The Plant's Capacity in Regulating Resource Demand

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Abstract: Regulation of resource allocation in plants is the key to integrate understanding of metabolism and resource flux across the whole plant. The challenge is to understand trade-offs as plants balance allocation between different and conflicting demands, e.g., for staying competitive with neighbours and ensuring defence against parasites. Related hypothesis evaluation can, however, produce equivocal results. Overcoming deficits in understanding underlying mechanisms is achieved through integrated experimentation and modelling the various spatio-temporal scaling levels, from genetic control and cell metabolism towards resource flux at the stand level. An integrated, interdisciplinary research concept on herbaceous and woody plants and its outcome to date are used, while drawing attention to currently available knowledge. This assessment is based on resource allocation as driven through plant-pathogen and plant-mycorrhizosphere interaction, as well as competition with neighbouring plants in stands, conceiving such biotic interactions as a "unity" in the control of allocation. Biotic interaction may diminish or foster effects of abiotic stress on allocation, as changes in allocation do not necessarily result from metabolic re-adjustment but may obey allometric rules during ontogeny. Focus is required on host-pathogen interaction under variable resource supply and disturbance, including effects of competition and mycorrhization. Cost/benefit relationships in balancing resource investments versus gains turned out to be fundamental in quantifying competitiveness when related to the space, which is subject to competitive resource exploitation. A space-related view of defence as a form of prevention of decline in competitiveness may promote conversion of resource turnover across the different kinds of biotic interaction, given their capacity in jointly controlling whole plant resource allocation.

Key words: Growth, allocation, allometry, competition, parasites, pathogens, fungi, mycorrhizae, mycorrhizosphere, soil micro-organisms, molecular mechanisms, modelling, trade-offs, trees, herbs.

1 Introduction

Regulation of resource allocation is receiving increased interest in plant science (e.g., Mooney et al., 1991; Schulze et al., 1994; Bazzaz and Grace, 1997; Poorter and Navas, 2003), as it is realized that evaluation of the biological significance of biochemical and physiological processes demands an integrative view of the resource fluxes that act across the whole plant (Bazzaz, 1997). The challenge is to understand trade-offs that occur as plants balance allocation between different, sometimes conflicting, demands, e.g., growth, reserve storage or fruiting, competitiveness with neighbours, but also defence against stress or subsistence of symbionts (e.g., mycorrhizal fungi; Stitt and Schulze, 1994; Andersen, 2003). While pursuing such a balance, plants face competition not only for external but also for internal resources, given the interactions with parasites, endophytes, and mycorrhizospheric organisms. One focal point is the balance between resource demands for staying competitive with neighbours and ensuring defence against parasites. Growth is regarded a basic affirmation of the plant's competitiveness with neighbours (Schulze et al., 1986; Schwinning, 1996; Grams et al., 2002). Hence, the *hypothesis* may be posed that, *independent of the factorial scenario, plants do regulate their resource allocation in a way that any increase in growth and competitiveness inherently leads to constraints on parasite defence*. This trade-off relates to the *"Growth-Differentiation Balance Theory"* (GDB) (Loomis, 1953; Lorio, 1988) as elucidated by Herms and Mattson (1992) and recently adapted (Matyssek, 2001; Matyssek et al., 2002). In addition, however, the above trade-off may be modulated by *"third party trade-offs"*, such as between resource demands of growth and reserve storage, or parasite defence and mycorrhizae (Stitt and Schulze, 1994; Heil and Baldwin, 2002; Stamp, 2003a).

The above hypothesis defines the essence of individual plant fitness, integrating the needs for sustaining competitiveness and defence – or, basically, for acquiring and retaining resources (Herms and Mattson, 1992; Zangerl and Bazzaz, 1992; Bazzaz, 1997). The question arises as to what extent the relative priorities of these needs may be regulated through one underlying mechanism (Fritz and Simms, 1992; Koch, 1996; Batz et al., 1998). The existence of a trade-off as outlined by the hypothesis has been supported by a recent meta-analysis by

Koricheva (2002) or findings by, e.g., Glynn et al. (2003) or Rüh-mann et al. (2002). However, evaluations sometimes also pro-duce apparently equivocal results (e.g., Oßwald et al., 2004; Fleischmann et al., 2002; Siemens et al., 2002, 2003). This may reflect deficiencies in our understanding of underlying mechanisms. Therefore, the evaluation of the hypothesis also requires the unravelling of underlying molecular mechanisms (Heil and Baldwin, 2002).

