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Growth and Parasite Defence in Plants; the Balance between Resource Sequestration and Retention: In Lieu of a Guest Editorial

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Abstract: **A hypothesis on regulation of the balance between growth and parasite defence in plants is formulated, namely that plants regulate their resource allocation in a way where stress tolerance and resistance inherently lead to constraints on growth and competitiveness. Seven reviews and the subsequent article in this issue of Plant Biology contributing to this problem are briefly introduced in context.**

Key words: **Growth, competitiveness, parasite defence, fitness, resource allocation.**

Research Issue

"Growth" and "Parasite Defence" – these keywords reflect one central challenge in the resource allocation of plants: the necessity to grow in order to stay competitive with neighbouring plants, and the necessity to defend against biotic stress as imposed by parasites (pathogens, herbivores; Herms and Mattson, 1999[16]; Zangerl and Bazzaz, 1992[39]). What are the mechanisms that partition energy, carbon, water and nutrients between these two demands and control the allocation of these resources within the plant's metabolism and amongst plants as they grow in stands? By what means do internal and external factors drive such mechanisms, and overall, what are the "cost/benefit" relationships in the control of resource allocation? *Growth* as one means of competitiveness and *defence* define the capacities for resource sequestration and retention – hence, they reflect the core of individual plant fitness (Bazzaz, 1997[2]), and they are conceived also to be intrinsically linked with common underlying mechanisms in resource allocation between the primary and secondary metabolism (Fritz and Simms, 1992[9]; Koch, 1996[18]; Batz et al., 1998[1]).

The starting point of an examination of "allocation strategies" may be a conceptual model as proposed by Herms and Mattson (1992[16]) which claims that increasing resource availability reduces the proportion of secondary metabolites along with an increase in primary production (Fig. **1**). Such a reduction is believed to occur at the expense of defence but in favour of growth and plant competitiveness. This concept may be expressed by the following hypothesis:

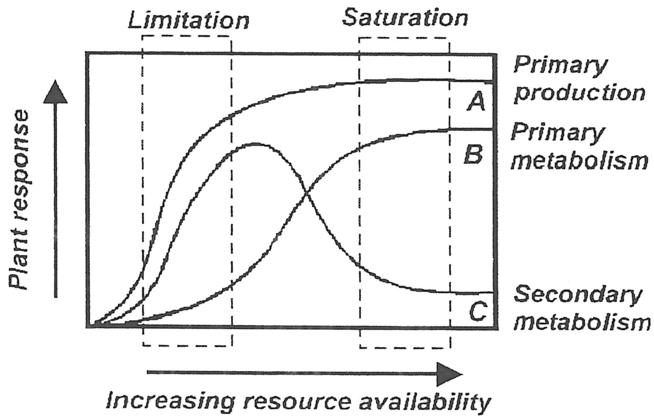

Fig. 1 Impact of resource availability on primary production, as well as on primary and secondary metabolism (adapted from Herms and Mattson, 1992[16]; Herms, 1999[15] and Matyssek, 2001[27]).

Regardless of the kind of impacting stress, plants do regulate their resource allocation in a way that increase in stress tolerance and resistance (in particular against pathogens and phytophages) inherently leads to constraints on growth and competitiveness.

Does a trade-off really exist, as suggested by this hypothesis, does it follow a linear relationship (as found between growth rate and lignification or reproduction: Sibly and Vincent, 1997[37]; Lerdau and Gershenzon, 1997[20]), and does it reflect a conflict rather than a balance or optimization in resource allocation? Clarification of the underlying mechanisms must resolve whether relationships as proposed in Fig. **1** possess general validity. The extent to which such mechanisms comply with the "Growth–Differentiation Balance Theory", which claims the capacity and quality in parasite defence to result from the ratio between productivity *versus* demand for carbon during organ differentiation (Loomis, 1953[22]; Lorio, 1988[23]), or if such mechanisms are consistent with the "Carbon–Nitrogen Balance Theory" (Bryant et al., 1983[4]), which predicts that the biochemical quality of defence is determined by adjust-

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ment between the carbon and nitrogen fluxes through the plant, are examined. These two theories are questioned (Feeny, 1976[8]; Rhoades, 1979[34]; Coley et al., 1985[7]; Lincoln and Couvet, 1989[21]) and may even be obsolete as soon as trade-offs, such as those in Fig. 1, are subjected to a "full cost analysis" – as has recently been postulated (Bazzaz, 1997[2]; Lerdau and Gershenzon, 1997[20]). In this latter case, "cost/benefit" relationships not only require the synthesis costs of metabolites to be accounted for, but also additional costs are relevant for maintaining the involved enzymatic apparatus, as well as the storage, transport and turnover of metabolites. The requirement for research regarding such trade-offs and cost/benefit relationships is evident (Bazzaz, 1997[2]).

