The Biosemiotics of Plant Communication

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Abstract: This contribution demonstrates that the development and growth of plants depends on the success of complex communication processes. These communication processes are primarily *sign-mediated interactions* and are not simply an mechanical exchange of 'information', as that term has come to be understood (or misunderstood) in science. Rather, such interactions as I will be describing here involve the active coordination and organisation of a great variety of different behavioural patterns — all of which must be mediated by signs.

Thus proposed, a biosemiotics of plant communication investigates communication processes both within and among the cells, tissues, and 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 will be seen in the cases under investigation, the context of interactions in which a plant organism is interwoven determines the content arrangement of its response behaviour. And as exemplified by the multiply semiotic roles played by the plant hormone *auxin* that I will discuss below, this means that a molecule type of identical chemical structure may function in the instantiation of different meanings (*semantics*) that are determined by the different contexts (*pragmatics*) in which this sign is used.

1. Introduction

Biosemiotics investigates the use of signs within and between organisms. Such signs may be signals or symbols, and many of them are chemical molecules. In the highly developed eukaryotic kingdoms, the behavioural patterns of organisms may also serve as signs, as for example, the dances of bees. Such signs obey the semiotic rules appropriate to their three level types. Thus: (1) their *syntax* determines the combinatory possibilities

of a given set of signs — whether physical and chemical (e.g., Watson-Crick-base-pairing), or spatial, temporal, and rhythmical (i.e., the relationship among the signs); (2) their *pragmatics* determines the relationship between a sign-user (within its interactional context) and the signs to be negotiated, and (3) their *semantics* (which is to say: their meanings) depend on the pragmatic interactional contexts within which a sign-using individual is, by necessity, interwoven — and, therefore, on the particular relation between the signs and the signified content that is required in the specific context.

Recent investigation into the biosemiotics of plant communication provides robust empirical evidence about *sign-mediated interactions* taking place incessantly both within and between plants, as well as between plants and non-plant organisms. As can be seen, there is a great variety of signalling processes in the organismic kingdom of plants, and this argues against the notion, held for too long now, that plants can be considered as automation-like organisms. With this article I hope to show that further investigation into the biosemiotics of plant communication may help us to better understand these fascinating organisms, in all of their communicative competence.

2. Plant Communication

Based on their apparently static life form, plants have often been viewed and studied as machine-like growth automatons (as evidenced by the practices of such leading agricultural biotechnology multinational companies as DuPont and Monsanto). Today however, it is increasingly becoming recognised that the coordination of development and growth in plants is made possible only by the use of signs, rather than by pure mechanics. Understanding the use of signs in communication processes requires us to adopt a semiotic perspective: for in the world of plant biology, as in the world of animal biology, chemical molecules are often used as signs. Such molecules, whether in a solid, liquid or gaseous form, function as signals, messenger substances, information carriers and memory media, in order to organise internal life processes and to guarantee agent-environment coordination.

Plants are sessile, highly sensitive organisms that actively compete for environmental resources both above and below the ground. As do all such living systems, they must somehow assess their surroundings, estimate how much energy they need for particular goals, and then realise the optimum variant. Similarly, they must take measures to control certain environmental resources, and as it has been shown that they perceive themselves and can distinguish between self and non-self (Trewavas 2003), this capability allows them to protect their territory. In short, like all organisms, plants process and

evaluate information, and then modify their behaviour accordingly (Trewavas 2003; Baluska and Mancuso 2007).

To understand these highly diverse competences, we must investigate those biologically necessary parallel communication processes that take place: within the plant body (*intraorganismicly*), between the same and different plant species (*interorganismicly*), and between plants and non-plant organisms (*trans-specifically*). Such successful communication processes allow plants to prosper; while unsuccessful ones have negative and potentially lethal repercussions. Similarly, intraorganismic communication involves sign-mediated interactions both within cells (*intracellularly*) and between cells (*intercellularly*). Intercellular communication processes are crucial in coordinating plant growth and development, as well as plant shape and dynamics. In order to be effective, however, such communication must function on both the local level and between widely separated plant parts, as we shall see.

