Plants: Unitary Organisms Emerging From Integration and Self-organization of Modules

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Abstract The organs roots, stems and leaves of plants have evolved under the challenges of the terrestrial environment where they are firmly rooted. Emergence of plants as unitary integrated organisms occurs by integration of these parts, organs or modules. Below this scaling level of morphology and the organs, there are modules on finer scaling levels, tissues at the level of anatomy, organelles and compartments at the level of cell biology, macromolecules at the molecular level and so on. Modules are connected and integrated forming the knots in networks. Networks at a finer scale can integrate, condense and self-organize to form knots in networks at the next coarser scale. In this way, hierarchies of networks are built up leading to the emergence of whole plants. Requirements for the integration are (i) signals carrying information, (ii) receptors for the signals, (iii) transduction of signals within systems and networks, (iv) cross-talk between different types of signals by their translation into each other and (v) configuration of information as instruction for reactions. Integration is organized during development where tight structural and functional correlations are built up under the systemic control of development. Self-organization uses both correlative inhibition and correlative stimulation, with homoiogenetic induction of self-resemblance and heterogenetic induction of unlike-self, respectively. Examples of integration are source-sink relations of water, nutrients and photosynthetic products, induction of flowering, orientation in space under gravity and light, environmental relations under herbivory and salinity. Plants are unitary organisms without a neuronal system. The whole is more than the sum of its parts (Aristotle 384–322 BC).

Parts and Modules of Plants

Figure 1 shows the scheme of a higher land plant between a giant brown alga of the genus *Laminaria* and the reconstruction from a fossil of one of the earliest land plants *Rhynia* in the fern allies Psilophyta. The major parts of higher land plants are

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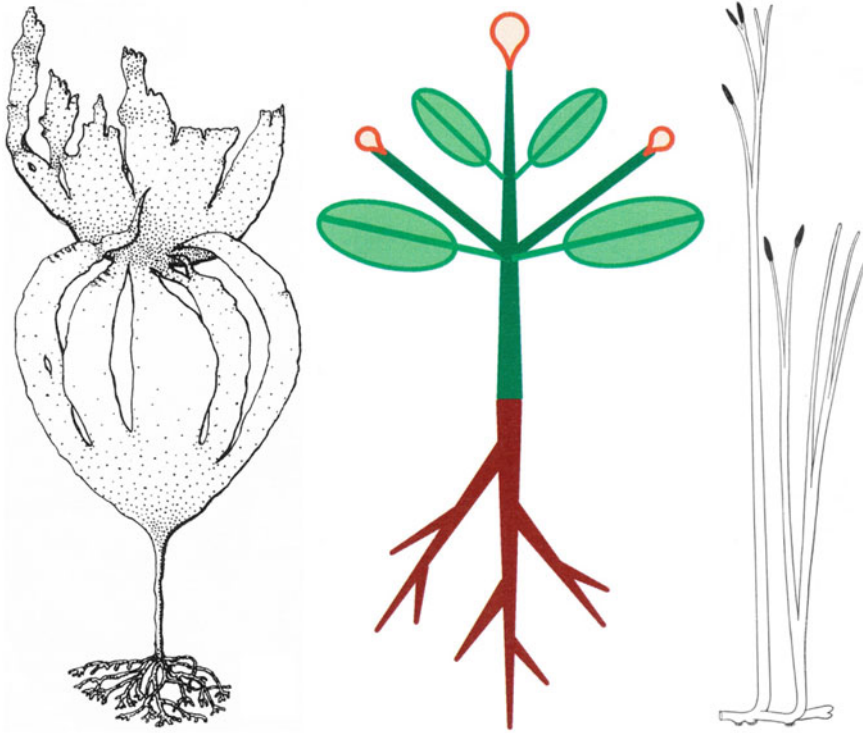e-mail: luettge@bio.tu-darmstadt.de

Fig. 1 Scheme of a higher land plant with its organs roots, stems and leaves between the brown alga *Laminaria* with rhizoids, a cauloid and a phylloid (left: After H. Schenck, from Kadereit et al. 2014) and the reconstruction of *Rhynia* from a fossil (right: From Zimmermann 1930)

the organs of roots, stems and leaves. We do not single out flowers here, because they are built up of metamorphoses of leaves. We may consider these organs as "modules," where we apply a very straightforward definition of modules as being parts or components of a system. This is a simple practical definition (Bolker 2000). The term module refers to "repeated, often semiautonomous … units" (de Kroon et al. 2005). The possession of roots, shoots and leaves appears as a general basic building principle of the gestalt of larger multi-cellular plants. The brown algae lineage is not directly linked to the lineage of higher land plants. The large bodies of brown algae or kelp have root-like ("rhizoid"), stem-like ("cauloid") and leaf-like ("phylloid") organs. They evolved parallel to and independent of roots, stems and leaves. It is a case of convergence (Morris 2003). However, *Rhynia* on the direct line to all higher land plants did not have roots and leaves yet. It consisted of slender about 1 m tall dichotomically branched shoots and had horizontal rhizomes, derivatives of shoots, in the soil.

