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Growth and Defence in Plants

Resource Allocation at Multiple Scales

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To our late colleague and friend,
Prof. Dr. Heinrich Sandermann jr.
(† August 18, 2009), who was one
of the initiators and members of the
interdisciplinary research program
SFB 607 "Growth and Parasite
Defence in Plants – Competition for
Resources in Economic Plants from
Agronomy and Forestry", giving rise
to this book project, but to whom it
was not granted to see its completion.

Prologue

A New View on Systems Biology: Information, Knowledge, Understanding

Cost/Benefit Scenarios and the Dilemma of Growth and Defence

Cost/benefit relations determine the functions of plants in natural ecosystems as well as anthropogenically formed agro- and forestry ecosystems. Under the influence of abiotic and biotic cues, they regulate the dynamics in the realm of the opposing forces of growth and defence (Chap. 1). In the competition for resources the dilemma has the costs of productivity on the one hand and of survival of stress on the other hand.

Talking of a dilemma we must ask the question if there are in fact options of ways out of it. Evidently, like all living organisms plants are also open systems subject to non-linear dynamics in space and time. This implies that spatio-temporal developments under a plethora of external cues and the opposing forces of growth and defence inevitably lead to branching points where alternatives or options are given, but where chance may eventually also lead the way into deterministic chaos. The latter is an inherent problem in evaluations of the degrees of possible predictability in all systems with non-linear dynamics (Schuster 1995). Options in spatio-temporal responses of plants under the dilemma of growth and defence and potential predictability are the central themes underlying the hypotheses and concepts evaluated in this book.

Scenarios are dominated by

- different life forms and types of habitats, viz. grassland and forest,
- competition (Chaps. 17 and 18), abiotic stress (ozone, elevated CO_2, nitrogen nutrition), pathogens (Chaps. 3 and 5), herbivores (Chap. 4), symbionts (Chaps. 5 and 10),
- ontogenetic development (Chap. 11),

- types of resources, e.g. originating from the soil (Chaps. 9 and 10), from aboveground components, from the atmosphere, of the solar radiation (Chap. 8), of space itself as a resource (Chap. 12, Grams and Lüttge 2010),
- allocation, partitioning and consumption of resources in allometry relations (Chaps. 6, 7, 9, 11–18).

These scenarios are elements of the formation of integrative networks within various scalar levels which are also connected between each other over both ascending and descending scales and thus can form supra-networks. This determines a new view on systems biology in an ecological context (Chap. 19), which must advance from information via knowledge towards understanding (Liessmann 2008), i.e. from purely descriptive compilation of data via correlative interpretation of processes towards reflection and causal assessment. Combining the approaches of experiment, theory and modelling develops predictive power on the basis of understanding observed past events.

An Architectural Metaphor

In a metaphoric way we may visualise the architecture of the Sonderforschungsbereich (SFB) "Wachstum und Parsitenabwehr – Wettbewerb um Ressourcen in Nutzpflanzen aus Land- und Forstwirtschaft", from whose work the present volume is emerging, like the knots and edges of networks. We may consider the experimental approaches on two basically different levels as two columns or towers (knots) which by long wings (edges) are connected to theory and modelling (knot).

I cannot imagine a better way of depicting this than choosing the Castle of Hirschberg above the city of Beilngries in the valley of the Altmühl in Central Bavaria. For more than a decade the SFB had regular internal meetings there for brainstorming and strategy planning. When we arrive at the castle we pass the two towers and we see the two wings of the building guiding our view in a remarkably suggestive way towards the entrance (Fig. 1). The architect managed this by having the two wings in an angle and much wider apart from each other at the start than at the end with the entrance. Let us consider the two towers as the two sections of the SFB. One of the towers (one knot) of the SFB or its section A (Chaps. 2–5) is linking molecular biology with biochemistry and physiology (Chap. 2) and, thus, is developing molecular ecology of

- gene induction and transcription,
- proteins and enzyme activities,
- primary and secondary metabolism,
- signalling by phytohormones and metabolites.

