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Opinion

Plant Growth and Development from Biocommunication Perspective

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Abstract: Different movement patterns are crucial behavioral motifs of plant organisms for reaching essential resources necessary for survival. This requires the accurate evaluation (interpretation) of information inputs regarding (i) abiotic factors such as gravity, light, and water; (ii) neighboring plants; (iii) various beneficial symbionts, including fungi and soil bacteria, as well as pests, which involve attack and defense strategies; and (iv) intraorganismic communication, including transcription, translation, immunity, repair, and epigenetic markings relevant to all regulation processes, finally outlined by a plethora of non-coding RNAs. The coordination of all steps and substeps in plant growth and development necessitates a complex organization of various levels of signaling processes within and between cells, tissues, organs, and organisms. Consequently, we can view a plant body as a coordinated entity that integrates these processes to thrive, representing a unique identity within its environmental niche.

Keywords: communication; signal-mediated interaction; coordination; growth; development

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1. Introduction

Is it possible for animals (including humans) to understand the biological communication of plant growth and development? Philosopher Ludwig Wittgenstein stated, "If a lion could speak, we could not understand him" [1]. Why? To understand a species-specific language in its real-life context, we would need to share the social lifeworld of that species from within, which is impossible for humans. Language use in communicative interactions relies on linguistic competence (the ability to generate correct sign sequences/sentences) and communicative competence (the ability to engage in social interaction), both of which are triggered and learned within species-specific social group behaviors. In the case of lion communication, we cannot achieve this in principle.

What does this imply for our goal of understanding plant communication? Charles Sanders Peirce proposed that to identify the "…meaning, we have, therefore, simply to determine what habits it produces" [2]. This suggests that we can understand a language without being part of the real social lifeworld of the species, but rather by observing the habits that follow signaling processes and statistically comparing and interpreting those actions that function as response behaviors. If we, e.g., identify auxin concentration, we may look at the habits that are performed with auxin as a signaling molecule, such as developmental processes, other movement patterns, or even immune reactions. The same molecule may generate various meanings depending on the context of use [3]. Close to Peirce's suggestion is Wittgenstein's pragmatic aspect of signal use: "The meaning of a word is its use" [1]. To identify the meaning of a sign sequence (such as a word), we have to look at its use in the real-life context of the signal-using agent. This contradicts mathematical theories of language and communication, which insist that the meaning of a word mechanistically depends on its unequivocal grammar or syntax, independent of

the sign-using agent. This view has been disproven. The unequivocal grammar of a sign sequence, such as "The shooting of the hunters", does not represent its meaning; rather, its concrete use in real-life contexts can lead to very different (and even contradictory) meanings [4].

To summarize this for investigations on plant communication processes in growth and development:

- We cannot understand plant language in communication processes as other plants do.
- We may identify the meaning of plant signaling by observing the habits (growth and development) it produces within real-life habitats.
- To identify the meaning of signaling in plant growth and development, we have to carefully examine the context of signal use within various interaction patterns.
- The context of use may vary according to the four levels of communication of plants: (a) signaling within the plant body, (b) signaling with other plants, (c) signaling with non-plant organisms, and (d) sensing and interpretation of abiotic influences.
- Actors in plant communication include various types of cells, tissues, and organs, all of which exhibit highly complex interaction patterns coordinated by various signaling processes.
- Biological communication in plants during growth and development is not a mechanistic process; rather, it is highly adaptable and context-dependent.

2. Growth and Development Through Biological Communication of Plants

Plants are sessile organisms, meaning that unlike nearly all animals (with exceptions such as corals or sponges), they have a fixed geographical location from the beginning of their life until death. However, plants are far from being immobile organisms or growth automatons. They grow through various movement patterns [5].