Self-organization leads to the formation of patterns (Johnson and Lam 2010). In this way, development can be a result of self-organization, where patterns originate
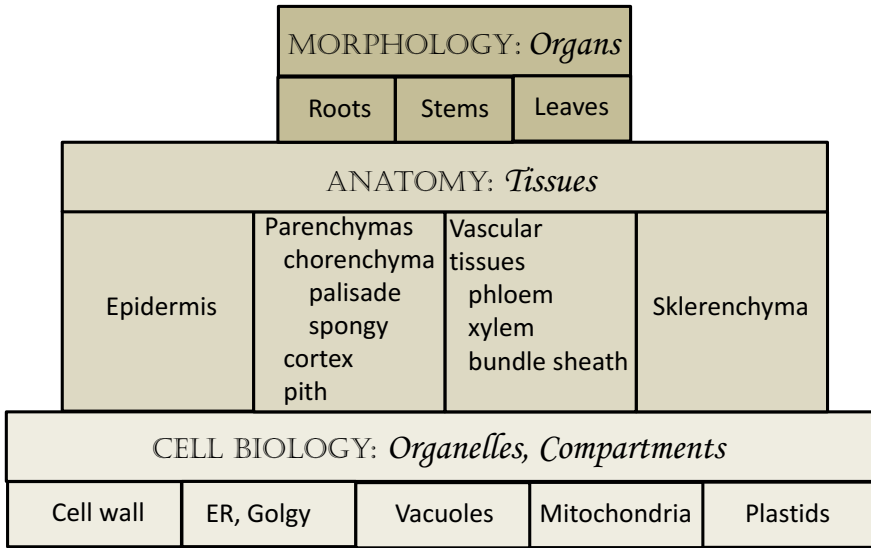
Fig. 2 Modules of plant structures at three different scaling levels

from divisions and differentiation of primordial cells. In morphogenesis, interaction of components of patterns creates new organized structures. The EVO-DEVO concept relates evolution and development. They are linked by feedback loops. There is "*evolution of development*" (Gould 2002). In return, development provides the material for natural selection. When Charles Darwin (1809–1882) developed the theory of evolution, many of his arguments were founded on development and growth (Friedman and Diggle 2011). He considered development and embryology as the most important aspects of natural history. Self-organization marks the frame within which evolution can select, and it is a tool of selection (Johnson and Lam 2010).
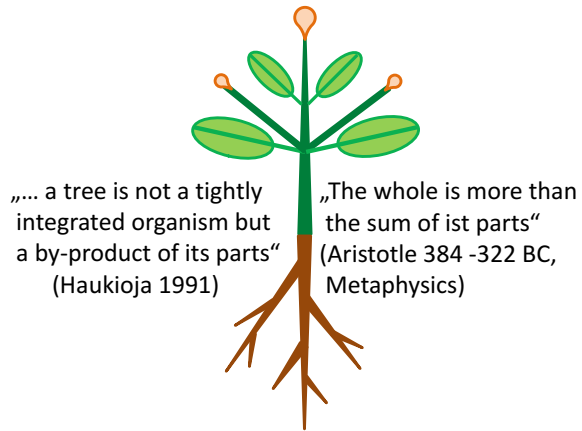
In addition to the modules or organs of the whole plant at the scaling level of morphology, Fig. 2 lists modules on two finer scaling levels, namely tissues at the level of anatomy and organelles/compartments at the level of cell biology.

Modularity Versus Emergence

Modularity

Modularity separates components of systems. The components are modules, and each module is regarded by itself. The view of modularity denies that plants with their "vegetative" life lacking integrating neuronal systems are unitary organisms (Fig. 3; Lüttge 2013). It considers plants as being the sum of their parts, where, for

Fig. 3 The points of view of modularity (left) and emergence (right)

„... a tree is not a tightly integrated organism but a by-product of its parts" (Haukioja 1991)

„The whole is more than the sum of ist parts" (Aristotle 384 -322 BC, Metaphysics)

example, a tree is just a "by-product of its parts" (Haukioja 1991). The study of separated individual modules is important, and it is essential. Their properties need to be known. Conceptually, the isolation of modules, however, is reductionism. It reduces the degrees of freedom given by interactions. Practically, it is an approach of specialization.

We know structural as well as dynamic functional modules, such as given processes or pathways (Bolker 2000). Going through levels of scaling, we realize that modules at finer scales are themselves composed of modules. Figure 2 shows this for three structural scaling levels of plants. The module "organ" is composed of the modules of tissues, and the module "tissue" is built up of the modules organelles or compartments.

Therefore, even when taken to lack external integration, individual modules clearly show internal integration (Bolker 2000). This leads us to distinguishing a hierarchy of modules over scaling levels. From Fig. 2, we can deduce the circles of Fig. 4. In the latter figure, each circle size would correspond to modules at a specific scaling level. The largest circle would represent the whole plant, which can be a module in vegetation or in an ecosystem, not to be treated in this chapter (but see chapters by Beck 2019 and zu Castell et al. 2019 in this book). The second largest circles would be the organs. Each one as a whole can be taken as a module at the level of morphology. The third largest circles would be modules of organs, i.e., the individual tissues at the level of anatomy. Again taken as individual modules, tissues would be composed of the fourth largest or smallest circles drawn, i.e., the modules of organelles and compartments. The consideration of such hierarchies could be continued for still finer scaling levels, i.e., compartments and organelles are built up of membranes and complex molecular structures, which again would consist of complex macromolecular components and so on.
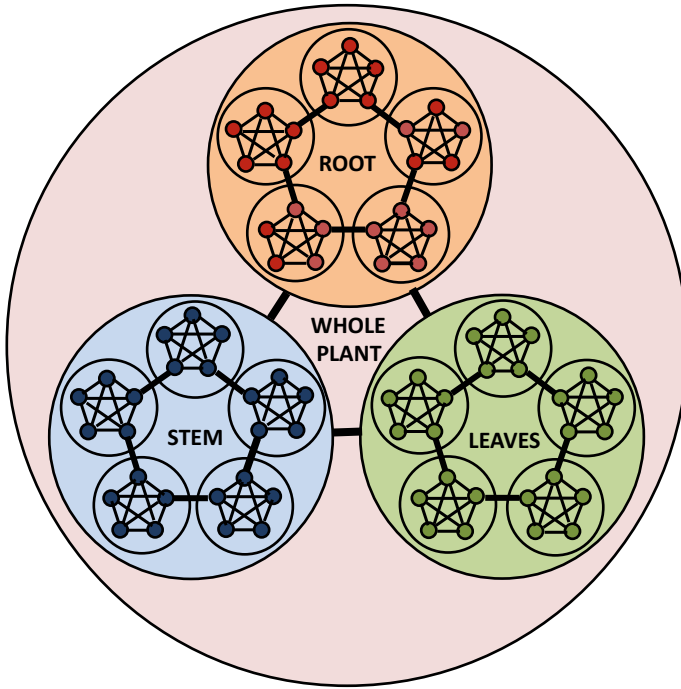
Fig. 4 Multi-scale hierarchical network models linking molecular networks to whole plant. Molecular networks are not drawn in the smallest circles. From smallest to largest circles: cells → tissues → organs → whole plant

