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
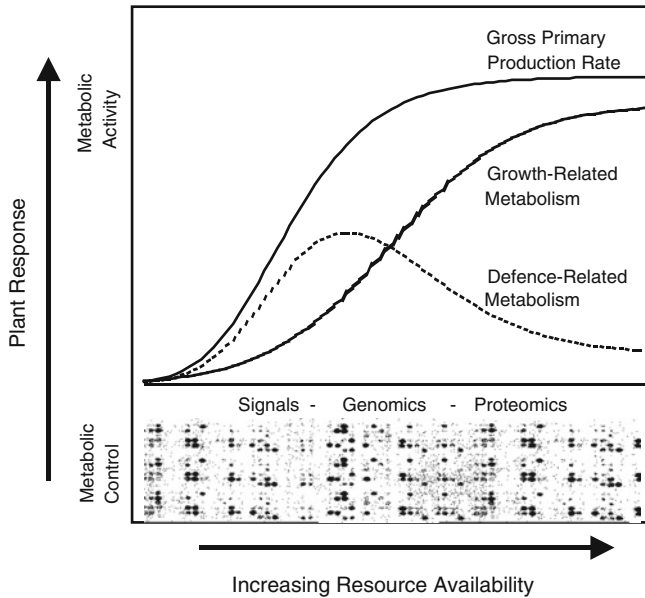
Fig. 1.1 Plant response in relation to increasing resource availability, expressed as variations in gross primary productivity along with such growth and defence-related metabolism. Note indicated trade-offs between growth (and competitiveness, see text) *versus* defence, according to the "*growth–differentiation balance theory*" (cf. Herms and Mattson 1992). Metabolic activity (biochemical and physiological process level) is linked with metabolic control at the molecular (gene) level through signalling, genomics and proteomics (from Matyssek et al. 2005, with staining pattern symbolizing genomics as macro-array based transcript analysis)

internal resource allocation between growth and defence. Differentiation means resource investment into the chemical and structural modification of biomass as opposed to growth, which represents irreversible biomass increment (Potters et al. 2009). Differentiation can serve both mechanical stability (being conducive to growth) and biochemical defence (Arnold and Targett 2003). Hence, differentiation implies that the functional transition between growth and defence is gradual. On such grounds, Fig. 1.1 schematically approximates the core of GDB, according to the extended view of Matyssek et al. (2005), in that increasing resource availability promotes gross primary productivity (GPP) towards a maximum level. In parallel, growth and defence-related metabolism respond in complementary ways to each other, in terms of a trade-off. This means, favoured defence at low resource availability at the expense of growth, but favoured growth at high availability when defence is low. Uncertainty may arise at severe resource limitation, which may constrain both the growth and defence-related metabolism (Glynn et al. 2007).

The processes associated with the three resource-driven functions of Fig. 1.1 are controlled by gene regulation (through signalling, transcription and protein synthesis). Haugen et al. (2008) underlined that the plant's capability of expressing trade-offs in growth/defence-related allocation is genotype-specific. The molecular

basis indicated in Fig. 1.1 (signals–genomics–proteomics) reminds of deficits in the understanding of the mechanistic link between metabolic control and metabolic activity (Matyssek et al. 2005; Ballhorn et al. 2008). In comparison to previous visualizations of GDB (Herms and Mattson 1992), choosing gross primary production rate (GPP) instead of net assimilation rate (NAR) as one measure of plant productivity stresses the paramount importance of respiratory demands in driving the trade-off (cf. Bolton 2009). Replacing, in addition, the previously used terms "primary" and "secondary" with "growth-related" and "defence-related" metabolism, respectively, overcomes the conceptual restriction of the conventional classification in that metabolites (or their precursors) may serve growth and/or defence regardless of their chemical nature (cf. Arnold and Targett 2003). As these two functions have to be achieved by the plant simultaneously, clarification of the role of metabolites in resource uptake (through competitive growth) and/or retention (through defence; Riipi et al. 2002) is crucial. Nevertheless, distinguishing between different types of secondary metabolites is important, because they reflect diversity acquired during evolutionary history, providing plants with the capacity of responding to specific ecological challenges (i.e. particular herbivores, pathogens). This evolutionary component in combination with the assumption of allocation trade-offs makes GDB a framework that allows understanding of departure from the core of the theory. In a strict sense, GDB views the availabilities of the resources (e.g. water and nutrients) as affecting the ratio between the pool size of photosynthate (i.e. the carbon pool) and the demand of growth for photosynthate (i.e. the sink strength for biomass formation; Koricheva et al. 1998). Resource limitation, predominantly by nitrogen (N) *sensu* GDB, but also by phosphorus (P; Sampedro et al. 2011), curtailing the sink strength of growth may lead to an accumulation of carbon, which then is available to differentiation processes including defence. Notwithstanding such kind of regulation, allocation is conceived to serve growth at a higher priority than differentiation.