The other tower (knot) of the SFB, its section B (Chaps. 6–14), is developing physiological ecology at the organismic, stand and ecosystem levels, with

Fig. 1 Hirschberg Castle of the bishopric of Eichstätt above the city of Beilngries in the valley of the Altmühl (photographs: K.-H. Häberle)

- primary production, allocation, partitioning and allometry,
- occupation of space above and below ground,
- the use of reserves under stress of resource availability, ozone pollution, elevated atmospheric CO_2, pathogen attack.

With the two wings the two towers are connected to the entrance, section C (Chaps. 15–19) of the SFB. What is this an entrance to? Transduction of the information and knowledge sensu Liessmann (2008) from the two sections, towers or knots A and B via the wings or edges into section or knot C enters the wealth of observations (information) and interpretations (knowledge) into understanding sensu Liessmann (2008) as probed and advanced by

- statistical modelling (Chap. 16),
- mechanistic modelling (Chaps. 14, 15, 17 and 18),
- integration via abstraction.

Thus, metaphorically we can see that, as in the most compelling way in which the two wings of the castle guide our anticipation to arrive towards the entrance, sections A and B of the SFB funnel our attention towards the integration by theory and modelling of section C.

What Is a "System" in Biology?

The extreme view is Gaia considering the whole biosphere as one single system or one mega-organism (Lovelock 1979, 2009).

In the life sciences the term "systems biology" originated from describing vast accumulations of data in "genomics", and in a noteworthy inflationary fashion it now covers all kinds of "-omics", such as transcriptomics, proteomics, metabolomics and channelomics. The present book presents examples of such databases (Chaps. 2–5). Remarkably comprehensive sets of data on mineral macro- and micro-nutrients in plants have also been obtained (Chap. 9). In the SFB this has been called "mineralomics". The term "ionomics" is somewhat of a misnomer in the literature (Salt et al. 2008) as long as it refers only to inorganic ions and does not comprise on the one hand the wealth of organic ions important in the functioning of organisms and realise on the other hand that many minerals in organisms occur and function in non-ionic bound or chelated states. In the vein of a certain omics-inflation we may also allude to the necessity of considering structural or functional complements, i.e. "anatomics" or "functionomics".

However, are such data bases "systems"? They are really nothing more than primary information. They constitute a necessary basis but themselves they have nothing to do with knowledge which must be advanced from the information.

Another way of looking from a molecular point of view to systems is to consider specific key functions which are often expressed by many different isogenes coding different isoenzymes. Interestingly abiotic stress due to ozone and biotic stress due to pathogen attack may elicit very similar reactions at the molecular level, viz. transcription (Chap. 2). The translational and post-translational regulation and modulation of isoenzyme activities as well as their localisation and compartmentation can characterise the spatio-temporal functioning of the systems of whole plants or even higher integrated consortia, such as host/parasite or host/symbiont associations. In the present book we find examples of this with respect to genes and enzymes involved in the growth/defence dilemma (Chaps. 2–4). Here, at levels of increasingly larger scale, we recognise systems as e.g. organelles or compartments of cells, cells, whole organisms, interspecies associations, ecosystems and so on. It is remarkable in this context that the term "ecosystem" coined as early as 1935 by Sir Arthur C. Tansley already refers to "system". With respect to the term anatomics suggested above we realise that in most complex regulation networks stress may not simply inhibit growth but rather redirect growth. Thus, a large diversity of different stresses via a plethora of pathways of hormonal regulation may result in remarkably similar morphological responses (Potters et al. 2009).

This already moves us forward from purely descriptive compilations towards correlative interpretation. Evidently the proof of a correlation is not yet showing a causal relationship, but conversely if there is no correlation there is no relationship. From another angle we can advance from pure information to knowledge if we fathom the processes governing the spatio-temporal functioning of systems, where we need to integrate a wealth of different approaches required to assess the dynamics of systems.

The climax realising effective understanding of systems must be seen in the combination of theory and modelling integrating past and present observation for future prediction (Chaps. 15–18). This comprises reflection opening a path towards abstraction which leads to deeper understanding (Lüttge and Hütt 2009). It is essential to note, however, that similar to empirical observation, theory is never completely definite. A continuous and iterative ping-pong like mutual input is required between experiment/observation on the one side and theory/modelling on the other side.

