Preface

Resource manager—this might be the "profession" of a plant, if one should assign one. The resources to be managed are carbon, nutrient elements, water and energy. Management here means distribution of resources to vital needs and to "arrange with" (i.e. acclimate to) the environment. Such needs imply to stay operational and competitive, to survive abiotic and biotic stress, to augment biomass and to reproduce. Management notably also comprises preventing premature loss of resources to consumers (pathogens, herbivores) as a prerequisite for meeting all other needs. Clearly, such kind of distribution requires priorities in management, i.e. the plant must make "decisions". The decision policy depends both on the plant's current developmental and metabolic status and on the environmental scenario, i.e. the site conditions. As the internal and external settings can be variable, so can apparently be the plant's response. This phenotypical variability in plant performance is termed "plasticity", and the prioritisation in the distribution policy is reflected in resource allocation and partitioning. In this book, allocation is defined as the process, and partitioning as the result of the resource management. To survive the plant requires to "modulate", i.e. regulate, the different needs through allocation by evaluating the diverse sources and sinks in resource fluxes *versus* the constraints associated with them. This regulatory process is complex, given the multifactorial world and impacts which set the stage for the individual plant's ecology, economy and for the process of evolution. Although one is aware that plants do not ponder on their regulation, the introductory allegory accentuates their challenge for survival and, hence, for empirical and theoretical assessment.

In such terms, how do plants cope in their resource management with complexity? This question is vital for the plant's persistence and fitness and so is the clarification of the functional grounds of resource allocation and its priorities in regulation (Mooney et al. 1991). Apparently, plants have been successful in operating their resource management, as can be concluded from their evolutionary history. However, how intense is the challenge on them in operating? Are they "jacks-of-all-trades, masters of all", as they have been termed in doing their "job" (Koricheva et al. 2004), seemingly in a virtuous way in spite of the complexity of the task? Or, do they encounter "dilemmas" in their "policy" on resource allocation

(Herms and Mattson 1992)? Then, prioritising would appear to be cumbersome. In either case, however, a mechanistic comprehension of resource allocation and its regulation at the whole-plant level evidentially is the prerequisite for understanding the existence and fitness of plants (Stamp 2003a). Nevertheless, attaining such an understanding still poses a major challenge for plant science (Bazzaz and Grace 1997).

The conventional view on the issue outlined above conceives plants as facing dilemmas, *sensu* predicaments in choosing from two or more vexing options, when prioritising the needs to be covered in resource allocation. A prominent, seeming dilemma is the one between the needs to grow to staying competitive in resource acquisition and to defend against stress for retaining the resources once acquired. Mostly stress by consumers such as herbivores or pathogens, but also by abiotic factors, is typically considered (Herms and Mattson 1992). Conversely, the awareness has also grown that allocation can be understood only in response to the continuum of biotic and abiotic impacts (Matyssek et al. 2005). This latter insight was originally founded on the assumed physiological trade-off in allocation at the individual plant level between growth and herbivore defence, represented by secondary metabolism—becoming part of the "growth–differentiation balance hypothesis" (GDB).

In its core, GDB claims such kind of trade-off in plant-internal resource allocation to materialise between growth and defence (Herms and Mattson 1992). Differentiation here means resource investment into chemical and structural modifications of biomass as opposed to growth, which represents irreversible biomass increment. As detailed in Chap. 1, increasing resource availability is presumed, according to GDB, to promote gross primary productivity (GPP) towards a maximum level (cf. Matyssek et al. 2005). In parallel, defence is claimed to be favoured at low resource availability at the expense of growth and growth to be favoured at high availability when defence is low. At severe resource limitation, defence may be constrained by GPP.

More explicitly, nutrient (and water) availability was claimed to have a parabolic effect on secondary metabolites, resulting in a unimodal optimum function with maximum concentration at about medium supply. At limitation, a positive correlation is predicted between growth and secondary metabolism, whereas the correlation should turn negative towards saturation (i.e. high carbohydrate investment into growth rather than defence). Having existed by now for about 60 years (Loomis 1953), GDB has experienced several extensions towards reaching a broad ecologically and evolutionarily relevant scope. As a result, GDB appears to possess, in comparison with other related, partly competing hypotheses, high integrative strength in incorporating a plethora of findings and strong potential for theory development (Herms and Mattson 1992; Koricheva et al. 2004; Stamp 2003a). On such grounds, GDB will be viewed in the remainder of this book as a theory on resource allocation in plants, being still on the way towards maturation (*sensu* science theory, given the unabated demand for integrating the challenging plasticity in the plant's biology and ecology; Stamp 2003b).

Given the current stage of GDB, a comprehensive, mechanistically founded treatment and timely update are missing. Evidence has increased, in addition, that plants appear to regulate resource allocation also beyond the scope of GDB. A holistic view, never presented before, is required, therefore, to integrate spatio-temporal process scaling (i.e. across hierarchical dimensions in structure and time) between cells, organs, whole plants and stands (cf. Ehleringer and Field 1993; Schulze 1994) along with ontogenetic stages and transition between controlled and field conditions of growth (Sandermann and Matyssek 2004). Such a perspective needs to account for links between molecular and biochemical/physiological processes and is reflected in the title of this book as *Growth and Defence in Plants: Resource Allocation at Multiple Scales*. Allocation control is to be clarified as an intrinsic component of interrelated plant–plant, plant–pathogen and plant–mycorrhizosphere interactions in approaching an extended mechanistic understanding. Regarding the biotic interactions, space-related cost/benefit relationships in resource turnover (i.e. investments vs. returns) will be highlighted to arrive at common underlying principles of resource allocation and to examine their validity across plant and interaction types, ontogeny and growth scenarios.