1.2.2 Carbon–Nutrient Balance Theory

In a sense that fluctuations in source/sink ratios as drivers of allocation trade-offs affect the relative availabilities between carbon and other resources, GDB indicates some conceptual proximity to CNB (Bryant et al. 1983). The latter, however, basically conceives growth/defence allocation trade-offs to be driven through changes in the carbon/nutrient ratio. Hence, rise of this ratio, as occurring under nitrogen limitation or at high light or elevated CO_2, is believed to favour differentiation. Mattson et al. (2005) suggested that climate change-associated atmospheric CO_2 increase will favour defence (e.g. as based on phenolics; cf. Koricheva et al. 1998), given the indications of a prevalently carbon-saturated metabolism, in particular, in trees (Körner 2003). Conversely, a decreasing ratio may curtail differentiation and defence. In addition, the sizes of C and nutrient pools relative to each other should determine, according to CNB, the chemical quality of defence

metabolites in view of N demand during synthesis. Overall, similar working hypotheses may be derived from GDB and CNB, in that, for example, plants regulate their resource allocation in a way that increase in growth and competitiveness leads to constraints on stress defence, in particular, of pathogens and herbivores (Matyssek et al. 2002, 2005).

CNB has been criticized recently for its inability to cover a wide range of ecological scenarios (Hamilton et al. 2001; Lerdau 2002; Koricheva 2002). Stamp (2003b) along with Herms and Mattson (1992) suggested to view CNB as a module of GDB, given some overlap between both theories. However, such a view would ignore that GDB rather than CNB can conceive different physiological interactions to result in similar C/N. In particular, GDB mirrors secondary metabolism to obey a parabolic dependency function in relation to resource availability, so that non-linearity in plant response is covered. In addition, GDB is specific in predicting the ways different environmental factors affect trade-offs through altering source/sink relationships, rather than being restricted to immediate effects on the carbon–nutrient balance. On such latter grounds, GDB has been evaluated as advanced in guiding a mechanistic analysis of allocation trade-offs, and in promoting theory development (Stamp 2003b).

1.2.3 Protein Competition Model

PCM (Jones and Hartley 1999) also pursues a mechanistic view on allocation trade-offs in plants and appears to be conceptually related to CNB and GDB because it considers N availability as one driver of allocation amongst nutrients. However, PCM differs from CNB and GDB theories by emphasizing the biochemical process level in the regulation of allocation, specifically, the competition between formation of proteins and phenolic compounds for the common, limiting precursor phenylalanine—which is the core of PCM. As a typical characteristic, plants possess the shikimic acid pathway producing phenyl-propanes, and hence, phenylalanine. Therefore, the trade-off can be claimed to originate from the inversely related allocation into protein *versus* phenolic substances formation, with phenylalanine-ammonia lyase (PAL) as the central metabolic switch. At increasing N availability, protein synthesis should drain, therefore, the carbon pool, creating a sink for growth, while curtailing the capacity for the formation of phenolic metabolites. In essence, and as opposed to GDB, the plant's N rather than C pool is conceived to limit phenolic synthesis, and hence, defence. It is believed that the concentration of phenolic compounds increases with declining sink strength for growth, either through environmental effects constraining N availability, or during advanced stages of organ maturation and ontogeny, or in plant species with inherently low growth rates (Jones and Hartley 1999). PCM was suggested to complement GDB in biochemical terms and to represent a viable alternative to CNB. Doubts arose, however, recently about the validity of PCM under elevated CO_2. According to PCM, the phenylpropanoid pathway should become limited

(i.e. with the N pool making proficient use of the high C supply for growth), whereas *sensu* GDB, C availability to the formation of phenylpropanoids should increase relative to the N pool. Respective evidence appears to support GDB rather than PCM (Mattson et al. 2005). In addition, phenylalanine was shown to be regenerated under N limitation through internal recycling of N in amination/desamination reactions (Pankhurst and Jones 1979; Graham 1983; Peng et al. 2007), which questions the regulation of the formation of phenolic substances through N availability. Furthermore, pool sizes of defence metabolites do not necessarily increase with ageing, as high levels in vulnerable young leaves have shown the plants' capability of decoupling defence from ontogeny (Herms and Mattson 1992).

In cross-evaluating growth/defence allocation theories, Koricheva et al. (1998) developed a hierarchical model of carbon allocation to plant secondary compounds. This model implies that resource-based theories as represented by CNB and GDB make valid predictions only about the total amount of carbon that can be allocated to carbon-based secondary compounds (CBSCs). Such theories cannot predict plant responses at lower hierarchical allocation levels, where carbon is shunted into various alternative synthesis pathways to different CBSC classes (e.g. phenolic compounds including lignins, terpenoids, alkaloids, tannins, phenylpropanoids). Instead, Koricheva et al. (1998) suggested that carbon allocation at lower hierarchy levels depends on specific evolutionary plant responses to the various types of biotic and abiotic stresses. Phenylpropanoids are an exception in that they are closely linked—through their precursor phenylalanine—with growth metabolism (see above). Hence, they tend to more distinctly reflect the resource trade-off between growth and defence (Rühmann et al. 2002) than do other compound classes. PCM may attain relevance in view of evolutionary specificities at low hierarchy levels.