Scalar Levels of Systems

We have seen above that when considering systems we inevitably arrive at changing levels of scaling. Ecology must cover a vast scope of systems in time and in space (Fig. 2). For an integrative view it is important to both descend and ascend the stairs or ladders of scaling levels or even jump up and down between levels. In the present volume throughout the various chapters this is documented by consideration of

- molecules and cells,
- plant tissues and organs,
- whole plants,
- intraspecific relations, e.g. relations between individual plants of a given species in stands,
- interspecific relations, e.g. relations between plants of different species in stands (Chaps. 12–14, 18), host/symbiont, host/parasite and host/herbivore relations (Chaps. 3–5, 10),
- ecosystems, e.g. grassland, forest (Chap. 12).

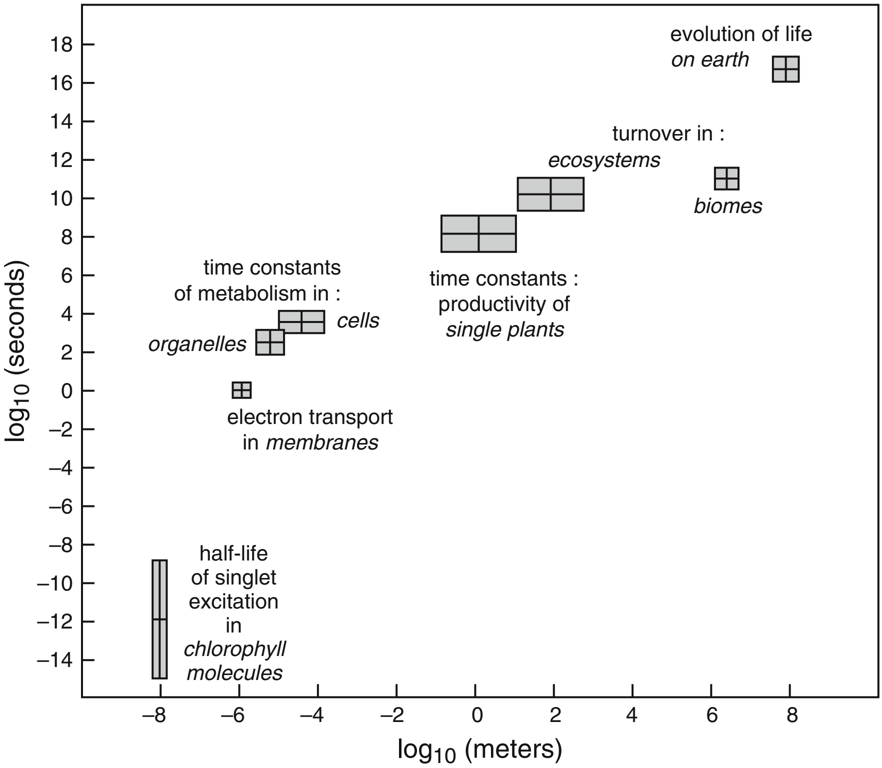

Fig. 2 Scalar levels of life in time (y-axis) and space (x-axis). Ecologically relevant levels range from molecules to the ecosphere (from Lüttge and Hütt 2009)

It is important to be aware of the fact that reductionism is not a reduction of scale size, e.g. from ecosystem to molecule. Complexity can be similarly overwhelming at any scale. Reductionism occurs at any given scale when the degrees of freedom are restricted, which is associated with a restriction of the number of different elements sampled and analysed or incorporated in mathematical models.

Processes and the Dynamics of Systems

Essential processes must be assessed comprehensively (“processomics”). The processes effective in creating and modulating the dynamics of systems in relation to the growth/defence dilemma treated in this volume are

- allocation and resource capture (Chaps. 12–14),
- partitioning and allometry (Chaps. 12 and 13),
- using the space as a resource (Chap. 12),

- competition and cooperation (Chaps. 2–5, 12),
- information biology:
  - Electrical signals (Lautner et al. 2005; Grams et al. 2009)
  - Chemical signals in the liquid and in the gas phase (Chaps. 4 and 5)
  - Light signals (Chap. 8)
  - Mechanical signals in space occupation