This article will not list all the signaling molecules involved in plant communication processes, such as hormones (e.g., auxin, cytokinin, gibberellin, ethylene, abscisic acid, and systemin), secondary metabolites (approximately 100,000 different substances), neurotransmitters (glutamate, glycine, histamine, acetylcholine, and dopamine), multiple re-usable components (nitric oxide and reactive oxygen species), etc. This was outlined in a previous article [6]. Instead, the focus here is on the various interactions (mediated by signals) that coordinate cells, tissues, and organs to achieve the goals of different movement patterns. This means that I will look here at the various communicative actions within the different behavioral motifs that lead to plant growth in the different cells, tissues, and organs, not at the abundance of molecular processes in detail [7]. This includes movement toward light, flower movements (opening and closing), and root movements in response to water and nutrient resources. Also, we must differentiate between the movement of whole organs and that of individual cells (motor cells such as guard cells or pollen) [8].

It is crucial to acknowledge that in all the abundant growth and developmental processes of all cells, tissues, and organs of plants, every step is part of a coordinated interaction mediated by signaling processes [9,10]. The prevailing perspective here is that developmental processes depend on successful communication [11,12]. If communication processes fail (becoming incomplete, damaged, or deformed), the final goal will not be achieved [13].

3. Various Levels of Signaling in Plants

First, we must differentiate the various levels of signaling in plants with which these organisms coordinate their behavior as cells within tissues and organs (Figure 1). This integrative model has been successful in categorizing biological communication across all domains of life [14–20]. It identifies all relevant levels of plant communication without

using mathematical theories of communication and their outdated sender–receiver narratives. Scientific arguments cannot continue to rely on concepts that have already been demonstrably disproven [4,21].

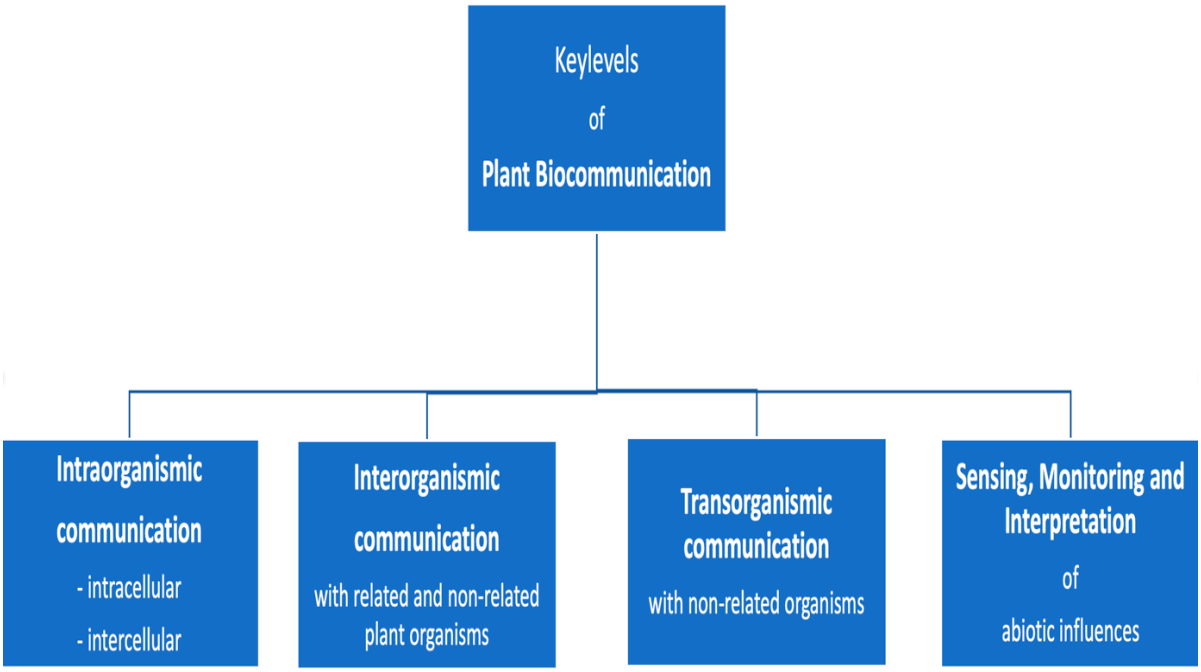

Figure 1. As in all domains of life, including plants, we can identify four different levels of biological communication.