Hierarchy of Module-Networks

Above we have already stumbled over "integration," i.e., the internal integration within modules (Bolker 2000). Going through the scaling levels of modules, this proved to be inevitable. When a number of modules at a finer level of scaling become a new module at the next higher level of scaling, we cannot avoid considering them as integrated. They form networks. When each of the networks at a finer scaling level condenses to give a module representing a knot in a network at the next coarser scaling level, it can be easily seen that we arrive at a hierarchy of networks (Souza et al. 2016) over the hierarchy of scaling levels (Fig. 4). Multi-scale network models linking molecular networks to whole-plant development present an integrated view (Lucas et al. 2011; Weston et al. 2012). From this, it is only a very small step toward understanding emergence. Studying individual modules, i.e., reductionism and specialization, is indispensible. We must know structure and function of modules well. However, with this alone, we would not comprehend life (Lüttge 2012). Life is an emergent category (see chapter by zu Castell et al. 2019). Per se, the modularity view of a plant stays short of understanding its life.

Emergence

Interactions of modules and their integration in clusters of modules can lead to a "fulguration" of systems with completely new innate qualities which cannot be predicted by even the closest examination of the modules per se and in isolation. The whole is more than the sum of its parts. This notion goes back to Aristotle (Fig. 3; Wikipedia 2012). The term fulguration was used by Lorenz (1977, pp. 47–48) to grasp the dramatic nature of the event of appearance of something new coming up like a flash of lightning. Regrettably the term fulguration has not found broad application in the literature, and we now speak of emergence. In the living world, it occurs on all levels of scaling.

For reasons of only graphical complexity, the molecular level is not included in Fig. 4. Genes and the nucleic acid macromolecules constituting them may be considered as the most basic and fundamental modules of life. However, by themselves, genes remain quiet modules. They are not life (see chapter by zu Castell et al. 2019). Life is emergent. The organization of genes by regulation of their expression leads to the emergence of gene products, the first ones of which are proteins. The hierarchy of network-based control of upstream and downstream events, or in other words feedback and feed forward, fosters the emergence of phenotypes and creates phenotypic novelties (Müller 2007; Marr et al. 2008; Lüttge 2012; Hütt 2013).

At the level of the gene products of proteins, we can witness most vividly how self-organization and emergence are linked. Self-organization creates fundamentally novel systems, which emerge from the interaction of the protein modules participating. Lipid and protein molecules can self-organize spontaneously to build up biological membranes with distinct properties and functions. Different individual proteins can be self-organized to form multi-subunit macromolecular structures functioning as enzymes. We may also call this self-assembly. Examples are the ATPases in the membranes of mitochondria synthesizing ATP driven by a proton electro-chemical gradient or the proton transporting ATPases building up a proton electro-chemical gradient at membranes by hydrolyzing ATP, e.g., the H^+-ATPase in the tonoplast membrane of plant vacuoles. Ribulose bis-phosphate carboxylase-oxygenase mediating CO_2 fixation in photosynthesis is built up of 8 small and 8 large protein subunits. The pyruvate and α-oxo-glutarate decarboxylases of respiration are also multi-subunit enzyme complexes. There are many other examples. In neither of these cases can their specific enzymatic function be predicted and derived from the particular nature of the individual subunits. Figures 2 and 4 may assist in illustrating the principle of emergence from self-organization with interaction and integration of modules on increasingly coarser levels of scaling: macromolecules → cells → tissues → organs → whole plant.

Mechanisms of Interaction and Integration

Proteins

The primary structure of proteins is given by the sequence of amino acids. The primary chains can undergo self-organization performing some simple folding of given amino acid strings. Parts of the primary chains are aligned, and this is stabilized by different kinds of bonds between amino acid side chains along them. This results in the secondary structure of proteins. These structures can undergo very complex further folding and coiling leading to a conformation called tertiary structure. Such self-organization often is not strictly spontaneous anymore and is regulated by various actions, such as binding of effectors and substrates, by interaction with other proteins, by incorporation into membranes. Special proteins catalyzing and regulating the correct folding are the chaperons (Buchanan et al. 2000; Alberts et al. 2002; Lüttge et al. 2010). When their conformations fit, tertiary structures of proteins can then self-organize into the quaternary structures of multi-protein complexes (section "Emergence").