What about *competitiveness* in this context – can it be conceived in a way to ensure quantitative evaluation of the above hypothesis? If growth is conceived as a resource investment into the sequestration of above- and belowground space, and hence as a pre-requisite for competitive resource exploitation, then competitiveness (i.e., the "competitive behaviour" of a plant) may also be analysed and quantified through a sequence of "cost/benefit" relationships:

- ***Efficiency in space sequestration:*** *Resource investment per unit of occupied shoot or root space (and in relation to the exploitable resource availability);*
- ***Efficiency in space exploitation:*** *Resource acquisition (gain) per unit of resource investment (or occupied shoot and root space);*
- ***Efficiency of maintenance costs:*** *Demand for resources (water, respired carbon, nutrients) per unit of resource gain (or occupied shoot and root space).*

These efficiencies express the "translation" of resource allocation into structural relationships and "cost/benefit" balances that result from space sequestration (Mäkelä and Vanninen, 1999[25]), and as such, represent the mechanistic basis of plant competitiveness (cf. Tilman and Grace, 1990[10]; Küppers, 1994[19]; Schwinning, 1996[36]; Bazzaz, 1997[2]; Hikosaka et al., 1999[17]). Is a competitive advantage arising from a high resource acquisition capacity (as one attribute of fitness) jeopardized by a simultaneous decline in defence capacity and hence the ability to retain resources (as one further attribute of fitness; cf. Bungerer et al., 1999[5])? Is such a scenario characteristic for plants under high resource supply, whereas increasing primary production at low supply might be associated with the stimulation of secondary metabolism (cf. Fig. 1; Herms, 1999[15])? The "translation" of resource allocation into shoot and root differentiation and space sequestration reflects an inherent link to defence, as the "value" of organs in defence may decline along with their increasing proportion in whole plant biomass (Zangerl and Bazzaz, 1992[39]). "Indirect costs" may complicate such interrelationships if constitutive defence *per se* already curtails the assimilate pool for growth (Pennypacker, 2000[32]). The issue of "cost/benefit" relationships has become part of theories and modelling concepts about resource allocation (e.g., Mäkelä, 1990[24]; Nikinmaa and Hari, 1990[29]).

Again, the need for experimental clarification is apparent, although the conception has gained in importance during the past decade that the development, ecology and survival of plants, i.e., their immanent system properties, can be understood only in terms of their allocation patterns (Mooney et al., 1991[28]; Schulze, 1994[35]; Bazzaz and Grace, 1997[3]). This research demand is similar both for wild and economic plants – or herbaceous and woody species. A number of research questions can be derived in line with this demand and the above hypothesis (cf. Bazzaz, 1997[2]):

- *How rapid and sensitive is allocation response to resource withdrawal by phytophages or pathogens, and how do shoot and root interact when re-adjusting the internal resource flux?*
- *In what ways do structural interactions between neighbouring plants result in modifications in allocation and allometric relationships and, by this, affect the basic mechanisms in plant competitiveness?*
- *Do "strategies" in allocation differ between plant life forms and environmental conditions?*
- *What kinds of signals are required for flux control, and how is the molecular level linked to the resource flux at the organ and whole plant level?*
- *By what means is fine root turnover controlled? Does resource allocation to root symbionts compete, internally, with that to parasite defence? What about the "opportunity costs", if resources are invested alternately between the needs for staying competitive, meeting the resource demands by root symbionts, and ensuring the defence against parasites?*

In particular, the final question reflects the transitions between the demands of individual plant fitness: sequestration and retention of resources. The role of parasitic and mutualistic interactions in allocation between plants and micro-organisms has been highlighted recently in a special issue of "Physiological and Molecular Plant Pathology" (Heath, 2000[14]), and mechanisms in signal transduction continue to be a focus in host/parasite research (Grant et al., 1996[12]; Ponchet et al., 1999[33]).

Need for Interdisciplinary Research

Assessment of the questions raised above requires interdisciplinary research, such as that of a special programme entitled "Growth and Parasite Defence – Competition for Resources in Economic Plants from Agronomy and Forestry", which the authors are organizing (*Sonderforschungsbereich* SFB 607, of *Deutsche Forschungsgemeinschaft*, DFG). Using Norway spruce, European beech, apple, grass and legume species, potato and barley, it integrates work on mechanisms of "plant–plant" interactions (intra- and inter-specific competition), "plant–mycorrhizosphere" relationships (potentially conducive to competitiveness), "plant–parasite" interactions (adverse to competitiveness) and the *underlying regulatory control* of allocation at the physiological, biochemical and molecular level. The analysis is being backed by mechanistic *modelling* as a tool for locating "black boxes" and establishing "cost/benefit" balances in resource allocation as well as performing sensitivity assessments under factorial impacts. A common focus on resource allocation as the basis of individual plant fitness is a *novum* in the applied, biological research of agronomy and forestry.