2.1. A Chemical Vocabulary

The amount of chemical communication that takes place within and between plants is complex. More than 20 different groups of molecules having communicatory functions have currently been identified, and up to 100,000 different substances, known as secondary metabolites, are actively used in the root zone. Such diversity, it has been proposed, is necessary due to the high abundance of microbes, insects and related or non-related plant roots in this zone, and all the interactions made necessary thereby (Bais et al. 2003). For purposes of this overview, I will focus primarily on the important role in plant life that is played by the phytohormone called *auxin* — this being only one example of the molecular vocabulary used in plant communication (e.g., hormones, RNAs and multiple reusable elements) which I have discussed in more depth elsewhere (Witzany 2007), but which would exceed the space limitations of this overview.

2.1.1. Context-dependent Auxin as a Neurotransmitter, a Hormone, and a Morphogenic Sign

It has been established that plant: (1) roots and plant shoots detect environmental signals as well as development levels, and that they communicate over long-distance pathways; and that (2) the decentralised nervous system of plants is advantageous for decentralized growth and development under constantly changing environmental conditions (Baluska et al. 2004, 2006).

The phtyhormone *auxin*, we will see, is involved in both of these phenomena, and is used in hormonal, morphogenic and transmitter pathways in plants (Baluska et al. 2005). Yet because the pragmatic context of use

can be very complex and highly diverse, identifying the momentary usage is extremely difficult for researchers (ibid). In the specific context of synaptic neuronal-like cell–cell communication, plants use *neurotransmitter*-like auxin (Schlicht et al. 2006) and, presumably, neurotransmitters such as glutamate, glycine, histamine, acetylcholine, dopamine — all of which they also produce themselves (Baluska et al. 2004). Yet auxin is detected as an *extracellular* signal at the plant synapse (Baluska et al. 2005) in order to react to light and gravity. In a different context, it also serves as an *extracellular messenger substance* to send electrical signals; while in yet another, it functions as a *synchronisation signal* for cell division (Campagnoni et al. 2003). In the context of intracellular signalling, auxin plays a role in *organogenesis*, i.e., cell development and differentiation. In the organogenesis of roots, for example, auxin enables cells to determine their position and establish their identity (Casson and Lindsey 2003), while the cell wall and the organelles it contains help regulate the signal molecules.

Auxin is — as the name suggests — a growth hormone. *Intra*-cellularly, it mediates in cell division and cell elongation. At the *inter*-cellular ("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, together with organ growth as well playing a vital signalling role in the phenomena of tropic responses and apical dominance (Friml and Wisniewska 2005). Thus, dependent on the different pragmatic contexts in which the plant organism is interwoven, the same chemical molecule, auxin, is used for different purposes. This allows for the instantiation and transportation of different messages which, in turn, trigger different response behaviours.

3. Interpretation of Mechanical Influences

As I have written about previously in my examination of the coordination of plants in defence behaviour (Witzany 2007), plants are able to distinguish between biotic and abiotic influences. As with all living systems, brute mechanical contact has an influence on the overall organism and on the cell level. Such contact can cause plants to react aggressively, for example (a) toward the animals that attempt to eat them, (b) to discard their pollen, or (c) to cause the plant stem to grow into the sunlight (Braam 2005). The entire configuration of a plant (i.e., its morphogenesis) is partially determined by abiotic mechanical inputs, for example wind and gravity (Morita and Tasaka 2004). Likewise, 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 to take place precisely within the expected period (Hellmeier et al. 1997).

Interpretation processes in the plant body are thus highly context-sensitive. In taller-growing plants, for example, the plants' overall *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 multi-levelled feedback — and feed-forward — system guarantees a plant-compatible water balance even under extreme environmental conditions (Zimmermann et al. 2004; Buckley 2005).

Similarly, all land 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., its altered growth) depends on the seconds-, minutes-, and hours-long dominating wavelengths of the incoming light, and on the combination of these wavelengths across the whole day. These abiotic influences trigger behavioural patterns which must be communicated within the plant body; thus, the roots receive constant signals from the above-ground parts of the plant for specific growth orientations (Baluska et al. 2006).