Requirements at Higher Levels

At higher scaling levels from cells to entire organisms like whole plants, there are a number of requirements for interaction and integration, namely (1) signaling, (2) receptors for signals, (3) transduction of the information inherent in signals, (4) cross-talk by translation of different types of signals into each other and (5) realization of the information by reactions of metabolism and growth. Figure 5 shows the sequence of events integrating modules for the emergence of higher unitary entities such as whole plants.

Signals can be external or internal cues. They carry information. Receptors are needed to fix this information of signals when they arrive at cells in a molecular structure. Often these receptors are specific proteins located in membranes or chromoproteins if the signals are light. Over shorter distances, i.e., within cells, transduction of the information from the receptors to regulation of protein activities and especially of gene expression is a very complex cellular process involving steps of protein phosphorylation catalyzed by kinases and mediated by waves of cellular calcium levels (Buchanan et al. 2000; Alberts et al. 2002; Lüttge et al. 2010). Over longer distances, transduction requires the transport of signals whose nature is mainly electric, hydraulic or chemical. Receptors are needed again at the locations where the signals arrive in cells. It is noteworthy that these three types of signals can be translated into each other before and after transduction (Lüttge 2013, 2016; Shabala et al. 2016). For example, electrical and hydraulic signals are more suitable for long-distance transduction and can be translated into chemical signals eliciting chemical reactions of metabolism and growth. In this way, the information is taken
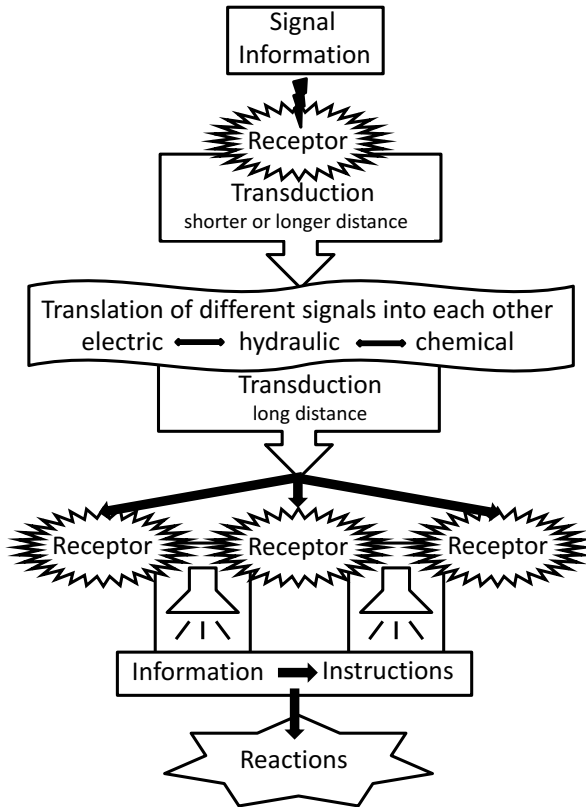
Fig. 5 Flow scheme of the sequence of events integrating modules for the emergence of higher unitary entities such as whole plants

as instructions to perform reactions in the integrated unitary organism. The following sections "Source-Sink Relations in Whole Plants" and "Developmental Relations" shall give some examples to illustrate how this general theoretical scheme is realized in whole plants.

Source-Sink Relations in Whole Plants

A major concept of whole-plant physiology regards source-sink relations mainly of water and various resources, such as mineral nutrients and organic compounds (Fig. 6). They illustrate the integration of roots and shoots for the emergence of whole plants as unitary organisms.

Fig. 6 Integrated allocation of water and resources in the whole plant
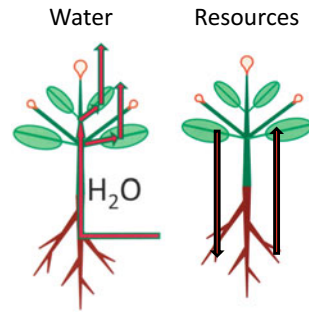

Water

The source of water is mainly the environment, i.e., the soil for rooted plants. The distribution of water within plants follows gradients of water potential from high water potential (source) to low water potential (sink). Sinks can be cells and tissues with high solute concentrations and hence low water potentials. The major sink for water is the dry atmosphere. The water potential gradient between the substratum, i.e., soil or a nutrient solution, and the atmosphere drives the flow of water flowing through whole plants, i.e., transpiration. Transpiration is regulated by the opening and closing of small pores, so-called stomata, in the aerial parts, especially the leaves of rooted plants. This process provides a very clear example of the whole-plant integration of the performance of roots and shoots.

Root-shoot signaling of soil drying is one of the most conspicuous features in whole-plant integration. A chemical agent, the phytohormone abscisic acid (ABA), accumulates and elicits stomatal closure when transpiration needs to be reduced to save water under stressful conditions. When the availability of water gets limiting, it is the soil water status rather than leaf water status which primarily controls transpiration of leaves (Turner et al. 1985; Davies et al. 1990; Wartinger et al. 1990; Zhang and Davies 1990). In the leaves, stomata can be warned early about that so that they may close even before the leaves experience water deficit (Davies and Zhang 1991; Gil et al. 2008). Experimental approaches to demonstrate this use split root systems or fence sitter plants. Plants are grown so that their roots develop in two different separated chambers, which looks like someone sitting on a fence and letting her or his legs hang down on either side (Fig. 7; Davies and Zhang 1991; Gersani et al. 1998). This allows it experimentally to subject different parts of the root system to different conditions. When half of the root system was subject to low water potential (Ψ), this elicited drought signals to the leaves, while the other half of the root system was kept at high Ψ and maintained their water supply. Thus, stomata began to close on transduction of a misleading signal, although leaves did not suffer from reduced supply. It was early recognized that a major signaling substance involved was ABA. Other chemical signals participate (Davies et al. 1994) including cytokinin phytohormones (Bano et al. 1993; Shabala et al. 2009), and also inorganic ions and