Perturbation of Systems by Investigation

Any researcher performing experiments or making measurements on empirical systems knows and the wave-particle dualism of quantum physics tells us most dramatically that any such investigation unavoidably always disturbs and perturbs the system studied. As also seen in the work presented in this book there are several degrees of severity of perturbation, which also cause methodological limitations:

- Perturbation is strong in experimental approaches primarily by direct manipulation of plant systems studied by the experimenters. However, this also includes implementing modes of access (cranes, towers, canopy walkways), e.g. affecting penetration of irradiance or introducing foreign substances (e.g. zinc from the metal of towers; Chap. 16), or using transplantations (controlled climate chambers, lysimeters).
- Perturbation is weak when non-invasive sensors are installed.
- Perturbation is weak when small size samples are taken en route or when sampling is performed destructively only at the termination of the study.
- Perturbation is close to inexistent in modelling and theory where modelling and its parameterisation on the one hand dwell on experiments and observations having perturbed the system under investigation and mathematical operations on the other hand play around and "perturb" the models, but modelling in itself never directly perturbs the empirical systems studied.

At all stages in a comprehensive approach as in the project at large covered in this volume perturbation needs to be evaluated carefully, which again documents the necessity of combining the three legs of the magic tripod experiment—mathematical model—theory.

Hypotheses and Predictability

In the foregoing we have seen that point after point we encounter a multiplicity of view points: scenarios, scalar levels and processes. The major hypothesis underlying the work presented in this book, derived from the growth–differentiation balance theory (GDB, regarded as a theory sensu Chap. 1; Herms and Mattson 1992), was:

> ***Independent of the type of scenarios and their effective factors the plant regulates its allocation of resources in a way that increased growth and competitiveness lead to reduced defence of stress and pathogen attacks***

(Chaps. 1, 19 and 20). Sub-hypotheses were developed. Among these hypotheses when looking at the growth defence dilemma we find three categories:

1. Hypotheses which are unanimously accepted from most or even all view points
2. Hypotheses which are clearly falsified
3. Hypotheses which are accepted at particular spatiotemporal levels but rejected at other levels

The reader will find detailed discussions within the volume. Among (1) we have statements such as

- that increased susceptibility to pathogen attack is reflected in different reactivity of primary and secondary metabolism and their genetic control,
- that independent of herbaceous or woody life form analogous metabolites and genetic and physiological mechanisms of regulation determine the degree of fitness,
- with slight reservations that efficiency in competitiveness and stress tolerance increase with carbon allocation to the rhizosphere and to mycorrhizae,
- with slight reservations that pressures of competition, scarcity of resources and pathogen attack increase the efficiency of the occupation of space by roots and shoots and the acquisition of resources,
- that competition, pathogen attack and symbiotic interaction in the mycorrhizosphere influence allocation by individual plants and biomass production as well as occupation of space.

Among (2) we find

- that an increase in primary metabolism is prerequisite for an increased intraspecific efficiency of competitiveness between neighbouring individual plants, which is rejected as space occupation and allocation are more decisive.

Among (3) we note

- that with increased resource availability species with low substrate turnover are supported in their competitiveness over species with high turnover but simultaneously more sensitive to parasite attack,
- that increased C/N ratios related to reduced nitrogen availability and to ontogenetic development increase pathogen defence,
- that pathogen sensitivity increases with increased stimulation of primary metabolism due to CO_2-concentration in the atmosphere as well as increased N-availability, while ozone treatment increases resistance due to increased secondary metabolism.

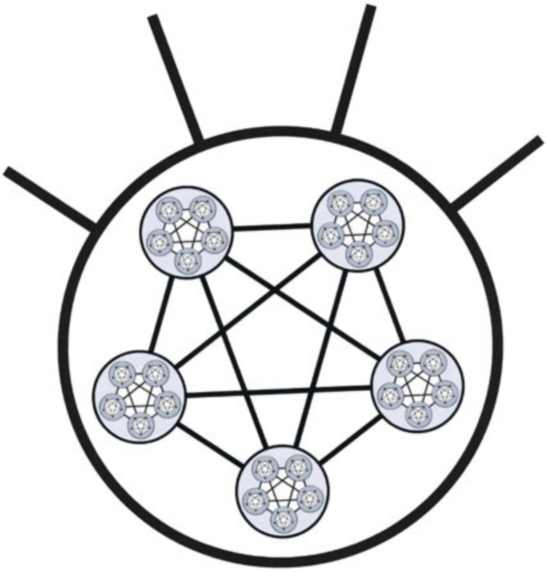

Fig. 3 Networks—macro networks—supra networks—mega networks, etc. where each *point* or *circle* is a system or knot at a particular scaling level and where at each level the output of its individual system is more than the sum of its parts. *Lines* are the connections or edges