4. Trans-specific Plant Communication

Sign-mediated interactions with organisms belonging to other species, genera, families and organismic kingdoms are vital for plants, and must be coordinated and organised in parallel (Baluska et al. 2007). Such interactions are almost always symbiotic or parasitic, and range from mutually beneficial to neutral to damaging behaviours (ibid). Such different forms of symbiotic communication represent *different pragmatic contexts* and require a great variety of different behaviours from the participating partners, often involving large numbers of complementary direct and indirect defence behaviours, as well as many mutually beneficial behaviours, as we shall see .

4.1. Coordination of Defence Against Pests and Injury

Chemical signal substances are the oldest form of signs and are used by all organisms: microbes, fungi, animals and plants (Witzany 2007). They are transmitted via liquids in the environment and can be distributed and perceived through the atmosphere. In the plant world, for example, plant leaves always

emit such volatiles in small doses, and in the specific context of pest infesta-
tion by parasitic insects, they emit these volatiles in greater quantities. This
allows them to attack the parasites, either directly by producing substances that
deter them semiotically, or indirectly by semiotically attracting other insects
that are natural enemies of the parasites. Such 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 meanings of the emitted scents clearly differ for
both the deterred or recruited insects and for the neighbouring plants (Pare
and Tumlinson 1999). In this way, plants coordinate complementary both
direct and indirect defence mechanisms in a step-wise manner, and tailor
them flexibly to the severity of the injury, or to the density of pest infestation
(Engelberth et al. 2004; Kant et al. 2004). Moreover, when plants are attacked
by pests, they develop immune substances that function in much the same
way as they do in animals (Nürnberger et al. 2004). Finally, injured plants
produce aromatic substances that effectively warn other plants to the source
of the injury. These warned plants rapidly produce enzymes that make their
leaves unpalatable for herbivorous insects. Thus, rather than being passive
prisoners of their surroundings, plants are active organisms (Peak et al. 2004)
that identify their pests and that in response take measures to solicit and
engage 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, these plants change their scent
to make them unattractive to the mites. Next, the plants emit scents that are
perceived by other plants, which then do precisely the same thing to warn
surrounding plants before the mites even reach them. Some of the emitted
substances have the effect of attracting other mites that eat the attacking mites
(Mithöfer et al. 2005). Similar defence processes have been described in to-
mato plants (Pearce and Ryan 2003; Kant et al. 2004). Similarly, many 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 even other (competing) 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 mimicing, signal block-
ing* and *signal-degrading* enzymes that respond to bacterial quorum sensing
(Walker et al. 2003). As a defensive manoeuvre, they can thus disrupt the
communication of parasitic microorganisms to the point that the internal
coordination of the parasitic group behaviour collapses.

4.2. Communicative Coordination of Symbioses

In contrast to the sign-mediated coordination of defence behaviour, the communicative coordination of symbioses takes place in a completely different pragmatic context. Here, a limited number of chemical messenger substances are available to maintain and to simultaneously conduct the communication between: (1) root cells of three different types, (2) root cells and microorganisms, (3) root cells and fungi and (4) root cells and insects (Teplitski et al. 2000; Callaway 2002; Dunn and Handelsman 2002; Bais et al. 2003; Walker et al. 2003; Dessaux 2004). Such communication processes in the root zone require a high level of communicative competence in order to be successfully interactive on all three levels (i.e., trans-specific, inter-organismic, and intra-organismic) and to distinguish biotic messenger molecules from molecules that are not part of biotic messages (Federle and Bassler 2003; Hirsch et al. 2003; Sharma et al. 2003).