Fig. 7 Split root system of a
fence sitter plant
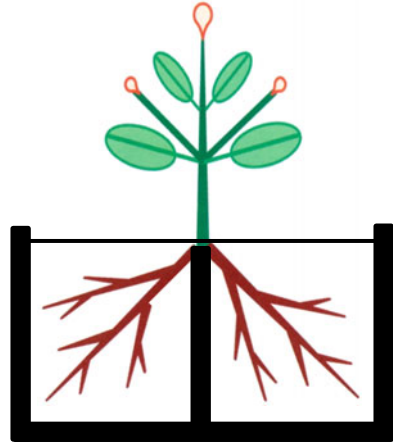
xylem sap pH (Schurr and Schulze 1996; Wilkinson and Davies 1997; Wilkinson et al. 1998), as well as hydraulic signals (Tardieu and Davies 1993; Tardieu et al. 1993). Hydraulic signals of soil drying can be translated into the chemical phytohormone signals which in turn may be translated into electric signals such as action potentials (APs), variation potentials (VPs) and system potentials (SPs) (Comstock 2002; Davies 2004; Lüttge 2013). Hydraulic signals such as pressure changes and hydraulic waves are rapidly transferred via the xylem (Matyssek et al. 1991; Cermak et al. 1993; Tang and Boyer 2003; Grams et al. 2007). Electrical action potentials are most rapidly propagated in whole plants along the veins via the phloem (Fromm and Eschrich 1993; Fromm and Fei 1998; Volkov 2000; Comstock 2002; Lautner et al. 2005; Fromm and Lautner 2007; Grams et al. 2009; Shabala et al. 2009; Lüttge 2013). Thus, chemical signals in the roots translate into hydraulic and electrical signals and after transduction to the leaves back to the chemical signal of ABA to elicit stomatal closure.

Nutrients

Whole-plant physiology boomed in the 1970s with studies of mineral nutrition (Pitman 1975; Sutcliffe 1976a, b; see Lüttge 2013). The important facts were that nitrogen and sulfur are available in the root medium in the oxidized forms of NO_3^- and SO_4^{2-}. These anions are taken up by the roots, but N and S are required in the metabolism of plants in reduced forms, and the reducing power within the roots is insufficient. It is photosynthetic electron transport in the leaves which provides enough reducing power of nicotinamide adenine dinucleotide phosphate ($NADPH + H^+$) for the reduction processes. If supply of NO_3^- is low, reduction to NH_4^+ can be managed by the plastids, the leucoplasts, in the roots, but at high concentrations, NO_3^- needs to be

transported into the leaves to be reduced in the chloroplasts (Wallace and Pate 1967; Kirkby and Knight 1977). Similarly, SO_4^{2-} reduction capacity is weak in roots, and SO_4^{2-} reduction needs to be driven by photosynthetic electron transport in the leaves (Rennenberg et al. 1979; Clarkson et al. 1983; Lüttge et al. 2010).

Nitrate nutrition requires a metabolic circle connecting and integrating roots and shoots. When NO_3^- is taken up by the roots, electrical charge balance of the ions is needed, which can be satisfied either by the release of bicarbonate HCO_3^- or by the uptake of K^+. KNO_3 is then transported in the xylem through the stems to the shoots and leaves. There the reduction of NO_3^- to NH_3 leaves behind a hydroxyl ion OH^-, which is neutralized by fixation of CO_2 and formation of malic acid via phosphoenolpyruvate carboxylase. The K^+ is returned to the roots by transport in the phloem and accompanied by malate anions for charge balance. In the roots, K^+ is available again for transport back to the leaves together with NO_3^-. Malate is decarboxylated. The pyruvate produced is funneled into respiratory energy metabolism, and the HCO_3^- obtained can be used for charge balance of NO_3^- uptake (BenZioni et al. 1971; Frost et al. 1978; Lüttge and Higinbotham 1979; Peuke et al. 1996; Lüttge et al. 2010; Lüttge 2013). Similar loops are envisaged for SO_4^{2-} nutrition.

There is systemic signaling. The Thornley model implies that nutrient deficiency favors photosynthate partitioning to the roots to improve nutrient acquisition capacity (Thornley 1972). With their transport, the chemical substrates involved in relations of whole-plant nutrition carry information. If in a split root system of fence sitter plants (Fig. 7) one chamber is kept under low or lacking provision of nutrients while roots in the other chamber are well supplied, the plants only develop a proliferate root system in the latter and reduce much of the growth of roots in the former (Gersani et al. 1998). Systemic signaling of sulfur status within the plants is mediated by the S-compound glutathione (Herschbach and Rennenberg 1994).

Photosynthetic Products

While nitrate and sulfate nutrition in the whole plant effectively is powered by source-sink relations of reduction potential (section "Nutrients"), the origin of source-sink concepts actually goes back to attempts of understanding long-distance phloem transport of photosynthetic products particularly sucrose, the major transport substance in the phloem (Münch 1930; Ziegler 1956). The mechanism is a hydraulic pressure-driven mass flow in the conductive elements, the sieve tubes of the phloem. The pressure gradient is maintained by the osmotic forces of sugar loading in the source tissues and unloading in the sink tissues, respectively. The source is photosynthetic production of sugars. The sinks are given by all kinds of metabolic consumption as well as storage of carbohydrates. The source is regulating the sinks via supply, and the sinks are regulating the sources via demand. The sink demand has feedback on source activity (Körner 2012). Not only partitioning and allocation of photosynthetic products but also of mineral nutrients are involved in the source-sink regulation. The

net rate of photosynthetic CO_2 uptake by leaves is reduced at low concentrations of NO_3^-, inorganic phosphate and K^+ (Longstreth and Nobel 1980).