1.2.4 Optimal Defence Theory

As opposed to GDB, CNB and PCM, OD (Rhoades and Cates 1976) is not related primarily to resource availability and associated phenotypic plasticity (including growth/defence allocation trade-offs). Rather, OD represents a life-history, i.e. adaptation-based explanation model that evaluates defence of plant organs in relation to risk by herbivory and value for plant fitness (Orians and Ward 2010). Economy in the regulation of allocation is presumed, viewing adaptations by their potential of decreasing defence cost, so that sufficient, i.e. "evolutionarily optimized", rather than abundant investment into defence is postulated (cf. Siemens et al. 2010). "Value" is defined by the fitness costs inflicted upon injury or tissue loss and tends to be negatively correlated with the abundance of a tissue or organ within the plant (Zangerl and Bazzaz 1992). "Risk" arises from the probability of vulnerability (by herbivore attack), as incurring in the absence of defence. High priority to defence is implied, if a tissue is exposed to consumers (e.g. peripheral tissue location in the plant), with the chemical quality and fitness costs being determined with the probability of discovery (Feeny 1976; Bustamante et al. 2006). Conversely,

low priority is suggested, if consumers are satiated by high tissue/organ abundance. In line are observations that determinate shoot growth, abundantly producing young foliage during short time periods, may not require enhanced defence, whereas leaves continually originating from indeterminate growth by low numbers may do so (Herms and Mattson 1992). OD is complementary to, and consistent with GDB in sharing the fundamental assumption that defence is costly. Both predict that given multiple defensive options of equal efficacy, the least costly is favoured, and that at equal costs, preference is with the most efficacious one. GDB provides a functional foundation to OD, when viewing phenotypic variation in defence as an adaptive trait in the response to nutrient availability (Glynn et al. 2007).

1.2.5   Preliminary Valuation

As the regulatory settings in plants are complex, one cannot *a priori* expect any of the theories introduced above to give a plain answer about the plant's "approach" to resolving the dilemma of resource sequestration *versus* retention. Plants may even invest resources into several different defence traits, being "jack-of-all-trades" *sensu* Koricheva et al. (2004), which may mitigate trade-offs of a particular trait. Haugen et al. (2008) postulate the clarification of allocation conflicts in relation to plant ontogeny and variable site conditions. Phenotypic plasticity in response may pretend plants to—or even makes them—perform in ways unrelated to resource trade-offs and respective theories (Bradshaw 2006; Ballhorn et al. 2008).

1.3   Constraints and Potential of Theory Development

For all theories introduced above, consistency with experimental evidence is limited (Koricheva et al. 1998; Koricheva 2002; Siemens et al. 2010). Scope and state of "theory maturation" attained *prior to* the recent gain in knowledge that will be reported in this book on the plant-internal growth/defence conflict will be outlined, therefore, both in view of science theory and empirical considerations. Constraints on and potential for theory development on plant resource allocation will be highlighted.

1.3.1   Aspects of Science Theory

1.3.1.1   Stages of Theory Maturation

Plants may express high phenotypic plasticity in stress response (Koricheva et al. 1998; Siemens et al. 2010; Cipollini and Heil 2010). The existence of this plasticity

has even led to questioning the suitability of the objective, i.e. the regulation of resource allocation between growth and stress defence, for theory building (Berenbaum 1995). The uncertainty relates to the rules of theory development and means of associated hypothesis testing. Theory development goes through early, immature and mature stages (Stamp 2003a). The early stage typically implies the formulation of relatively vague and qualitative hypotheses which cannot be accurately and unambiguously tested. Conclusions are at risk to be caught in conceptual conflicts, because the underlying mechanisms are still unclear. Increasing empirical evidence is one means of promoting sharpness in hypothesis formulation and testing towards approaching the immature stage. If predictions stay vague, competing hypotheses and theories on same, but inadequately understood phenomena tend to prevail (Berenbaum 1995), and intellectual progress may become exhausted in reconciling findings, which typically lack overarching conceptual and experimental frameworks. Novel statistical tools, linking generality of findings with deterministic strength, along with rigorous examination for plausibility and inherent consistency can mitigate seeming conflicts (Chap. 16). Overcoming "immaturity" means posing and falsifying hypotheses on mechanisms that underlie the challenging phenomena, i.e. *sensu* Karl Popper (1989) hypothesis (and theory) elimination through falsification is the pre-requisite for intellectually approaching the actual nature of research objectives. The frontier in research on growth/defence-related allocation has arrived at intensifying this selection process (Stamp 2003a), and it is one aim of this book to explore recent progress in approaching "maturity" in theory development.