From the viewpoint of science theory, hypotheses like that giv-en above reflect an "immature" state, given the complexity of their subjects and the limitation of their databases (Stamp, 2003 b). The broad range of ecologically relevant scenarios can only be covered in part when formulating and testing such hypotheses, and knowledge on pre-conditioning of study ob-jects is often scant (Heil and Baldwin, 2002). Gene cohorts rather than single genes affect the regulation between re-source demands, and *"third party trade-offs"* or *"ecological costs"* may interact through feedbacks with the key processes addressed by hypotheses (Felton and Korth, 2000; Heil and Baldwin, 2002; Glynn et al., 2003; Stamp, 2003 a). *"Third party trade-offs"* may include increasing stress tolerance at the ex-pense of reserve storage, involving *"ecological costs"* associat-ed with variable defence such as those resulting from interac-tions between pathogens, competitors, and mycorrhizospher-ic organisms. Progress in mechanistic understanding can be achieved, however, through integrated experimentation, mod-elling, and hypothesis testing at the various spatio-temporal scaling levels in biological organization, keeping in mind that relevant mechanisms are based on genetic control and cellular metabolism while driving, in sum, the resource flux at the stand level (Matyssek and Sandermann, 2003; Sandermann and Matyssek, 2004). Fig. 1 illustrates the core of the intro-duced hypothesis and can guide design of experiments and modelling: the interrelationship between gross primary pro-duction (GPP) and growth, and defence-related metabolism is conceived as being under control at the molecular level (sig-nalling, transcription and proteomics). Based on this concept, clarification is approached on the biotic and abiotic interac-tions that challenge plant life in the field (Heil and Baldwin, 2002).

Scaling approaches may prevent authors from reaching pre-mature conclusions about the validity of hypotheses (Herms, 2002; Stamp, 2003 b), as given, perhaps, in the context of the *"Carbon-Nutrient Balance Theory"* (CNB) (Bryant et al., 1983; Hamilton et al., 2001). CNB states that the biochemical quality in defence is determined by the relationship between C and N availability. A recent assessment suggested that CNB is part of GDB (Stamp, 2003 a) and states that organ differentiation (in-cluding defence) is determined by a "surplus" in production that is not used in growth-related metabolism (being in line with the introduced hypothesis and Fig. 1). Stamp (2003 a), in her critical review, claimed that GDB is the most differentiated and capacitive theory on trade-offs in resource allocation.

It is tempting to assess energetic-biochemical or ecological costs of trade-offs (cf. Fig. 1). *"Full cost analyses"* of the associ-ated cost/benefit relationships (opportunity costs), not only covering the immediate but also indirect "inconspicuous" costs (e.g., of storage, transport, or repeated metabolite turn-over), appear to be a promising possibility (Lerdau and Ger-shenzon, 1997). However, this turns out to be rather idealistic,
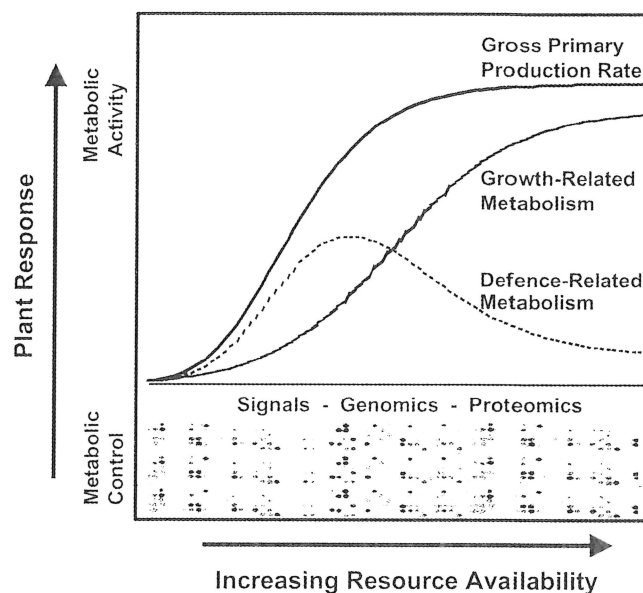