For whole-plant integration of source-sink states, the concept of recirculation is decisive. It is based on phloem-xylem cycling of all kinds of solutes. Parenchyma rays mediate the exchange between the two pathways of long-distance transport, i.e., phloem and xylem (van Bel 1990). The concept has been developed and much propagated by Pate and Jeschke and their collaborators in the 1970s. The important cycling of mineral nutrients has been much studied by them (Jeschke et al. 1985, 1987; Peuke et al. 1996; Jeschke and Pate 1991b) as well as by other authors who have also contributed to the demonstration of the cycling of organic nitrogen and sulfur compounds (Cooper and Clarkson 1989; da Silva and Shelp 1990; Larsson et al. 1991; Geßler et al. 2003).

The role of concentration gradients of solutes and of pressure gradients resulting from them implies that information for the regulation of the cycling in whole plants is directly contained in the substrates themselves. Arrival of a substrate in a sink is a signal from the source. Demand of a sink is a signal to the source. Evidently, however, these are rather coarse signaling functions although their effectiveness should not be neglected. Beyond that, there is also more finely tuned signaling where substrates and metabolites participate. Nitrogen, phosphorus and sulfur compounds are involved in metabolic signaling systems (Longstreth and Nobel 1980; Scheible et al. 2004). Of particular importance in systemic signaling are sugars, not only the monosaccharide glucose but also the disaccharides sucrose and trehalose (Rolland et al. 2006). Glucose affects mitotic activity and acts analogous to a morphogen controlling development. It also interacts with regulation of hormone signaling at the level of transcriptional regulation by phytohormones. Sucrose affects gene expression and activity of enzymes and regulates processes of differentiation and development of plants. Sensors involved are various enzymes of sugar metabolism and sugar transporters in membranes (see Lüttge et al. 2010).

Developmental Relations

Intimate integration of parts is characterized by building up correlations between them. With "correlation," we mean here the systemic control of development (Ziegler 1998; Kost 2014). Correlations are mutual physical and functional relations and interactions of parts within whole plants. These come about by the determination of development. If a part or module of the integrated whole of a plant is subject to such determination from outside of itself, we call it aitionomic determination. It can be either positive or negative, i.e., an induction or a blockade. Aitionomic determination from neighboring cells or tissues can be an induction of the formation of similar cells or tissues, named homoiogenetic induction, or an induction of the formation of different types of cells or tissues, named heterogenetic induction.

An illustrative example of aitionomic correlative blockade or inhibition is apical dominance (Fig. 8). Normally, the bud at the top of a plant grows faster than the

lateral buds. This drives the vertical growth of the plant. It is due to a domination of the lateral buds by the terminal bud. The latter produces the phytohormone indole acetic acid (IAA), which is transported downward and carries the information for the lateral buds to retard growth or even remain dormant. If the terminal bud is injured or removed experimentally, IAA transport from the top ceases. Then the lateral buds germinate and increase their growth until one of them wins the race, seizes the lead in producing a downward stream of IAA and takes over apical dominance again. Aitionomic correlative stimulation is observed in trees at the beginning of the growing season. Developing buds of branches when starting to grow out are signaling to the cambium in the stems to resume their secondary growth.

In secondary growth of the trunks of trees, we also see correlations (Fig. 8). Within intact stems, the meristem cylinder of the cambium produces the elements of the wood toward the center and the elements of the cortex toward the periphery. Other potential developments are suppressed by aitionomic correlative blockade. Such blockade is relieved if, for example, a fallen beech tree is cut in spring time. Then one can see that the cells of the cambium are in fact totipotent (Fig. 9). When the correlative inhibition is removed, the cambium cells at the cut surface begin to divide, first forming a callus of non-differentiated cells, which, however, rapidly begin differentiation and regenerate complete small beech trees.

Another example is induction of flowering (Fig. 10). We distinguish short day or long night (SD) and long day or short night (LD) plants. They flower if the duration of the night is above (SD plants) or below (LD plants) a certain threshold length which is specific for individual plant species. A flowering signal, the phytohormone-like florigen which is presumably the transcription factor "flowering locus T," is elicited by the leaves if night length is appropriate and transported to the top of the plant inducing the terminal bud to produce flowers. Experimentally, it is enough to put one leaf under the appropriate SD or LD conditions to induce flowering in the SD or LD plants.