Not surprisingly, then, it has been postulated that the origin of root cells in plants (which forms the basis for the youngest organismic kingdom on our planet) arose through the symbiogenesis of fungi and algae (Jorgensen 1993; Zyalalov 2004; Baluska et al. 2006). 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. Vital Symbiosis of Plant Roots with Bacteria, Fungi and Insects

It has recently been discovered that plants use their plant-specific synapses to conduct neuronal-like activities and to establish symbiotic relationships with bacteria (Denison and Kiers 2004; Baluska et al. 2005), while 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 (Estabrook and Yoder 1998; Yoder 1999; Keyes et al. 2000; Kahmann and Basse 2001; Imaizumi-Anraku et al. 2005; Baluska et al. 2006). Electrical signals can reinforce chemical signals and can 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 the roots of leguminous plants (Samaj et al. 2004). This symbiotic relationship between legumes and rhizobial bacteria leads to the formation of nitrogen-binding nodules in the root zone of the leguminous plant, with node factor

signalling and thigmotrophic responses of root hairs playing a decisive role in the symbiotic interaction here as well. This once again shows the biological importance of *context-dependency* in sign use — i.e., how the same signalling pathways are used for different sign-content transfer (Guerts et al. 2005).

Today, several hundred species of fungi colonise more than 100,000 different plant species, and this type of cohabitation also requires complex symbiotic signalling (Lammers 2004). For example, many 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, for example, live in plants without triggering disease symptoms (Brundrett 2002). And, of course, plants, insects and microbes share a particular repertoire of signals. Interestingly, some of these repertoires are also employed strategically. Thus, plants also use insect hormones (prostaglandins) for specific defence behaviour. Such signal theft is common, but 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. Interorganismic Communication

As I have mentioned earlier, it has now been scientifically established that plants can distinguish between self and non-self (McCubbin 2005). Thus, in the context of defence behaviours, defence activities are initiated against 'foreign' roots in order to protect the plant's 'own' root zone against intruders. This is so because 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 into the root zone that hinder this advance (Dunn and Handelsman 2002; Bais et al. 2003; Walker et al. 2003; Dessaux 2004). Such defence activities are also deployed as antimicrobial substances against deleterious microflora in the root zone. Similarly, research has shown that plants can distinguish between damage caused by insects and by mechanical injuries. Mechanically injured plants emit substances that are *ignored* by neighbouring plants, i.e., do not trigger any kind of response behaviour, whereas these same plants all reacted immediately to communicated pest infestation (Bais et al. 2003; Walker et al. 2003).

Plant roots produce a wide range of chemical substances for different purposes: some enable species-specific interactions; some are released tens of centimetres into the surroundings; some have strong but not necessarily negative effects on animals, bacteria, viruses and fungi; some have a defensive

function against other plants; and some have absorptive characteristics that reduce the negative effects of substances (Bais et al. 2003). Plants use such 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 appear to 'remember' the identity of their former closest neighbours for several months (Turkington et al. 1991). The presence of previously formed ('recognition') patterns in the plant's neuronal-like networks are one possible explanation for this phenomenon.

6. Intraorganismic Communication

In contrast to the central nervous system of animals, which controls metabolism and reactions centrally, such control in plants is decentralized. This enables plants to start independent growth or developmental activities in variously relevant regions of their body — influencing, for example, how a particular branch should grow, depending on the prevailing wind and light angle vis-à-vis the current overall 'architecture' of the plant body at that point (Trewavas 2005). Similarly, the cellular organisation of the root is determined during the plant's embryonic development and is controlled by intercellular communication. Bonke et al. (2005) provide a particularly good overview of the processes of communicative control specific to each of a plant's ten distinct phases of embryogenesis.

6.1. Intercellular Communication

Short-distance communication differs considerably from long-distance communication; yet as a rule, these processes tend to complement each other. Intercellular communication in the root zone (i.e., in the soil) differs from that in the stem region above ground (Baluska et al. 2004; Bonke et al. 2005; Golz 2005). Yet both of these processes are necessarily coordinated with one another in order to enable life that must take place simultaneously in these very different habitats. Accordingly, intercellular communication informs other plant parts about events in specific organs or regions of the plant (especially in large plants). Examples of this phenomenon include signalling representing the current state of sugar production in leaves, reproduction in flowers, and resource utilisation 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). Most

interestingly from a biosemiotic standpoint, however, is the fact that such plasmodesmata integrate various *communication* types and functions, as allowing for both local and long-distance communication.