Fig. 1 Plant response in relation to increasing resource availability, ex-pressed as variations in gross primary production along with such changes in growth and defence-related metabolism (i.e., primary and secondary metabolism *sensu lato*, respectively). Note, indicated trade-offs between growth (competitiveness, see text) and defence. Meta-bolic activity (biochemical and physiological process level) is linked with metabolic control at the molecular (gene) level through signal-ling, genomics, and proteomics (redrawn from Matyssek et al., 2002, following Herms and Mattson, 1992).

as the latter authors also needed to rely on assumptions, to some extent at least, when illustrating a *"full cost analysis"*. Shortcomings involve quantifications of inducibility costs of defence and ecological costs that mask resource investment into defence (Heil and Baldwin, 2002) as well as metabolic compounds that are assignable to either growth or defence-related metabolism (cf. Herms and Mattson, 1992). It is un-certain whether defence costs may generally be regarded as low (Gayler et al., 2004). The intrinsic limitations in compre-hensively quantifying cost/benefit relationships led Stamp (2003 a) to the conclusion that *"...focus on costs per se will be less useful than that on mechanisms of cost..."* for unravelling trade-offs in resource allocation and resolving conflicts in hy-pothesis evaluation.

Based on Fig. 1, Matyssek et al. (2002) and Sandermann and Matyssek (2004) have developed an integrated research pro-gramme at different scaling levels, i.e., SFB 607, which is being highlighted in this special issue (see editorial). The concept (Fig. 2) focuses on the regulatory mechanisms of resource allo-cation between and within herbaceous and woody plants (cov-ering plant ontogeny) under the influence of plant competitors as well as symbiotic and parasitic organisms. Resource alloca-tion is being analyzed as a process driven by host-parasite in-teractions, mycorrhizospheric relationships, and competition with neighbouring plants in stands, by assessing the cost/ben-efit relationships of resource turnover and exchange with the environment and alternative uses within plant metabolism. Hence, competition for resources exists both plant-internally (between the different demands for the three major ranges of biotic interaction and within the resource pool of primary and
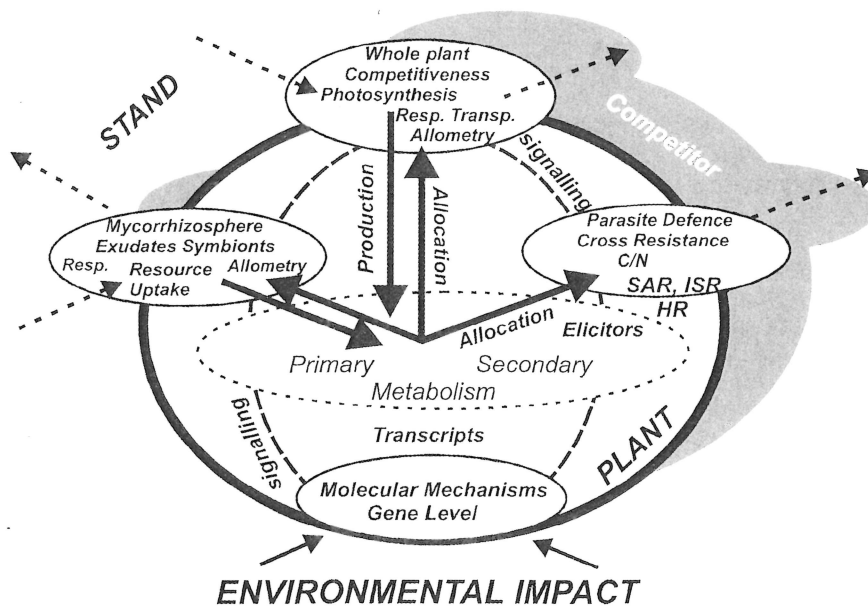
Fig. 2 Conceptual model underlying the interdisciplinary research programme "SFB 607: Growth and Parasite Defence – Competition for Resources in Economic Plants from Agronomy and Forestry". Arrows indicate major pathways in resource allocation between physiological demands within the plant and in exchange with the environment, as being under the control of environmental impact and molecular processes (see text for details; from Sandermann and Matyssek, 2004).