The orientation of plants in space is achieved by tropisms (Fig. 11). These are growth reactions directed along external signals. Positive phototropisms of shoots
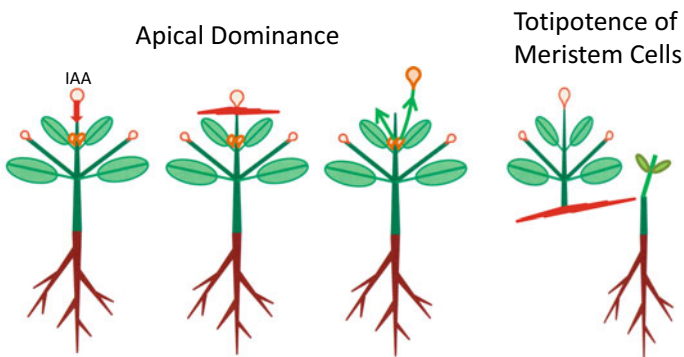

Fig. 8 Correlations

Fig. 9 Cut stem of a beech tree in spring with regenerating beech plants from the cambium

Cambium of secondary growth

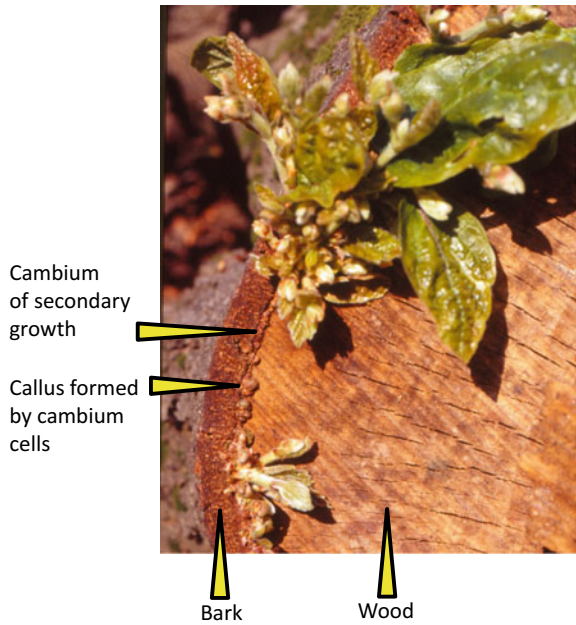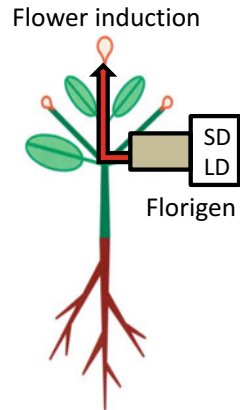Callus formed by cambium cells

Bark   Wood

Fig. 10 Flower induction. If one leaf (dark box) is given short days (SD) or long days (LD), the plant is induced to flower if it is a short day or long day plant, respectively

Flower induction

SD
LD

Florigen

are directed toward the light and negative phototropisms away from it. Gravitropisms directed to gravity are orthotropic positive of main roots and orthotropic negative of main shoots, plagiotropic (horizontal) of rhizomes and tillers, negative plagiotropic of side branches and positive plagiotropic of side roots.

The positive gravitropism of primary roots is particularly well studied at the molecular level. This is also an example for the translation of electrical and chemical phytohormone signals into each other in whole-plant performance. When the roots of the plants are in the normal vertical position, there is a symmetrical distribution of IAA coming from the shoot and back to the shoot from the roots. This is regulated by

Fig. 11 Orientation in space by gravitropism (left) or phototropism (right)
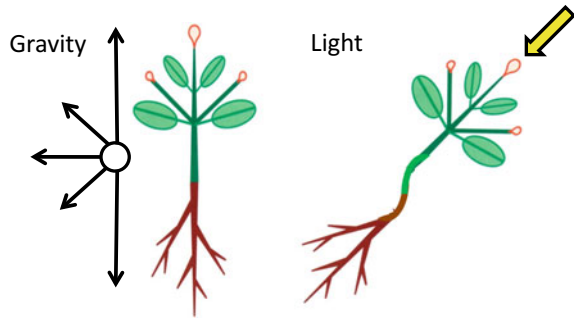
the *PIN* genes. The name originates from the needle- or pin-like growth observed in *PIN*-deficient mutants, which cannot form leaves (Paponov et al. 2005; Grieneisen et al. 2007). *PIN1* and *PIN4* genes regulate IAA transport from the top down into the root tips within the central cylinder, *PIN2* genes control transport back up in the cortex, while *PIN3* genes determine distribution within the root tip (Friml 2003; Benková et al. 2003; Friml et al. 2003; Blilou et al. 2005). When the root is moved out of the vertical position, the signal of the changed direction of gravity is perceived by a system of amyloplasts functioning as statolytes and lying on cushions of endoplasmic reticulum in specific cells of the root cap, the statocysts. The products of the *PIN* genes are IAA efflux facilitators of cell membranes. Responses to changed direction of gravity lead to building up an asymmetrical distribution of IAA where IAA levels are higher at the physically lower side of cells. Electrical signals are associated with asymmetrical IAA distribution. The lower side of the roots gets less negative (Brauner and Bünning 1930; Behrens et al. 1985; Stenz and Weisenseel 1991, 1993). While signal perception is located in the root cap, the reaction of gravitropic bending, however, occurs further up in the elongation zone, where growth is inhibited at the lower side of the roots, and asymmetric cell elongations in the upper and lower sides lead to bending down of the root and acquiring the normal vertical position again. The signaling from the root tip to the elongation zone involves the asymmetric PIN3-regulated backflow of IAA which is enhanced at the lower side and flow of another phytohormone, i.e., cytokinin, from the root tip upward (Aloni et al. 2004) functioning as a growth inhibitor at the lower side. Electrical signals most likely are also involved.

These few examples mainly chosen from the textbook literature (Ziegler 1998; Kost 2014; Lüttge et al. 2010) may suffice here to illustrate that developmental biology provides principal concepts and is extraordinarily rich in examples underlining the tight interactions between the parts integrated in the emergent whole-plant systems (see also chapter by Layer 2019 in this book).

