

Part II

Revisiting Principles of Plant Life – Integration of Whole-Plant Functionality Under Ecological and Evolutionary Perspective

The conceptual perception of plant life has gained new impetus towards functionally understanding the inextricable “eco–evo” interrelationships (Müller 2007; Gilbert and Epel 2009). For Higher Plants, which are sessile and cannot escape stress, survival at their sites is a big challenge. They need high plasticity in effective stress response, higher than in mobile animals. Indeed, response plasticity turns out in plants to represent a functional regularity on its own (Matyssek et al. 2012; Souza and Lüttge 2014). High plasticity inherently requires high degrees of internal functional integration of the plant as a whole, i.e. multi-scale systemic ability of control. The control is challenged externally and determined by biotic interactions, i.e. through competition, parasitism, and mutualistic relationships. Multi-organismic associations prove to drive resource allocation and, as a consequence, the diverse functions of plants (Matyssek et al. 2012).

Evolution teaches us that plants master that challenge at their firm rooting sites quite successfully. Plant science has been caught in a tradition that tended to address plants (i) under a more “static” and “modular” perspective than animals regarding internal functional organization, and (ii) in the field of plant (eco-) physiological research, in aut- rather than syn-ecological terms. The aut-ecological emphasis is owed to the analytical research with its reductionist tendency of reducing degrees of freedom while neglecting the systemic synthesis of evidence within and across spatiotemporal scales. To take the latter step, one needs to comprehensively embrace whole-plant functioning in ecologically meaningful ways, both *per se* and as part of environmental contexts. Overcoming deficits of (i) and (ii) requires merging reductionist and systemic approaches. The new impetus of conceptual perception of plant life has gained momentum recently in breaking (i) and (ii) related restrictions in understanding whole-plant performance under ecological and evolutionary perspectives. This present volume 77 of “Progress in Botany” gathers ten contributions reflecting this recent momentum.

Regarding (i), the contributions by Lüttge (2016a) and Lüttge and Thellier (2016) each elucidate the highly integrated functional interrelationships at the level of whole plants, enabling for rapid, variant-rich, and highly differentiated performance within and responsiveness to the environment. One central means of

functional whole-plant integration are transport processes at various organizational levels within plants from membranes and cells to organs in the whole plant (Lüttge 2016a). The vitally essential water fluxes at membranes, cells, and tissues and the pathways of long-distance transport of not only the xylem but also the phloem are integrated in the functional network of the phenomenon of root pressure (Singh 2016). These transports carry the distribution of nutrients and assimilates within plants and with that the resource-supply-based information for whole-plant performance. For fine-tuned regulation, the transports are the intrinsic platform of phytohormonal plant-level signalling, beyond electrical and hydraulic signalling.

How is this plethora of signalling evaluated and “distilled” into highly coordinated whole-plant response, as plants do not have a nervous system specialized for signal pulsing? Neither a central processing unit of information exists. Instead of a “central processing unit”, a diffuse information-processing network of cells may serve whole-plant integration. For example, the systemic regulation of photosynthesis in response to light and CO₂ operates with the integration of chloroplasts and green cells at the whole-plant level (Matsuda and Murakami 2016). Hence, the evolutionary approach would contrast with that of animals but may be similarly effective, perhaps differentially “tuned” during evolution to the particular ecological needs of the life form of plants. Doubtlessly, information storage exists in plants, as demonstrated by Lüttge and Thellier (2016), and the highly specific and differential memory of internal and external signalling is controlled by multiple metabolic mechanisms, including biological clocks that rely on regular matching with phenological and ontogenetic stimuli. Such kind of memory remarkably is systemic, mirroring the evolutionary approach in plants of diffuse information processing.

Regarding (ii), evidence suggests that individual-centred views of aut-ecology fall short if trying to unveil ecological and evolutionary mechanisms crucial in promoting adaptability and niching as prerequisites of genotype evolution and persistence. This has been shown in research on biological invasions (Heger et al. 2013), in restoration ecology (Zaplata et al. 2013), and during biodiversity experiments (Allan et al. 2011; Scherber et al. 2010). Rather, evolutionary significance arises from multi-organismic associations as the ecologically relevant entities which apparently possess emergent functional features that are conducive to niche formation as an intrinsic aspect of fitness. Such biological systems are hierarchically organized. Their irreducibility is explained by the flow of information across the various hierarchical levels, where we must abandon the conception of a one-way hierarchical order and realize that hierarchy works not only top down but also bottom up (Souza et al. 2016).