For long-distance signalling, so-called 'movement proteins' perform an important role in plants. 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 and thereby move into the phloem flow (phloem is a specific plant tissue important for nutrition transport). Once the mRNA has entered this transport system, it can reach all parts of the plant relatively rapidly. These mRNAs can control the levels of other proteins, and the status of such levels contain 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).

Likewise, a wounded plant organises 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' (read: sign-mediated and context-specific) response by plants (McClintock 1984). Not surprisingly, there are about 1000 known protein kinases. phosphatases, and numerous secondary messengers — as well as many thousands of other proteins — necessary to the life of plants (Trewavas 2005). And 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, to later utilise themselves (Trewavas 2005).

Goh et al. (2003) claim that even small plants store stress experiences in their 'memories', and then use these memories to coordinate future activities. Especially during growth, key information about the current state of affairs is often subordinated to future-oriented processes. For example, information about early root growth and nutrient supply is used to secure future developments such as larger leaves (Trewavas 2003). From this perspective, plants must 'plan' for the future and coordinate growth, food uptake and communication with symbionts (Trewavas 2003). Finally, 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 own position within this larger communicative matrix. They accomplish this task by, among other methods, detecting and identifying signals from neighbouring cells (Coupland 2005).

6.2. Intracellular Communication

Last but not least, a few words must be said about sign-mediated interactions which occur *within* the plant cells. Intracellular communication in plants transforms and transmits external messages into internal messages that exert a direct epigenetic influence on the DNA storage medium, and that trigger genetic processes — and this, in turn, leads to the production of signal molecules that generate a response behaviour. Via endocytosis, however, bacteria, viruses and viroids can interfere with this intracellular communication community of a plant and can disrupt or even destroy it. Such exploitation of the plant's own intracellular communication system enables 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.

And yet, the ability of viruses to integrate different genetic data-sets probably plays a major role in symbiogenetic processes (Villarreal 2005; Witzany 2005). This is because the eukaryotic cell is composed of a multicompetent nucleus as a basic building block of life and a cell periphery 'apparatus' that is itself most likely symbiogenetically descended from other endosymbionts. Interestingly, both viruses and the eukaryotic nucleus have several similar features and capabilities — most notably, they both lack their own dedicated protein synthesis pathways and fatty acid-producing pathways. Viruses were probably thus very important in the evolution of eukaryotic cells because they were able to conduct cell–cell 'fusion' (Baluska et al. 2005). Thus, 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 in the biological community (Andersson 2005). Yet 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). In a similar vein, 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 the case in animals, synaptic cell–cell communication in plants is based on rapid endocytosis and vesicular recycling (Samaj et al. 2005).

Perhaps most interestingly of all, 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; Pearson 2005; Weigl and Juergens 2005). This contradicts the traditional DNA-textbook conviction that offspring passively receive combinations of the genes carried by their parents. For now a 'backup'

genetic code has been found — and under certain stress influences, the plant can bypass unhealthy genetic sequences inherited from its parents and revert to the healthier sequences borne by their grandparents or great-grandparents (Lolle et al. 2005; Pearson 2005; Weigl and Juergens 2005).

7. Future Outlook

Plantae is the youngest of the organismic kingdoms and, perhaps, the main success story of evolution. Land plants (embryophytes) 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. Plants make up 99 percent of the biomass on our planet; of this, nearly 84 percent are trees. Their lack of mobility is often construed as a disadvantage vis-à-vis representatives of the animal kingdom. Yet from a biosemiotic perspective, such immobility and the accompanying sessile lifestyle must have been of some evolutionary advantage, for it led to a multilevel communicative competence which does not act in a serial, but in a parallel manner. Thus, although plants maintain a lifestyle with environments, body physiologies, and vital symbiotic partnerships that are completely different to those found in the organismic kingdom of *Animalia*, the preceeding biosemiotic overview shows that plant organisms, like animal organisms, organise and coordinate all *life* processes through the *communication* processes of *sign-mediated interaction*.

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