The current stage requires the definition of predictive limits of hypotheses under examination rather than the exploration of the entire scope of theories. Findings upon passing comprehensive quality assessment, combining plausibility and consistency evaluation with hypothesis testing, have been adopted, in addition, too rarely into frameworks of mathematical modelling. Such latter abstractions advance hypothesis formulation and testing towards enhanced integration levels to foster further empirical progress. Interaction between experimentation and modelling has been neglected in promoting theory building. Advancements in this field are a subject of this book. In the forefront, none of the introduced theories has reached "maturity", given the shortcoming that most knowledge has not been elaborated in view of theory development, but circumstantially originated from the pursuit of conceptually non-related research questions.

1.3.1.2   Hypothesis Formulation

How to formulate hypotheses and design research in view of theory development? Making research questions operational for testing requires streamlining hypothesis formulation, while preventing simplification prone to misinterpretation. Simulations by mechanistic modelling, representing hypotheses themselves, may provide demanding predictions beyond the scope of experimentation, being testable against empirical evidence. Still, theories can only reflect excerpts from the wide range of biological reality, being defined by plant behaviour and ecological scenario.

Research outcome beyond hypothesis prediction represents falsification, and hence, in terms of science theory, gain in understanding (cf. Popper 1989). The appropriate balance between simplification in hypothesis formulation as an expression of attained intellectual comprehension and aptitude to falsification, therefore, is crucial. In particular, growth/defence resource allocation with its metabolic specificities across stress and plant types (see Sect. 1.2) offers potential for (rather than hinders) theory development, as will be elucidated in this book.

1.3.1.3 Sub-theories

Theories can be viewed as integrative constructs of sub-theories that are insertions for facilitating analysis (Stamp 2004). Such insertions dealing with pre-requisites of the overall construct support focused hypothesis formulation on, e.g., gene regulation, biochemical pathways, biotic interactions—or, often neglected, but fundamentally important—on the roles of genotype, pre-history, plant ontogeny, allometry, phenology or bifurcation in resource allocation. Derived hypotheses are applicable to explicit developmental or ecological settings and can be hedged or interconnected to argumentative chains or statistically ascertainable relationships. At this stage, statistical modelling (Chap. 16) as a tool complementary to mechanistic modelling can foster hypothesis development and testing. Advancement of such kind is constructive, unless intellectually unassimilated findings merely accumulate. Recent evidence reported in this book originated from an approach as suggested here. Only inconclusive stagnation would pretend plant functioning to be governed by exceptions and lead to questioning suitability for theory development.

1.3.2 Biological Aspects

1.3.2.1 Steady-States *versus* Stages of Transition

Theory development is constrained also by the complexity of plant life and related challenges in experimentation that needs to ensure potential for hypothesis testing. One key assumption behind the theories on growth/defence resource allocation typically is steady-state in plant metabolism (Stamp 2004, "steady-state" used here *sensu* pseudo steady-state, as plant are open systems in terms of thermodynamics, cf. Sect. 1.1). However, plant life at field sites is hardly determined by steady-states. Although these are conducive to facilitate and standardize experimentation and hypothesis testing (Koricheva et al. 1998), evolutionary understanding gained about plant performance is limited (Glynn et al. 2007). Complication in conceptually relying on steady-states may arise due to plants' use of reserves from pre-experimental periods (Siemens et al. 2010), while acclimating to experimental treatments (Glynn et al. 2007). Defence costs inherited from the preceding generation through non-genetic parental effects may also bias steady-states (Purrington 2000).

In addition, resource supply *versus* demand can change due to experimentation and/ or plant development, which altogether underlines the dynamic rather than steady-state character of resource allocation. In this sense, empirical studies conducted so far tended to neglect the evolutionary dimension of growth/defence allocation which in fact resembles a "moving target" (Glynn et al. 2007). Moreover, plants were often "overloaded" with stress (e.g. parasites) in order to provoke distinct response, which not necessarily was ecologically meaningful (Bolton 2009; cf. van Dam and Heil 2011). Recent assessment by Glynn et al. (2007), however, showed predictions of GDB to stay robust about changes in plant metabolism, as transitioning to new equilibrium upon alteration in resource availability. Hence, the scope of GDB can reach beyond the argument of Stamp (2004) that growth/ defence allocation theories are bound to steady-state presumptions. The subsequent account in this book is guided by envisioning dynamics in plant response.