4. Intraorganismic Communication: Intra- and Intercellular Signal-Mediated Interaction

Intracellular communication ensures the coordination of various steps of genetic transcription, translation, repair, and immunity. The genetic storage medium of plants consists of three components: (i) mitochondria, which are relevant for cellular respiration, immune functions, and oxidative phosphorylation; (ii) chloroplasts, which are responsible for photosynthesis, transforming water and light into glucose; and (iii) the nucleus, which oversees replication and gene expression. The mutation rates of these three genetic storage media are similar. Research on the roles of circadian clocks has identified several genes that code for chlorophyll-binding proteins of the light-harvesting complex [22,23].

4.1. Intracellular Communication: Non-Coding RNAs Are Key Players

Non-coding RNAs were long considered junk DNA, remnants of former evolutionary genetic stages. This misconception was corrected in the last decades of the 20th century when it became increasingly evident that only 2% of transcribed RNA is translated into proteins, while most of the remaining non-coding RNAs serve as essential tools for gene regulation in eukaryotic genomes [24].

Research has since shown that nearly all regulatory processes in eukaryotes are outlined by RNAs in transcriptional and post-transcriptional gene expression [25]. Whether long non-coding RNAs, short RNAs, or small interfering RNAs, RNAs are expressed in a tissue-specific manner according to a dynamic regulation of developmental timing [26–29]. A variety of repetitive sequence grammar and transposable elements indicate a viral-infection-derived evolutionary origin, which have been co-opted into a persistent status, serving as beneficial regulatory tools for host purposes [30–32].

RNAs carry out various protein functions derived from the genetic text according to the environmental needs of the specific (contextual) life world of the plant, indicating alternative splicing after transcription. This activity ensures a variety of possible proteins from an identical genetic DNA sequence [33]. RNA regulatory elements are involved in all cellular processes of transcription, translation, immunity, repair, and epigenetic markings (including their modification) [34,35]. They constitute the toolbox of biological communication in plants, essential for organization and coordination within and between cells, tissues, organs, and even organisms [36–38]. Particularly, transcription-derived microRNAs are crucial for a variety of regulatory processes in plant growth and development [39–44].

Interestingly, RNAs not only serve as intraorganismic and interorganismic communication tools but also play significant roles as communicative signals with non-plant organisms. Their ability is not restricted to transport from cell to cell via phloem or plasmodesmata; they can also be secreted outside the plant body [45]. This role means that RNAs serve as communication tools between plants and, for example, insects, filamentous fungi, nematodes, parasitic plants, and microorganisms in the rhizosphere; endophytic microorganisms; and microorganisms in the phyllosphere. Additionally, extracellular vesicles are important signal-trafficking tools for RNAs, hormones, and metabolites [46].

In all cases, communication does not imply mere information exchange but concrete interaction mediated by signals with various goals [47]. Some studies have also demonstrated that plant microRNAs, when orally acquired by animals, can pass into the mammalian gastrointestinal tract and regulate gene expression in mammals [48–50].

4.2. Epigenetic Programming

Epigenetics examines how environmental factors influence gene expression [51]. This encompasses not only abiotic influences but also the biotic impacts of other plants, animals, fungi, bacteria, and viruses. To generate appropriate response actions, plants must sense, monitor, and interpret these impacts and then decide on the signaling pathways for an appropriate reaction [52,53]. Whether plants face pests or other threats, strong winds, drought, or flooding, these factors can alter growth and developmental processes. After correctly interpreting the sensed information, the organization of an appropriate response can be coordinated.

Changes in DNA methylation, histone modification, and chromatin structures serve as appropriate (re)action tools to adapt to informational impacts. The programming and eventual reprogramming of these epigenetic markings are outlined by various RNAs. RNAs, therefore, regulate plant defense actions and dynamically alter DNA methylation in response to abiotic stress. RNAs drive epigenetic markings and adapt these markings to changing environmental influences, whether abiotic or biotic. The epigenetics of plants represents the ultimate layer in which various plant cells are regulated in a spatial and timely manner, meaning that they are precisely positioned within the relevant tissue and organ [47].