In this way, research issues of currently high priority are being addressed, i.e., control of resource allocation, competitiveness and stress sensitivity at the individual plant and stand level (Bazzaz, 1997[2]; Matyssek and Innes, 1999[26]; Ceulemans et al., 1999[6]; Norby et al., 1999[30]), effects of parasitic and mutualistic interactions on assimilate flux (Hall and Williams, 2000[13]; Heath, 2000[14]), mechanisms of signal transduction in plants (Grant and Loake, 2000[11]), genetic basis of plant defence against parasites (Oberhagemann et al. ,1999[31]) and control of differential gene expression (Yang et al., 1999[38]). Consequently, SFB 607 provides the postulated link across molecular biology and ecophysiology (Zangerl and Bazzaz, 1992[39]), with the individual plant representing the "interface" between internal and external resource partitioning. Process scaling reaches the stand level while covering resource fluxes which are involved in competition.

The following seven reviews in this issue of Plant Biology (having emerged from a symposium sponsored by SFB 607) provide insights into approaches of assessing overall integration and concluding validation of the central hypothesis outlined above. In particular, Rühmann et al. (this issue) show that young apple trees display high susceptibility to the pathogenic impact of *Venturia inaequalis,* when growing vigorously at high N availability. Resistance is increased by enhanced phenylpropanoid biosynthesis and accumulation of phenolic compounds, when growth is constrained by low N supply. The ratio between the availability of sugars and N supply apparently controls enzymatic regulation within the phenlypropanoid pathway. Fleischmann et al. (this issue) direct the issue of defence *versus* production towards forest trees, showing that beech seedlings rather than saplings are susceptible to *Phytophthora* pathogens, in terms of photosynthetic and transpiratory performance. The response strongly varies with the *Phytophthora* species, in some cases proving the physiological sensitivity of the foliage to be unrelated to the extent of root injury. In saplings, the leaf gas exchange indicates infestation only one year after inoculation, exhibiting breakdown in photosynthesis and transpiration a few days *prior* to the onset of wilting.

In view of the central hypothesis, growth performance needs to be quantified with respect to plant competitiveness. Grams et al. (this issue) present a concept applicable to juvenile and adult beech and spruce trees for assessing the above outlined efficiency ratios in space sequestration, resource exploitation and associated maintenance costs. Consistencies across plant age and species are demonstrated that indicate efficiency in space sequestration, rather than exploitation, to be crucial for the functional interpretation of competitiveness in mixed plantations. The competitive interaction apparently diminishes specific tree responses to CO_2/O_3 regimes, these gases being employed as experimental disturbants of resource allocation and, hence, analytical tools for unravelling regulatory mechanisms. As the aboveground interaction is dominated by competition for light, Reithmayer et al. (this issue) have developed a novel methodology for assessing the quantity and spectral quality of PAR across the canopy of old growth beech/spruce mixed forest. About 260 fibre optics, each 30 m in length, are connected to a high-resolving, computerized spectrometer at one end, while the other end is inserted into ball-shaped diffusors positioned in the sun and shade crowns and serving as light sensors. Approaching the stand level, Pretzsch (this issue) raises the question of whether ontogenetic progression in the spatial allometry of woody and herbaceous plant systems may be unified into one common law applicable to both forestry and agronomy. Theoretical deduction and data-based proof are presented that show the relationships between production and stand density to indeed be consistent in both forests and agricultural systems. Mathematical treatment proves that the self-thinning ("– 3/2 power") rule is the common, underlying principle. Rules previously derived for forests are shown to be a special case of independently formulated principles in herbaceous systems.

The integration of the research concept is backed by mechanistic modelling approaches, one of which is introduced by Grote and Pretzsch (this issue). The presented model depicts three-dimensional tree and stand development based on carbon, water and nitrogen balances and structural architecture of crowns and root systems, as well as the resource allocation between the plant organs. The model accounts for the seasonal interactions between neighbouring trees so that a tool is created that can evaluate environmental influences for any kind of species mixture and stand structure. Integration is also achieved by applying stable isotope analysis to the different kinds of plants and experimental scenarios of this research, locating and quantifying resource pools and fluxes, source–sink relationships and metabolic regulation. The analytical and integrative potential of this latter methodology, which is gaining in importance during the ongoing research programme, is highlighted by Ehleringer et al. (this issue) who have contributed to the SFB symposium on further perspectives of the research concept.

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