1.3.2.2 Phenotypic Plasticity

In addition to dynamics in allocation, resource availability if severely limiting GPP challenges empirical analyses. Given such a setting to limit both growth and defence, plants apparently obey the principle of "optimal phenotypic plasticity" (Glynn et al. 2007) in assigning high priority to compensatory growth. For example, nutrient or water shortage typically drives below rather than aboveground production (Mooney and Winner 1991). During growth adjustment, growth/defence trade-offs hardly become substantiated. Absence of trade-off may also be explained by high variation in resource acquisition *versus* allocation (van Noordwijk and de Jong 1986). Once adjustment being accomplished, plant performance was found, however, to conform to trade-off predictions by GDB (Glynn et al. 2007). It was proposed, therefore, to extend GDB by including the concept of phenotypic plasticity to enhance the theory's predictive strength. This concept communicates why GPP and allocation to defence and growth can positively correlate while approaching the plant-internal set-point of balanced resource flux *sensu* Mooney and Winner (1991): The constraint on GPP (i.e. production of photosynthate) apparently becomes relieved to a higher degree than on growth (in terms of irreversible biomass increment) so that the eventually resulting surplus in C availability can stimulate defence. Such grounds may explain inconsistencies in theory predictions by ascertaining the parabolic dependency of defence, as postulated by GDB, on the transition from limiting to non-limiting resource availability (cf. Fig. 1.1; Glynn et al. 2007). Complication represents, however, scarcity of knowledge on belowground plant defence and variable competitive interference during successional progression (Luedemann et al. 2005; Rasmann et al. 2010; Hakes and Cronin 2011).

1.3.2.3 Driving Factors

Misinterpretation of growth/defence allocation theories can arise from confounding driving factors. Exemplifying GDB, these are nutrients and water rather than

carbon (Koricheva 2002). The distinction is crucial in understanding growth (biomass increment) rather than GPP (productivity of photosynthate) to be limited by incipient shortage of water and/or nutrients (Kramer and Boyer 1995). The latter drive the sink induction of growth, and by this, are the primary determinants of potential allocation trade-offs. Mitigated sink induction, however, enhances the internal carbon availability which then fosters structural and functional differentiation, including defence. Nevertheless, there is no strict "either-or", regarding the potential usage of resources in growth *versus* defence processes, as some metabolites may serve both plant functions (Riipi et al. 2002; cf. Vannette and Hunter 2011). Phenylpropanoids, however, appear to mostly mirror allocation trade-offs under the fluctuating influence of driving factors (see Sect. 1.2.3 and Chap. 3). Within this compound class, trade-offs may even occur between metabolites, if precursors share same biosynthesis pathways (Koricheva et al. 2004). Trade-offs tended to become conspicuous within the whole-plant phenylpropanoid pool (Koricheva 2002). However, metabolic whole-plant assessments have been rare, despite their high integrative value in theory development.

1.3.2.4 Productivity Parameters

Another challenge is the adequate assessment of photosynthetic productivity and growth parameters in view of growth/defence allocation theories. NAR and RGR (relative growth rate), respectively, have been chosen as substitutes, like in the case of early definitions of GDB (cf. Herms and Mattson 1992). This increases the conceptual uncertainty in addition to ambiguous distinctions between secondary and primary metabolites (cf. Matyssek et al. 2005; Stitt and Schulze 1994; see Sect. 1.2). NAR may be viewed as mirroring the balance between respiratory demand and the remaining portion of carbon, upon the respiratory mitigation of GPP, eventually available to growth (Glynn et al. 2007). The circumstance of NAR and RGR being linked to each other *via* LWR (leaf weight ratio) within the framework of growth analysis (Nobel 1983) is conducive, however, to interpreting predictions of GDB (Glynn et al. 2007), as LWR is an indicator of the plant's phenotypic plasticity (see above). Theory development has neglected, though, the capacity of plants under stress for inducing additional sinks for carbon related to defence. Such sinks require enhanced supply of primary carbon compounds (Schwachtje and Baldwin 2008; Bolton 2009). Photosynthesis can be up-regulated in such cases (Murray and Walters 1992; Williams and Ayres 1981), augmenting the carbon pool available to allocation through enhancing GPP (i.e. the supply of photosynthate). Increasing GPP de-escalates growth/defence trade-offs, i.e. helps the plant to "escape" from the dilemma (in addition to reasons suggested by van Noordwijk and de Jong 1986; see above)—albeit reducing conformity to prevalent theory predictions. Photosynthetic up-regulation may be a trait of defence beyond GDB, unless parasites profit from the enhanced carbon availability (Bolton 2009).