The major hypothesis above belongs to category (3): Trade-off between growth and defence is dependent on specific mechanisms and scenarios, and such trade-off is not always expressed. It is an essential result of the work compiled in this book that GDB may basically continue to serve as a basis provoking observations, experiments and thought but that at the same time it needs critical re-evaluation, modification and extension. It is also shown where and how the critique of GDB is becoming effective and where future study is needed. This is achieved by Chap. 1 introducing GDB and Chaps. 19 and 20 putting it under scrutiny with the flesh given by Chaps. 2–18 in between.

That there are hypotheses, including the major hypothesis, which receive positive, negative or neutral answers from different view points or at different scalar levels must not be seen as a failure of the work. On the contrary, it is an intrinsic consequence of the fact that the performance of a whole integrated system is usually not just reflecting the simple sum of its parts. If we consider the impact of the output of a single system in a network of several systems placed at a certain scalar level, we may receive a different answer than when we are seeing the output of several systems of that particular scalar level integrated as one of several parts in a new supra-system at the next higher scalar level. Graphically this can be illustrated by considering the knots (individual systems) of a network at a certain scalar level and unite them into a new macro-knot of a macro-network on the next higher level and taking that macro-network as a knot for a supra-network at the next higher level advancing to a mega-network and so on (Fig. 3; Watts 1999).

Hence, we really must expect that we encounter many scenarios where we receive different answers at different scalar or hierarchical levels as it were for such systems as investigated here. In addition to non-linear behaviour and branching or options between alternative mechanisms, this reflects plasticity and diversity. This is relevant to the assessment of the problem to which extent predictions can be made (Chap. 19). With all success of attempts for predictions (confirmed hypotheses) it documents intrinsic in-determination of systems (open hypotheses), which often makes systems more robust with respect to perturbations by abiotic and biotic stress as fathomed in this volume. In-determination also is keeping the systems challenging, intriguing and interesting. Research is never finished and closed, and curiosity is never satisfied.

Darmstadt, Germany Ulrich Lüttge

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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".

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Part I
Introduction

Chapter 1
The Balance Between Resource Sequestration and Retention: A Challenge in Plant Science

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1.1 Setting the Stage

Plants like all other organisms require sustaining a state of structural and functional order, i.e. to prevent loss of control on internal entropy, and by this warrant the crucial pre-requisite for—what is called—life processes. Such grounds represent energetic pseudo steady-states which are established by a continuous flux of energy and matter through plants as open systems, mirroring dynamic equilibria between

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intake of resources (energy, carbon, water, inorganic nutrients) *versus* release back into the environment after temporary use (Bazzaz and Grace 1997). Upon anabolizing the resources, usage is facilitated through complex metabolic processes and eventually leads into catabolism, unless biomass is shed and becomes subject to decomposition, as does the whole plant body at the end of its life span. Hence, a resource turnover exists, which is operated through input/output balances along time scales specific to the different plant functions. Resource gains from the environment are invested internally to ensure growth, survival and reproduction, and for warranting physiological acclimation and genetic adaptation to the environment. However, the input/output balances are constantly at risk from abiotic (e.g. wind, fire, frost, drought) as well as biotic stressors (competitors, pathogens, herbivores). Therefore, plants must also preserve some of their resources for stress defence, i.e. preventing impediment of uptake and loss. Additional resources are invested into symbionts (like mycorrhizal fungi or N-fixing bacteria) or beneficial soil micro-organisms (van Dam and Heil 2011; Vannette and Hunter 2011) or insects in tritrophic settings (cf. Chap. 4), which together with the plant form the "holobiont" as the co-evolutionarily effective unity (cf. Zilber-Rosenberg and Rosenberg 2008) that determines both resource gain and retention (e.g. Ericsson et al. 1996). The priorities of the different plant functions are dynamic (typically driven by fluctuations in the most growth-limiting factor) so that regulation of the internal resource flux is required. For preventing critical limits in regulation, i.e. ensuring resource supply to vital functions, a buffering component must be sustained, which is the plant's reserve storage. The latter can be intrinsic to defence and reproduction, but is particularly important to plants with prolonged life spans (Schulze 1982).