secondary metabolism) and externally amongst neighbouring plants at the stand level (Fig. 2). The internal resource pool is – via transcription – under the control of molecular processes which, in turn, respond to environmental impact. Signal transduction across the whole plant system ensures that the plant functions as an integral entity. The extent to which central mechanisms in the control of resource allocation behave similarly in woody and herbaceous plants, young and mature individuals, and under laboratory and field conditions is yet to be clarified (*"three dimensions of scaling"*, Matyssek, 2001; Kolb and Matyssek, 2001). Such concepts that stress the mechanistic entity of plant, parasite, and mycorrhizosphere within trade-offs of resource allocation have the capacity to bridge the functional gap between molecular and ecophysiological processes and to resolve conflicts in hypothesis evaluation. The concept requires mathematical modelling for fostering synthesis of experimental evidence, promoting hypothesis formulation and evaluation, examining functionality of mechanisms across scaling levels, and simulating plant performance under scenarios too complex for experimentation. In this way, questions may be tackled about variability in resource needs, optimization principles in *"trade-offs"*, and costs of defence.

The following account will focus on the gain in knowledge which has derived, in SFB 607, from experimentation following the conceptual outline of Fig. 2, highlighting *"plant-plant"* (section 2), *"plant-parasite"* (section 3), and *"plant-mycorrhizosphere"* interactions (section 4) and their mutual interrelationships, the underlying regulation at the molecular level (section 5), and modelling to approach holistic integration (section 6). The context will be exemplified for each section to arrive at the present status of evidence in this field of research.

2   Allocation Related to "Plant-Plant" Interaction

From the viewpoint of the single plant, the role of internal allocation is first examined in fostering competitive interaction with neighbours – or, more precisely, in warranting competitiveness. Findings are highlighted in woody and herbaceous

plants, before raising the question to what extent allocation in single plants is relevant for resource competition at the stand level (i.e., associated population dynamics), and if woody and herbaceous plant systems conform to common principles. To this end, competitiveness is examined in terms of resource investments *versus* returns in relation to above- and belowground space, as it is recognized that competition between plants is inherently linked to the structural allometry for occupying and exploring the site and to the fluxes along shoot and root structures during the process of resource sequestration (Schulze et al., 1986; Küppers, 1994; Matyssek et al., 2002). Hence, competitiveness is analyzed and quantified through a sequence of *"cost/benefit"* relationships: (1) *Efficiency in space occupation,* i.e., resource investment per unit of occupied shoot or root space (or exploitable resource availability); (2) *Efficiency in space exploitation,* i.e., resource acquisition (gain, return) per unit of occupied shoot and root space (or available resource); and (3) *Efficiency of "running", e.g., respiratory and/or transpiratory, costs* for sustaining above- and belowground structures (as posed by SFB 607: Matyssek et al., 2002; Grams et al., 2002). According to definitions in physics (Lide, 2003), efficiency is conceived as a ratio of gain *versus* concurrent resource use (such as photosynthetic water or light use efficiency, cf. Larcher, 2001), where (1) occupied space is the gain from resource investment, (2) yield is the return from occupied space, and (3) the space sustained in competition is the return from "running costs". Such efficiencies relate internal resource allocation to external resource availability (Mooney and Winner, 1991; cf. Fig. 2), *"translate"* resource allocation into *"cost/ benefit"* ratios that result from space occupation (i.e., investment/gain balances sustaining structural and functional integrity in resource acquisition) and, from this, provide a quantitative and mechanistic framework for the assessment of plant competitiveness, which has long been postulated (cf. Roloff, 1986, 2001; Grace and Tilman, 1990; Küppers, 1994; Schwinning, 1996; Bazzaz, 1997; Hikosaka et al., 1999). Nevertheless, such efficiencies have hardly ever been assessed, in particular, for woody plants (Küppers, 1984; Matyssek and Schulze, 1987; Grams et al., 2002).

