

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

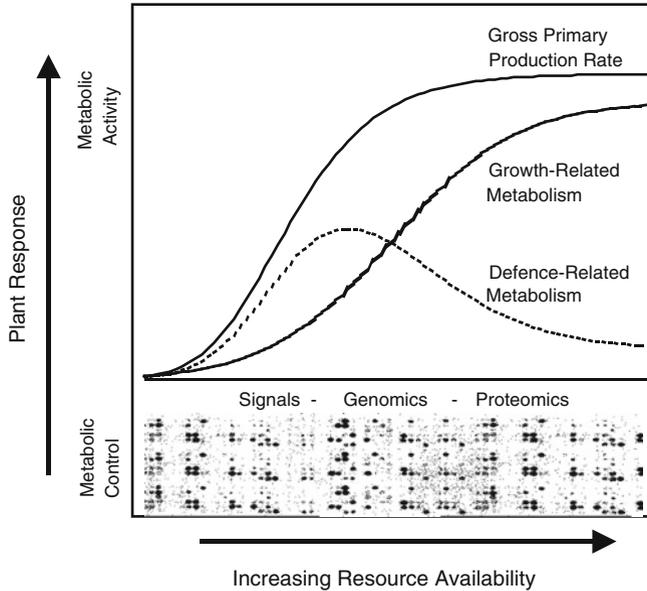


Fig. 1.1 Plant response in relation to increasing resource availability, expressed as variations in gross primary productivity along with such growth and defence-related metabolism. Note indicated trade-offs between growth (and competitiveness, see text) *versus* defence, according to the “*growth–differentiation 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 CO₂, is believed to favour differentiation. Mattson et al. (2005) suggested that climate change-associated atmospheric CO₂ 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



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