1.3.2.5 Respiratory Costs

Within frameworks of growth/defence allocation theories, the amount of respiratory carbon as a determinant of productivity and substantial component of GPP has largely remained unaccounted for. This deficit is severe as primary carbon compounds do not only feed differentiation and defence, but are crucial also for the associated respiratory demand of both (Bolton 2009). Unlike other aspects of defence, e.g. metabolic pathogen recognition, signalling or biochemical stress responses, the energy recruitment of defence has scarcely been investigated (Schwachtje and Baldwin 2008; Bolton 2009). On such grounds, the concept of GDB was widened by Matyssek et al. (2005) in replacing NAR with GPP (acknowledging respiration) and stressing the potential multi-functionality of metabolites, mediating between rather than separating growth and defence-related metabolism (cf. Fig. 1.1). This considers the actual scope of GDB in a more realistic view, as "full resource costs" of trade-offs must include respiration, and as multi-functionality of metabolites is a basic feature of the plants' biology. Häberle et al. (2009) approximated the substrate disposable for defence to be about 2–5 % of GPP. Estimating full costs of defence and growth is difficult (Gershenzon 1994; Bazzaz 1997), but important for further theory development. Quantification of respiration is relevant also to costs before metabolites deploy their ultimate and specific function (Purrington 2000), as incurred from transport, storage or synthesis and turnover of precursors (Lerdau and Gershenzon 1997). Given the methodological challenges, however, to be overcome, "full-cost" studies hardly have been pursued (Lerdau and Gershenzon 1997).

1.3.2.6 Direct *versus* Indirect Defence Costs

Growth/defence allocation theories typically focus on costs which are directly associated with resource investment to defence *versus* such to growth and other plant functions (allocation costs). Direct costs of *constitutive* defence (being preformed in the absence of stress impact) must not conceptually be confounded with such inducible defences. Costs of these two types of defences may be negatively correlated, representing another kind of trade-off (Koricheva et al. 2004). Conclusions about "inexpensiveness" of inducible defence in relation to plant fitness appear to be premature (Heil, and Baldwin 2002; Koricheva 2002) and perhaps result from limitations in statistical resolution (Purrington 2000). Instead, expenses are likely for sustaining the plant's capacity for inducing defence, if intermittently needed (Purrington 2000; Cipollini and Heil 2010). As this capacity relies on plant properties provided by the growth-related metabolism (e.g. storage structures, defence precursors, multi-functionality of metabolites; Arnold and Targett 2003), and as *inducible* defence tends to be locally restricted in plant tissues, costs may be lower, however, than of constitutive defence (see Chap. 3).

However, indirect costs of defence may also be relevant for plant resource allocation to growth *versus* defence (Koricheva 2002). One type are "opportunity costs" associated with constitutive defence, denoting foregone opportunities (e.g. Stitt and Schulze 1994) upon investing resources into defence instead of growth—*sensu* the additional biomass increment (beyond the equivalent effect of resource partitioning per se) that would have occurred in the absence of defence. Such costs are manifested in the presence of competitors (Baldwin and Hamilton 2000; Hakes and Cronin 2011). Of indirect nature also are "ecological costs" of defence (Koricheva 2002). These denote enhanced defence against one stressor at the expense of other defences (Purrington 2000; Strauss et al. 2002; Haugen et al. 2008). Third-party trade-offs between the different kinds of defences may arise (Koricheva et al. 2004; Ballhorn et al. 2008). The significance of ecological costs has been overlooked in terms of plant evolution and ecology, although indirect and direct costs appear to be equally important (Koricheva 2002). If plants developed multiple stress defences at low ecological costs instead of switching defence within rigid frameworks of allocation trade-offs (Koricheva et al. 2004; Novriyanti et al. 2010), low conformity to current allocation theories would not be surprising (Cipollini and Heil 2010; Siemens et al. 2010). Ecological costs require awareness as incurring under contrasting ecological scenarios, including varying extents of competition or facilitation as modifiers of defence capacity (Baldwin and Hamilton 2000; Siemens et al. 2003; Hakes and Cronin 2011).