Environmental Relations

The establishment of plants in their environment with their responses to abiotic factors and their biotic interactions with other organisms is a wide field. Plants can only perform effectively as integrated unitary organisms. Since this essay restricts itself to emergence of the whole plant per se, it would go beyond our scope to consider higher ecological scaling levels (see, e.g., the holobionts and the holobiont-like systems (chapter zu Castell et al. 2019)). Instead, two examples shall be chosen to illustrate the within-whole-plant integrations during responses to environmental challenges, namely herbivory—defense and salinity (Fig. 12).

Defense

Defense under biotic attack requires structural modifications and in plants particularly chemical efforts. These are costly, and the energy and resources going into defense mechanisms are lost for growth. This dilemma is addressed by the growth-defense-balance hypothesis (GDB; Loomis 1953; Herms and Mattson 1992; Matyssek et al. 2002, 2005). The choice between defense and growth is a typical whole-plant accomplishment. The GDB is based on observations which suggest that at high affluence of resources and energy provided by vigorous photosynthesis, the choice is preferential propagation of growth as an irreversible increase in plant biomass, while at scarcity of resources and low energy supply, activation of defense is preferred to maintain and preserve the status given by resources already incorporated. Although due to the very high plasticity of the performance of plants the dilemma of growth-defense is not all that absolute and strict and the GDB hypothesis needs to be modified in this respect (Matyssek et al. 2012a, b, 2013; Souza and Lüttge 2015), responses can only be orchestrated by within-plant integrations, which in view of versatility are even more subtle than for the strict dilemma alone.

Fig. 12 Whole-plant performance under environmental stress of herbivory (left) or salinity (right)
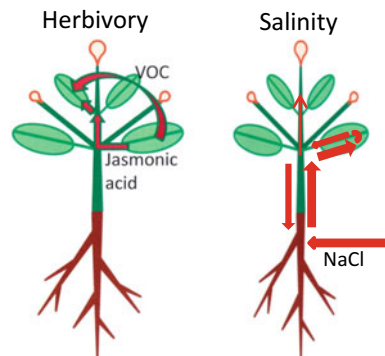
In addition to this general view, an example of within-plant signaling is worth considering here. Plants often react to herbivore attack by producing chemical defense compounds that repel the aggressors when they start feeding. Such compounds are, for example, phenolics, phenyl-propane derivatives, terpenoids or tannins (Oßwald et al. 2012; Kolosova and Bohlmann 2012). When biting by herbivores occurs, there is systemic signaling to other parts of a plant to elicit production of defense compounds there before the herbivores arrive. The stress hormone jasmonic acid is carrying such information. However, it needs to be transported over long distances within the plant away from the site of first attack toward other parts to be conditioned and prepared for possible attack. This long-distance transport takes time which may prove to be too long for immediate protection. This is overcome by production of volatile signaling compounds, so-called pheromones, which alert the parts of a plant almost instantaneously via diffusion in the gas phase (Heil 2010). The methylated form of jasmonic acid, methyl jasmonate, is also volatile (Nincovic 2010). In ecological systems, this signaling proves to be also effective between different plants of the same and even of other species establishing preparedness intra- and inter-specifically (Ruther and Kleier 2005; von Dahl and Baldwin 2007; Baluška and Nikovic 2010; Bruce 2010; Nincovic 2010).

Salinity

Salinity, especially of sodium chloride (NaCl), is a common environmental problem in the substratum of plants. Plants can adapt (i) by excluding salt uptake at the root level (salt excluders), (ii) by taking salt up and excreting it via salt hairs and salt glands or (iii) by taking salt up and sequestering it in the vacuoles of cells at sites of salt storage (salt includers). The salt excluders run into problems of osmoregulation and need specific other adaptations. The salt includers can use the cheaply available NaCl for stabilizing their osmotic relations. They are particularly worth mentioning here in relation to whole-plant integrations because they use salt recirculation based on phloem-xylem cycling (see section "Photosynthetic Products") of NaCl. Salt is partitioned in the whole plant in a way protecting the most important centers of metabolism from salinity stress. Salt transported to the leaves in the transpiration stream via the xylem is recycled via the phloem and accumulated in the less sensitive parts. In an experiment with plants of *Ricinus communis* (Jeschke and Pate 1991a), more than two-third of the NaCl taken up was kept within the roots. During transport in the xylem, much Na^+ was accumulated in the old lower leaves and most of the Na^+ arriving in upper mature leaves was recycled in the phloem. The salt load of the growth zone of the apex and the young leaves and also leaves which were still growing and importing assimilates for growth was kept very low.

Higher Plants: Unitary Organisms Without a Neuronal System

Higher land plants cannot move around to visit optimal external conditions. Plastic responses to the dynamically variable features of and the input from the environment where they are firmly established are essential. Obviously for this, the simple stems, also called telome, of the psilophytes *Rhynia* (Fig. 1) were not a solution sophisticated enough. Specialization for the different sections of the environment, most notably the soil and the atmosphere, respectively, appeared advantageous. Thus, selection from morphogenetic patterns bore out the evolution of roots and leaves. By their integration via the stems, the modern higher land plants became emergent on the structural level of roots, stems and leaves (Figs. 1 and 2). Integration of a plethora of capacities completed the emergence of the plants as unitary organisms at the functional level (Figs. 6, 8 and 10). With the exception of neuronal systems, all kinds of mechanisms of integration are expressed in plants. There is systemic signaling (Figs. 5, 6, 8, 10 and 11). Partitioning and allocation of resources are optimizing the fulfillment of the demands of the parts in close mutual interactions (Fig. 6). The parts cannot perform independently and maintain their existence and integrity. The whole is more than the sum of its parts (Fig. 3).

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