The individual plant's success in growth, survival and reproduction in relation to competitors is associated with cost/benefit relationships in resource turnover (Schwinning 1996). It is conceivable, therefore, that marginal fluctuations in such cost/benefit relationships, i.e. in the efficiencies in resource management, are crucial for plant competitiveness. Such an "economic" view on the plant's existence (e.g. Givnish 1986 and review articles therein) reflects the core of ecology, as expressed by Ernst Haeckel, a founder of the research discipline, *sensu* ecology as the economy of organisms (Haeckel 1870). In such terms, survival of the fittest during the evolutionary process (Darwin 1859) results from efficient resource use, which might be more decisive than maximum resource sequestration relative to competitors (e.g. Schulze et al. 1986; Matyssek and Schulze 1987; Küppers 1994; Schwinning 1996; Grams and Andersen 2007).

Given the ecological need for efficient resource use, the plant faces the challenge that any resource can only be spent once at a given instant, although "recycling" for same or different functions is possible. Examples are storage, which postpones the ultimate investment, and metabolites with rapid turnover or precursors of several usages (Stitt and Schulze 1994). Therefore, plants may encounter a dilemma in resource allocation to various concurrent needs, giving rise to potential trade-offs, i.e. favouring some functions at the expense of others in terms of inverse relationships. A crucial trade-off is associated with investment into growth (for ensuring competitiveness) *versus* that into defence against stress with risks of resource loss. In such terms, the plant has to balance resource uptake and incorporation *versus* resource retention (Matyssek et al. 2005). This balance is the expression of individual plant fitness by providing the ability and extent of reproduction through the capacities in competitiveness and defence as crucial prerequisites. The balance is evidently fed from the whole-plant resource pool with all its metabolites (regardless of being conventionally classified as "primary" or "secondary"; Schwachtje and Baldwin 2008). It is tempting to conceive underlying mechanisms through which the required balance is accomplished and the potential dilemma in resource allocation is resolved.

In the following, we will first highlight theoretical concepts that give guidance to understanding resource allocation in plants. "Theory maturation" will be examined in view of the available knowledge *prior to* the recent progress reported in this book—or, in other terms, of capacities for hypothesis formulation and falsification in promoting and consolidating knowledge. Empirical aspects will then be viewed both in terms of constraints on and potential for theory development. The stage will be set for demonstrating recent empirical and theoretical progress on the outlined subject in the subsequent book chapters.

1.2 Theories on Whole-Plant Resource Allocation

Amongst analytical concepts which view resource availability as a driver of whole-plant allocation, three prominent ones focus on the "*growth–differentiation-balance*" (GDB; Herms and Mattson 1992), the "*carbon–nutrient balance*" (CNB, Bryant et al. 1983) or on the role of protein synthesis ("*protein competition model*", PCM; Jones and Hartley 1999). Conceiving allocation by different regulatory principles, these will be featured in this section *prior to* also introducing the concept of "*optimal defence*" (OD, Rhoades and Cates 1976), which is based on the value of organs for plant fitness *versus* their risk of loss. Such concepts, each of them claiming to reflect specific evolutionary outcome, have been termed hypotheses, although it is debatable of whether they may also be viewed as theories. Classification of the above concepts as theories appears to be justified to the extent that guidance to experimental clarification and mechanistic explanation is provided (Stamp 2004), as will be elucidated in the following. On such grounds, the introduced concepts will be termed as "theories" in the remainder of this chapter, while being aware of their present "immature" state (Stamp 2003a; also see Sect. 1.3).

1.2.1 Growth–Differentiation Balance Theory

As introduced by Loomis (1953; also see Lorio 1988) and extended by Herms and Mattson (1992) and Matyssek et al. (2002, 2005), GDB states a trade-off in plant