resource utilization by the roots (Xoconostle-Cázares 1999).

Plant cells are connected by plasmodesmata. These connecting channels enable the flow of small molecules as well as ions, metabolites and hormones, and allow the selective exchange (size exclusion limit) of macromolecules such as proteins, RNAs and even cell bodies (Baluska et al. 2004). Plasmodesmata integrate various communication types such as local and long-distance communication.

For long-distance signalling movement proteins play an important role. Movement proteins convey information bearing RNA from the stem and leaves to the remote roots and flowers. The movement protein allows the mRNA to enter the plasmodesmata tunnel, into the phloem flow. Phloem is a specific plant tissue important for nutrition transport. Once it has entered this transport system, it can reach all parts of the plant relatively rapidly. These RNAs can control the levels of other proteins. The level contains information for local tissues, for example about the general physical condition of the plant, the season or the presence of dangerous enemies (Xoconostle-Cázares 1999).

A wounded plant organizes an integrated molecular, biochemical and cell biological response. This strategy enables information to be transported across great distances, for example in tall trees (Schilmiller and Howe 2005). Proteins that can be detected by receptors enable a 'thoughtful response' (McClintock 1984) by plants. There are about 1000 known protein kinases/phosphatases, numerous secondary messengers and many thousands of other proteins (Trewavas 2005). Through their life cycles and their growth zones, plants develop a life history of environmental experience that they can pass on to later generations and, should they themselves live to be several hundred years old, utilize themselves (Trewavas 2005). Even small plants store stress experiences in their memories and then use these memories to coordinate future activities (Goh et al. 2003). Especially during growth, key information about the current status often takes a back seat to future-oriented processes, for example early root growth and nutrient supply to secure future developments such as larger leaves. From this perspective, plants must plan for the future and coordinate growth, food uptake and communication with symbionts (Trewavas 2003). The complementary differentiation of communication types into short-distance and long-distance signalling – with their different yet ultimately complementary tasks – requires cells to identify their position. They accomplish this by, among other things, detecting signals from neighbouring cells (Coupland 2005).

6.2. Intracellular communication

Last but not least, sign-mediated interactions which occur *within* the plant cells are considered here. Intracellular communication in plants transforms and transmits external messages into

internal messages that exert a direct (epigenetic) influence on the DNA storage medium and trigger genetic processes. This leads to the production of signal molecules that generate a response behaviour. Via endocytosis, however, bacteria, viruses and viroids interfere with this intracellular communication community of a plant and can support, disrupt or even destroy it. Intracellular communication offers viruses the opportunity to integrate certain genetically coded abilities of the host into their own genome or to integrate their own genetic data sets into the host genome. The ability of viruses to integrate different genetic data sets probably plays a major role in symbiogenetic processes (Villarreal 2005, Witzany 2005).

The eukaryotic cell is composed of a multicompetent nucleus as a basic building block of life and a cell periphery 'apparatus' that symbiogenetically descended from other endosymbionts. Interestingly, both the nucleus and viruses have several similar features and capabilities: they both lack the protein synthesis pathway and the fatty acid-producing pathways. Viruses were probably very important in the evolution of eukaryotic cells because they were able to conduct cell–cell 'fusion' (Baluska et al. 2005). There are powerful reasons to believe that the eukaryotic nucleus is of viral origin (Bell 2001, Villarreal 2005).

Reports on the transfer of mitochondrial genes between unrelated plant species caused some surprise. While gene transfer is an extremely rare event in animals and fungi, it is common between plant mitochondria (Andersson 2005). Variations in repetitive DNA that manifest themselves as variation in the nuclear DNA complex have far-reaching ecological and life history consequences for plants (Meagher and Vassiliadis 2005).

Plant endocytosis and endosomes are important for auxin-mediated cell–cell communication as well as for gravitropic responses, stomatal movements, cytokinesis and cell wall morphogenesis. Similar to in animals, in plants synaptic cell–cell communication is based on rapid endocytosis and vesicular recycling (Samaj et al. 2005).

Interestingly plants can overwrite the genetic code they inherited from their parents and revert to that of their grandparents or great-grandparents (Lolle et al. 2005, Weigl and Juergens 2005, Pearson 2005). This contradicts traditional DNA-textbook conviction that children simply receive combinations of the genes carried by their parents. Now, a backup code has been found; under certain stress influence it can bypass unhealthy sequences inherited from the parents and revert to the healthier sequences borne by their grandparents or great-grandparents.

Outlook

The youngest organismic kingdom and, perhaps, the main success story of evolution are plants. They originated about 350 million years ago, and terrestrial plants, which flower and bear fruits (a key prerequisite for feeding in larger animals), only evolved 150 million years ago. Higher plants make up 99% of the biomass on our planet; of this, nearly 84% are trees. The lack of mobility is often construed as a disadvantage vis-à-vis representatives of the animal kingdom. From a biosemiotic perspective, such immobility and the sessile lifestyle must have been an advantage. It led to a multilevel communicative competence which does not act in a serial but in a parallel way.

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