All signal-mediated interactions in epigenetic programming and reprogramming are outlined by RNAs. Particularly, the coordination of plant defense mechanisms is orchestrated by small RNA-mediated epigenetic modifications. If biotic stress is the cause, dynamic DNA methylation helps the plant adapt to this context. The various response behavioral motifs that orchestrate defense mechanisms are outlined by histone modifications in coordination with DNA methylation [47]. Interestingly, plant memory plays a crucial role in defense and disease resistance, as epigenetic markings from previous experiences may be adjusted to enhance responses to similar experiences in the future [51,54]. It has also been found that plants can “overwrite” their inherited genetic text and revert to that of their grandparents or even great-grandparents. If certain genetic sequences lead to

unhealthy expression patterns, plants can replace those parental genetic sequences with similar codes possessed by their grandparents or great-grandparents [55,56].

4.3. Transgenerational Inheritance of Epigenetic Variations

All cell types in all plant tissues are regulated epigenetically, which means that methylated chromosomes represent the functional identity of the cells and ensure the orchestrated interaction of the tissues during all developmental stages. These epigenetic states represent memory functions of the contexts experienced in real-life situations. Such epigenetic markings can be inherited transgenerationally [57]. Transgenerational inheritance represents reversible non-genetic patterns transferred from grandparents to grandchildren, which may change according to adaptive purposes. We know that certain epigenetic changes are induced by environmental and genomic stress experiences [58]. Various examples of transgenerational inheritance of epigenetic variation have been documented during plant evolution, breeding, polyploidy evolution, and the domestication and de-domestication of crops and rice [59]. Some mechanisms for transgenerational inheritance have been identified in hybridization-induced epialleles [57]. Transgenerational inheritance of memorized experiences may help progeny better adapt to forthcoming challenges [60].

4.4. Intercellular Communication: Coordination of Tissues and Organs

Plant movements must be coordinated within the plant body through signaling processes between various cell types [61–63]. Short- and long-distance signaling is coordinated throughout the plant body and works complementarily [64–66]. The successful communication processes ensure appropriate coordination among the various cell members [67]. If communication is disturbed or deformed, the communicative interaction leads to less successful coordination, and the movement in developmental or growth processes will not achieve their intended goals.

This fact is relevant in all coordination organizations of cells that are part of specialized tissues, such as in the plant embryo (seed coat, endosperm, cotyledons, hypocotyl, and radicle), various types of root cell tissues (bulbous, prop roots, pneumatophores, epiphytic roots, or haustoria), and stem cell types (nodes and internodes, apical buds, and auxiliary buds) such as herbaceous, woody, unbranched, and branched stems or leaf parts (tip, midrib, margin, vein, lamina, and petiole). Each action of each cell in a tissue is coordinated with the others through signaling processes [68].

Plant movements, growth processes, and development are investigated across a variety of tissues and organs [69,70]. The most prominent tissues include dermal tissue with important roles in protection, gas exchange, and water absorption; vascular tissue (xylem and phloem), which is essential for transporting water, minerals, and sugar to all parts of the plant; and ground tissue, which serves various context-dependent functions. The most prominent organs are roots (dermal tissue: root hairs and epidermis; ground tissue: cortex, endodermis, and pericycle; vascular tissue: xylem, phloem, and cambium), stems (dermal tissue: epidermis; ground tissue: cortex and pith; vascular tissue: xylem and phloem; meristematic tissue: cambium), and leaves (dermal tissue: cuticle and epidermis; ground tissue: palisade mesophyll; vascular tissue: xylem and phloem; ground tissue: spongy mesophyll). When plants develop flower buds, this process is organized from meristem tissues in various coordinated steps, such as forming rings, sepals, petals, stamens, and pistils. The apical bud dominates, and its signaling determines the dormant phase of the axillary buds. Apical buds produce auxin, which is lost if this bud is damaged or destroyed. The absence of auxin triggers growth and cell division in lateral buds.