The three stages in theory building will be covered:

1. Examination in view of new empirical evidence from a spectrum of ecological scenarios
2. Exploration of conflicts and validity ranges
3. Extension followed by re-examination of the theory

In such a way, based on methodological advancement and recent gains in evidence, data analysis and modelling, the ultimate aim of this book is a rigorous validation of GDB that may result in a mechanistically founded revision or extension of this theory within ecophysiologically relevant contexts.

An integrative and unique view across forest and orchard trees, herbaceous crop plants and grassland species will be developed on this research issue. Conceptual links will be demonstrated and emphasised between empirical and theoretical approaches as powerful means for hypothesis building and evaluating and theory development. Covered ecological scenarios include competitors, pathogens, herbivores, mycorrhizae, soil microorganisms, CO_2/O_3 regimes, N and light availabilities, as well as drought.

Given the mechanistic perspective and ecological scope of this book volume, the presented new evidence is relevant for the biology of both wild and economic plants. Basic knowledge is augmented as a starting point for applied research on food production and quality, plant breeding and disease control, production of renewable resources and plant system management, altogether within contexts of changing environmental conditions. On these grounds, the focused aims of the book are to

– gather a timely understanding of resource allocation and its regulation in herbaceous and woody plant systems, linking molecular with biochemical and physiological process levels,

– clarify allocation control as an intrinsic component of plant–plant, plant–pathogen and plant–mycorrhizosphere interactions,
– integrate ontogeny and contrasting growth scenarios into spatio-temporal scaling,
– clarify extents of common underlying mechanisms in resource allocation across plant types, ontogeny and growth scenarios,
– evaluate the potential for advanced mechanistic and ecophysiologically relevant theory development as one result of the integrative analyses and hypotheses testing in relation to GDB.

The review character of this book profits from the outcome of interdisciplinary case studies on the subject, e.g. of SFB 607 (an integrated research centre, supported by the German research funding agency, DFG, from 1998 through 2010 in the Munich area/Germany, on *Growth and Parasite Defence – Competition for Resources in Economic Plants from Agronomy and Forestry*) and from the contributions of invited external experts: C. Anderson (Corvallis, USA), J. Bohlmann (Vancouver, Canada), R. Hampp (Tübingen, Germany), J. Koricheva (London, UK) and C. Mathews (Palmer Stone North, New Zealand). Their valuable contributions to this book project are highly appreciated.

Book publications reviewing and comprehensively updating knowledge on resource allocation in plants have been missing for more than one decade. None of the preceding books had pursued a comparably holistic and focused rationale towards theory maturation on resource allocation in plants, inherently addressing joint mechanisms of resource flux and turnover across plant–plant, plant–pathogen and plant–mycorrhizosphere interactions. Part I of the present book elucidates the theoretical grounds of resource allocation between growth and defence. This sets the stage for Part II, presenting the new evidence. Part III then strives to arrive at an integration of the achieved state of knowledge, promoting theory development and introducing into the conclusions of Part IV. To readers who prefer to obtain an overview on the essentials elaborated by this book volume as a whole, a glance into the summarizing Chaps. 19 and 20 is recommended before visiting the detailed explorations of the other chapters. Prominent intention of the book is the re-consideration of research strategies towards a mechanistic and ecologically relevant understanding of the plants' "resource husbandry".

Freising and Neuherberg, Germany

Rainer Matyssek
Hans Schnyder
Wolfgang Oßwald
Dieter Ernst
Jean Charles Munch
Hans Pretzsch

References

Bazzaz FA, Grace J (1997) Plant resource allocation. Academic, San Diego, pp 303
Ehleringer JR, Field CB (1993) Scaling physiological processes – leaf to globe. Academic, San Diego, pp 387
Herms DA, Mattson WJ (1992) The dilemma of plants: to grow or defend. Q Rev Biol 67:283–335
Koricheva J, Nykänen H, Gianoli E (2004) Meta-analysis of trade-offs among plant antiherbivore defenses: are plants Jacks-of-all-trades, masters of all? Am Nat 163:E65–E75
Loomis WE (1953) Growth and differentiation – an introduction and summary. In: Loomis WE (ed) Growth and differentiation in plants. Iowa State College Press, Ames, pp 1–17
Matyssek R, Agerer R, Ernst D, Munch J-C, Osswald W, Pretzsch H, Priesack E, Schnyder H, Treutter D (2005) The plant's capacity in regulating resource demand. Plant Biol 7:560–580
Mooney HA, Winner WE (1991) Partitioning response of plants to stress. In: Mooney HA, Winner WE, Pell E (eds) Response of plants to multiple stresses. Academic, San Diego, pp 129–141
Sandermann H, Matyssek R (2004) Scaling up from molecular to ecological processes. In: Sandermann H (ed) Molecular ecotoxicology of plants. Ecological studies, vol 170. Springer, Heidelberg, pp 207–226
Schulze E-D (1994) Flux control in biological systems. Academic, San Diego, pp 494
Stamp N (2003a) Out of the quagmire of plant defenses hypotheses. Q Rev Biol 78:23–55
Stamp N (2003b) Theory of plant defensive level: example of process and pitfalls in development of ecological theory. Oikos 102:672–678

http://www.springer.com/978-3-642-30644-0

Growth and Defence in Plants
Resource Allocation at Multiple Scales
Matyssek, R.; Schnyder, H.; Oßwald, W.; Ernst, D.;
Munch, J.C.; Pretzsch, H. (Eds.)
2012, XXVI, 474 p., Hardcover
ISBN: 978-3-642-30644-0