Multi-organismic associations comprising a highly evolved host and microorganisms (MOs) have been termed “holobionts”; however, such notion is much more introduced and functionally understood by means of animal (including humans) than plant systems (zu Castell et al. 2016). Such holobionts are represented through their “hologenome”, responding as a functional entity to environmental impact. The ecological and evolutionary strength of such systems is anchored in the hologenome responding, via MOs, rapidly and effectively to stress as compensating

for the sluggishness in host responsiveness. The holobiontic performance is concluded to promote acclimation and adaptation to changing environmental conditions, with the holobiont being the actual platform of selection and (co-) evolution. Environmental information can be stored and inherited in holobionts not only in the conventional genetic way, but also through structural and functional changes, e.g. in the multi-organismic assembly.

Holobiontic principles in plant systems begin to gain attention in ecological research (Vandenkoornhuysen et al. 2015) and provide the functional grounds of plasticity in stress response, highlighted above as a crucial feature of plant persistence.

Souza and Lüttge (2014, last vol.) elucidate functional stability at the plant and ecosystem level as a phenomenon that emerges—as a new synergistic quality of system functionality—from the holobiont plasticity in combination with the complexity and diversity of the underlying ecophysiological responsiveness. Lüttge (2016b) demonstrates such principles as the functional grounds of the natural self-management of ecosystems and as guidance for stand management in agronomy and forestry. Such considerations lead us to spatiotemporal scales hierarchically higher than that of holobionts *sensu stricto*.

The question arises, if holobiont-like principles are realized in scale-invariant ways. If so, the holobiont *sensu stricto* would represent just one variant of holobiont-like systems (HLS) and its principles of biotic interactions would represent an intrinsic and generic characteristic of any biological system. Such considerations are further propagated by zu Castell et al. (2016). Respective consistencies appear to be keys to understanding the systems' self-organization, pseudo-steady states, and self-maintenance, perhaps mediated through particular settings of driving forces, feedback or feed-forward mechanisms, and organismic control components. Clearly, we have left the scale now of holobionts *sensu stricto*, and we may be inclined of thinking in terms of the conventional hierarchically vertical spatiotemporal scaling of interaction principles (Souza et al. 2016). However, the hypothesized scale invariance of HLS principles also—and in particular—demands for functional cross-linking within spatiotemporal scales. The demand reflects adaptive cycles that are nested one within the other within scales and extending beyond.

For such kind of interrelationships, the term “panarchy” was coined by Holling (2001) and Gunderson and Holling (2002). The “panarchical” view becomes compelling in recognizing HLS principles and potential scale invariance to complement and ultimately replace the hierarchical perspective (zu Castell et al. 2016). To the extent that such overarching principles may substantiate through upcoming research, a quality of evidence would become available casting new bridges in the understanding of biotic interaction in the interrelated “eco–evo” research field, i.e. unifying explorations of ecology and evolution (Müller 2007; Lüttge et al. 2012). Hence, the new impetus to plant science may turn into a fundamental driver of theory building about plant life.

A prerequisite towards such goal is a new understanding, however, of “systems biology” for becoming “syn-ecological” ecosystem biology. For this to be achieved,

“systems biology” needs to embed molecular biology into ecophysiological, multi-organismic, and ecosystem-level networking. This means that genomic biology must also advance to exploring different aspects of plant biology, such as elaborating the role of genetic diversity (Larrañaga and Hormaza 2016) and its functional analysis (Fladung 2016) in relation to evolutionary aspects, where the evolution of flowering has eminent eco–evo implications (Lucas-Reina et al. 2016). We wish the addressed collection of contributions to this present volume 77 of “Progress in Botany” to provide a stimulating input towards reaching the outlined goal.

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