The ultimate foundation of every kind of cell growth and development lies in the apical (tips of shoots and roots), lateral (secondary growth), and intercalary (in the middle

of stems and leaves) meristem cells [71]. If resources are available, plants will develop new roots, stems, and leaves without limitation. Meristem cells build differentiated and specialized tissues at the vascular, ground, or dermal levels. These meristem cell actions encompass growth and development in both height and breadth, meaning that plants will grow taller and broader (primary and secondary growth). This process begins with root growth following embryo development from seeds. Of particular interest is the coordination of organizing the root tip with its cell layers: root cap, and the zones of cellular division, elongation, and cellular maturation (root hairs) [72,73]. The root system, which explores, measures, and interprets available resources, communicates dynamically, which is crucial for further growth and development in the shoot zone.

When the coordination activates lateral meristems, the goal shifts from vertical growth to horizontal expansion [74]. Intercellular communication is not divided but runs in parallel. In forests with high trees, this is more critical than in non-woody plants, because the production of strength and structure is essential for the survival of these types of plants [75,76].

5. Interorganismic Communication

Plants are typically part of a community of similar, related, or unrelated plant organisms. A variety of species-specific signaling processes ensure adaptation to environmental niches, balancing competition and cooperation [77]. This activity may also include parasitic behavior as well as altruistic (kinship) support for survival, as observed in various tree species within forests.

Plants must ensure growth and development in the root zone. They can distinguish between self and non-self, producing substances in their roots, which are emitted into the surrounding soil. In most cases, these substances act as defense strategies against other plant roots [78,79]. Other substances mitigate the negative impact of foreign substances from other plants.

Research into interorganismic interactions among similar, related, and even unrelated plant organisms has revealed that plants can warn each other by emitting volatiles, which neighboring plants sense as alarm calls, triggering the production of protective substances even before pests attack [80–83]. This behavior exemplifies mutualistic action, which depends on high sensory quality for monitoring, interpretation, and reaction, all coordinated through step-by-step signaling processes.

6. Transorganismic Communication

Transorganismic communication encompasses all signal-mediated interactions between plants and non-plant organisms. These interactional motifs may involve active actions to achieve goals such as nutrition or attracting essential symbiotic partners through various pheromone-like substances and color patterns for pollinators, or passive responses in the case of pests or even mimicry [84,85]. As mentioned earlier, signaling that initiates defense against pests includes communication to related plants as warning signals, enabling them to produce repellents before pests reach their plant bodies. Signaling molecules (semiochemicals) are typically liquids that can be transmitted through the air (volatiles) or even underground [86]. Such defense actions deter parasites directly or indirectly, as emitted volatiles may attract the enemies of the parasites. The airborne semiochemicals, as well as the repellent substances that accumulate in the leaves to render them unpalatable for herbivorous insects, are tailored flexibly according to the nature of the injury or the intensity of the parasite attack.

Plants face various types of bacteria, fungi, and animals (insects, mites, and nematodes) that can cause injury in plants with a range of disease consequences. For example, plants can

emit substances in the root zone that disrupt the communication of parasitizing microbes. All these different attacks must be sensed, monitored, and interpreted by the plant to organize an appropriate, step-by-step defense action.

Simultaneously, plants have several essential symbiotic interaction networks, without which they would not survive [87]. The best-known examples are found in the symbiotic signaling in the root zone with mycorrhizal fungi and soil bacteria, as well as above ground with various animals specialized in pollinating plants, such as bees and birds [88–93]. Through symbiotic partners, communication ensures the availability of nutrients essential for plant growth and development.

Such signaling processes are crucial for the movement of plants. It guarantees normal development and growth processes. A massive attack by pests may damage leaves, buds, stems, or roots, adversely affecting plant growth and developmental processes [94]. Various plant enemies, such as parasitic plants, must also be defended against, as they can pose serious threats to plant growth and development [95].