1.3.2.7 Mechanistic Perspective

Given the methodological constraints on "full-cost" analyses (cf. Gershenzon 1994; see above), the mechanistic understanding of costs is a pre-requisite for promoting growth/defence allocation theories (Purrington 2000; Stamp 2003b). The cause–effect related "down-link" from phenotypic expression to gene regulation, however, represents a research frontier in plant science. A challenge is posed, in particular, for understanding the genotype determining trade-offs in growth/ defence allocation and ecological costs (Purrington 2000), as exemplified for defence–drought interrelationships (Haugen et al. 2008). Gene clusters rather than single genes respond to external stress and/or internal resource demands, hindering proofs of cause–effect relationships (Potters et al. 2009), because both at the gene and process level, straight-forward relationships can be lost and embedded in complex interaction networks (as determined, e.g. by demands for reserve storage, reproduction or by symbionts like mycorrhizal fungi, N_2-fixing bacteria or soil micro-organisms and insects; van Dam and Heil 2011). As a consequence, "third-party trade-offs" can arise, so that the one on growth/defence allocation needs to be viewed as part of the continuum in whole-plant allocation (Fig. 1.2, Matyssek et al. 2005). This continuum is represented by one resource pool (as the sum of primary and secondary metabolites) concurrently serving growth as a means of competitiveness, defence for retaining competitively acquired resources, and (below-ground) symbionts in support of competitiveness and reproductive success
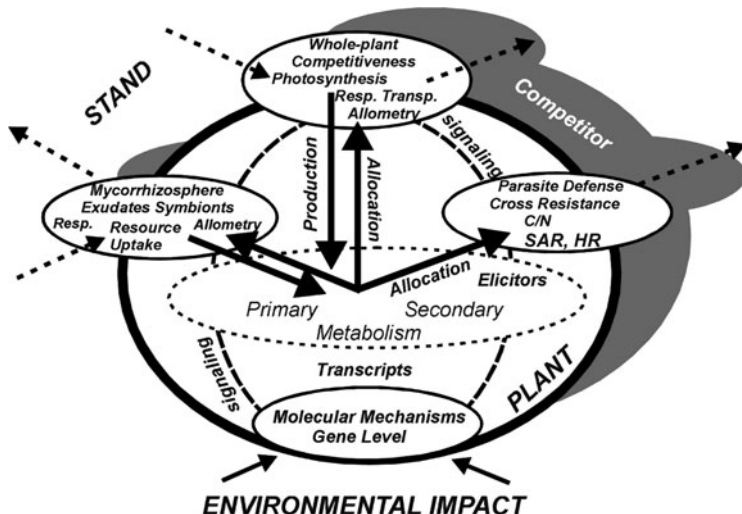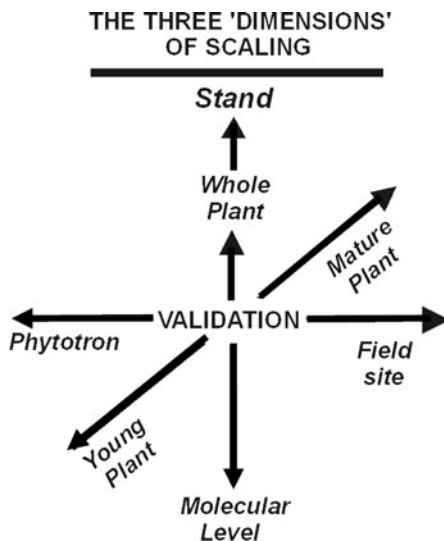
Fig. 1.2 Conceptual model visualizing whole-plant resource allocation. *Arrows* indicate major pathways in resource allocation between physiological demands within the plant and in exchange with the environment, as being under the control of environmental impact and molecular processes (see text for details; from Sandermann and Matyssek 2004)

(van Dam and Heil 2011; Vannette and Hunter 2011). Ecological benefits counteracting trade-offs have been reported, as some kind of facilitation, from mycorrhizae in enhancing defence (Bonello et al. 1993; Ericsson et al. 1996; Bi et al. 2007; Pozo and Azcon-Aguilar 2007), although the mechanistic basis is unravelled only in parts and also mitigation of defence has been reported (Koricheva et al. 2009). However, such kind of factorial and mechanistic complexity represents the actual, biologically relevant stage of growth/defence theories.

1.3.2.8 Spatio-temporal Process Scaling

"Timing" of mechanisms in growth/defence allocation is another aspect of relevancy in related theory development. Gene regulation can proceed instantaneously, whereas the induced metabolic processes may evolve with delay and develop prolonged momentum (regarding growth, up to weeks or months). Conversely, only prolonged factorial impact may end up in gene induction, as well as more than one gene induction event may be necessary for sustaining defence (Purrington 2000). Hence, the temporal coupling between gene expression and physiological response can be weak or even appear to be absent under the influence of factorial networks (Glinski and Weckwerth 2006). The plant's metabolic status may even more readily be assessable through principles of thermodynamics than the pursuit of process pathways (Potters et al. 2009; cf. Sect. 1.1). Process scaling is intrinsically linked with increasing time scales (Sandermann and Matyssek 2004) and

Fig. 1.3 Three spatio-temporal axes ("dimensions") of process scaling (adapted from Matyssek 2001)

THE THREE 'DIMENSIONS'
OF SCALING

Stand

Whole Plant

Mature Plant

Phytotron — VALIDATION — *Field site*

Young Plant

Molecular Level

decreasing strength of cause/effect relationships in approaching hierarchically high levels of integration (Baldocchi 1993). Mechanistic consistency may be lost when bridging neighbouring scales within the integration hierarchy (see Fig. 3 of the Prologue; Watts 1999). Such scaling characteristics interfere with growth/defence analyses. In addition, ontogeny affects process scaling as one additional driver in resource allocation (see above, Haugen et al. 2008). Also within-plant scaling has prevailed (linking factorial impact with phenotype and gene regulation), although plants in parallel do affect the ecosystem fluxes and site conditions, which in turn set the stage for the plants' performance (Hendriks et al. 2009). Matyssek (2001) stressed, therefore, the "three dimensions of scaling" in developing growth/defence theories on mechanistic grounds (Fig. 1.3), i.e. integrating (1) the gene-to-ecosystem axis and those of (2) ontogeny (in association with plant allometry, see Chap. 13) and (3) growth conditions, i.e. from controlled (phytotrons, glasshouses) and semi-controlled environments (e.g. field lysimeters; Schloter and Matyssek 2009) to actual field sites. Axes (2) and (3) are borne by the experience that juvenile plants physiologically and structurally differ from mature ones, and that plant behaviour displayed under controlled growth conditions does not necessarily conform to field performance. Evidence remains rudimentary, therefore, as long as physiologically and ecologically meaningful validation is missing.

1.3.3 Theoretical Outset of This Book Project

Amongst theories on growth and defence-related resource allocation, GDB has been considered as the one with the highest integrative and explanatory potential

(Stamp 2003b). The conceptual strength is based on the advanced framework character in comprehending available knowledge from the cell, tissue, organ and whole-plant levels, across ontogenetic stages, ecological scenarios including stand-level interactions, and beyond steady-state conditions (Glynn et al. 2007). On such grounds, advancement towards "theory maturity" appears to be promising, given the plants' repertoire in answering stress in plentiful and variable ways (Schwachtje and Baldwin 2008), i.e. by means of more than one defence strategy. Challenges will be coped with in this book that originate from dynamics and plasticity, making plant resource allocation and defence "moving targets" both for theoretical treatment and the ecology and evolution of host–parasite relationships (Glynn et al. 2007). In striving for mechanistic understanding, the ecological perspective, neglected in the past, on growth/defence-related allocation will be fostered in the following chapters in combination with and relative to the molecular analysis (cf. Schwachtje and Baldwin 2008).

1.4   Gain in Knowledge Presented in This Book: An Outlook

Recent gain in knowledge, both in empirical and theoretical terms, will be united in this book on one of the plant's and plant research's fundamental challenges, as pointed out above, i.e. the regulation of allocation across physiological demands. Allocation may culminate towards growth (mediating competitive resource sequestration) *versus* defence (enabling for resource retention) so that focus is directed to GDB as a reference, being one leading theory on plant allocation with integrative capacities for mechanistic foundation and extension (Stamp 2003b; Herms and Mattson 1992; Koricheva 2002). Part II will then comprehend advancements across diverse spatio-temporal dimensions of mechanisms in resource allocation, according to the book's sub-title. Relevancy will be examined for herbaceous and woody plants and stands in view of the introductory considerations of the Sects. 1.1–1.3 of this chapter.

Starting point of Part II will be the extent of progress in linking the molecular with the biochemical and physiological level, accounting for plant–pathogen, plant–herbivore and plant–mycorrhizosphere interactions in determining, individually and in combination, allocation control through gene regulation. Resource costs and benefits will be viewed in relation to symbiontic organisms and extended to respiratory costs as further determinants of whole-plant allocation. State-of-the-art methodology will be highlighted for resource tracing so that cost/benefit relationships can be integrated across spatio-temporal scales. Scaling will then be extended by plant ontogeny and growth scenario as driving factors of allocation. Growth/defence-related effects by plant competition will be shown to allow mechanistic understanding only, if resource fluxes of plant–pathogen and plant–mycorrhizosphere interactions are integrated into the analysis. Space-related efficiencies of resource investments into *versus* returns from plant structures will be introduced as determinants of competitiveness and a feature of growth. The extent will be

examined to which space may become a "currency" in comparing costs of growth with such of defence when viewing the latter as a means for sustaining the plant's access to space and hence, external resources. Space relates to allometric plasticity in shaping the plants' three-dimensional structure and associated resource flux at the stand level. The extent will be assessed to which stand development mirrors resource allocation within and between plants under abiotic and biotic stress, including such by parasites. Embedding growth/defence allocation in Part II into the different kinds of interactions and scenarios between the molecular and hierarchically higher spatio-temporal scales will convey the issue about resource conflicts *sensu* GDB towards a mechanistically founded and ecologically relevant comprehension.

Part III will examine the capacity of the attained empirical knowledge for theory building on resource allocation in plants. Mechanistic and statistical modelling as complementary components of an integrative analysis will be assessed, regarding compensation for experimental shortcomings and usability for theory development, on the basis of scenario simulations upon parameter variation. Capacities and limitations of empirical and theoretical approaches will be elucidated in promoting clarification and predictability of plant system behaviour. The extent of common underlying mechanisms in resource allocation across plant types, ontogenetic stages and growth scenarios will be examined in conclusion (Part IV). Arguments will be evaluated about a "unifying theory" on plant resource allocation, reconciling the breadth of evidence and knowledge.

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