7. Sensing, Monitoring, and Interpretation of Abiotic Influences

Essential for coordinating the growth and development of plants are the sensing, monitoring, and interpretation of abiotic influences. This activity includes not only nutritional requirements, which are vital for survival (light and water), but also adaptation to changing circumstances in the real world, such as drought, temperature fluctuations, deficient nutrients, flooding, or salinity [96]. Plants must be able to sense changing conditions, monitor them, and interpret them to generate appropriate response behaviors [95]. If sensing, monitoring, and interpretation are insufficient, the response behavior may be inappropriate. Appropriate response behavior must be coordinated between root and shoot zones in a timely manner, encompassing immediate, medium-term, and long-term reactions.

Coordination requires various levels of context-dependent signaling within and between cells, tissues, and organs of the plant [97]. All of this communication has consequences for the various plant parts according to their goals in development, growth, reproduction, epigenetic markings, and, finally, evolution.

The transport of water (up and down) creates significant pressure on cell walls, which is an important input for cell wall growth and development and must be coordinated within the cells in accordance with other cells within the tissue. As plants need solar energy and CO_2 to produce carbon compounds that can be transformed into polysaccharides and/or proteins, there is a coordinated interaction to transport these resources to the growing parts of the plants. Some of these resources may be stored for later needs. To achieve this goal, there must be a response to the monitoring and interpretation of the timely available resources to maintain a good balance between transpiration and photosynthesis. All of this must be coordinated between leaves and roots in a timely manner. Not only short-distance signaling within the various tissues but also long-distance signaling (via hormones) guarantees successful coordination [98–101]. Monitoring and interpretation of nutrient deficiencies lead to changes in the shoot–root ratio, meaning that young leaves will age more slowly while old leaves and roots may grow faster, adapting growth to the altered environmental conditions.

Sensing, monitoring, and interpretation (SMI) of changes in nutrient availability drive plant activity in the root zone to explore other regions. This communicative action is driven by nitrogen, sulfur, and phosphor signaling pathways. When nutrients limit growth, soil nutrient uptake is strongly selected [102]. SMI in the case of flooding changes root growth near the underground surface. Additionally, (a) root anatomy is altered to achieve the goal of better oxygen transport in the root tips; (b) hormonal changes occur in ethylene synthesis; (c) metabolism adapts to lower oxygen dependence; and (d) various minerals in the soil

are excluded [103,104]. SMI in response to heat or cold improves cold tolerance pathways, maintenance of pollen fertility, respiratory acclimation, and metabolism slowing [105,106]. SMI in the case of salinity leads to reduced spatial cell division and changes in root uptake management to support the uptake of fresh water and nutrients. Root signaling may also reduce shoot growth and exclude salt uptake by root cells [107,108]. SMI in response to drought leads to reduced transpiration by the leaves, changes in leaf and root development, enhanced shoot-root signaling according to water availability, increased photosynthesis, and decreased respiration [109–111].

It has been observed that in the case of abiotic stress, there is an increase in reproductive growth and a decrease in vegetative growth, which means the shoot apex does not develop leaves but floral buds. All these communicative actions, mediated by a variety of selectively used signaling molecules, require signaling processes within each cell of a tissue, according to transcription and translation, in a highly coordinated manner that ensures the relevant role of each cell within its tissue [112].

8. Conclusions

The presented overview of the key levels of biocommunication in plant growth and development serves as a framework for research on any issue of signal-mediated interaction in plants. It enhances an integrative understanding of the variety of signaling processes relevant to different goals of plant movement patterns. Additionally, it ensures that the context of the signaling process is in focus to identify the meaning of the signals for the relevant cells, tissues, and organs. To better understand plants, it is essential to recognize that biological communication (biocommunication) is not a mechanistic process that functions like a machine. What were previously termed mechanisms in all detailed steps and substeps are highly coordinated and organized signaling pathways, each of which can be varied according to RNA regulation and epigenetic markings (memory and learning), depending on the real-life context. Communication ensures high adaptability in every detailed signaling process, as the meaning of signals depends on the context of use within the abundance of growth and developmental actions. If we adopt this explanatory model in the future, plant growth and development will provide us with a new perspective on the rich signal-mediated interactions of plant organisms.

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