This concept was examined at the SFB 607 field site "Kranzberg Forest" (Pretzsch et al., 1998; Nunn et al., 2002) on adult trees of *Fagus sylvatica* and *Picea abies* which represent, in Central Europe, contrasting extremes in foliage type and crown structure (Schulze et al., 1977; Ellenberg, 1996). The foliated space around branches and within crowns was regarded as the volume relevant in aboveground resource availability (Grote and Reiter, 2004; Reiter et al., 2005). Occupied crown space per standing foliage mass was higher in shade than sun branches of beech, but not so in spruce. Although beech occupied more space per foliage mass than spruce, the C gain per occupied crown volume did not differ between species, nor did the amount of occupied space for "running" respiratory and transpiratory costs. Respiratory costs distinctly increased, however, in the shade foliage, rendering the latter costly so that only low or even negative C balances were achieved, and conflicting with the claimed C autonomy of branches (cf. Sprugel, 1991; Dickson and Isebrands, 1991; Grossman and DeJong, 1994). Late-successional species like beech and spruce appear to differ in this respect from light-demanding pioneers (Matyssek and Schulze, 1988; Witowski, 1997). Sustaining unproductive branches may reflect a "sit-and-wait" strategy, foraging for the incidental occurrence of canopy gaps (de Kroon and Hutchings, 1995; Falster and Westoby, 2003) which drive ecosystem development (Remmert, 1991). Competitiveness appeared to be determined by space-related standing foliage mass and annual volume increment rather than annual mass investment in foliage (Reiter et al., 2005). Remarkably, contrasting productivity at the level of deciduous versus evergreen leaves (Matyssek, 1986) vanished when C gains and costs of branch foliage were related to space, emphasizing space as a resource in itself and an object of competition (cf. McConnaughay and Bazzaz, 1991; Grabherr, 1997; Grams et al., 2002).

Do such principles also hold for differing ontogenetic stage and growth conditions? This was investigated on beech and spruce saplings in mixed and monoculture under phytotron conditions (Payer et al., 1993), where allocation was also disturbed using combinations of ambient and elevated CO_2/O_3 regimes (Kozovits et al., 2005 a, b). The gaseous regimes may affect competitiveness, given their capacity for altering shoot architecture (Matyssek et al., 1992; Pritchard et al., 1999; Dickson et al., 2001). Also, in the phytotrons, the ability to enlarge crown volume at low structural cost determined competitiveness rather than did the space-related C gain or "running" costs (Kozovits et al., 2005 a, b). Given the phytotron conditions, spruce constrained increments in biomass and volume of beech when growing in a mixture (depending, however, on plant age and size). Profiting from elevated CO_2 (Liu et al., 2004), the competitve strength of spruce did not just result from the acidic soil reaction (Egli et al., 1998; Spinnler et al., 2002), as the growth performance of beech was similar to that of spruce across the gaseous regimes when growing in monoculture (Kozovits et al., 2005 a, b). In mixtures, the lowered competitiveness of beech was related to a decline in foliage/shoot axes biomass ratio, being a size-independent effect (cf. Müller et al., 2000; Gedroc et al., 1996) in the presence of spruce and fostered by enhanced O_3 levels (Kozovits et al., 2005 b; cf. Fuhrer et al., 2003; Grantz and Yang, 2000). Hence, exacerbating biotic and abiotic stress overruled the allometry-related ontogenetic (i.e., size-dependent) control of resource allocation. This latter kind of control of resource allocation

was otherwise dominant over the responses in the root/shoot biomass ratio of beech to the gaseous regimes (Kozovits et al., 2005 b; cf. Weiner and Fishman, 1994). Consequently, shifts in biomass partitioning do not *per se* indicate metabolic re-adjustment in resource allocation (Weiner, 2004). The lowered aboveground competitiveness of beech was paralleled belowground, as declining efficiency in the space occupation of beech roots favoured N uptake in spruce, the latter species taking advantage through unchanged carbohydrate availability and non-limited growth (Liu et al., 2004; cf. Körner, 2003). Belowground competition appeared to become less crucial under concurrent conditions of canopy closure, when constraints from ozone on production and crown extension in beech tended to be counteracted by elevated CO_2 (Kozovits et al., 2005 a; cf. Grams and Matyssek, 1999; Volin et al., 1998; Karnosky et al., 2003). In general, interspecific competition enhanced the atmospheric treatment effects, with spruce profiting from elevated CO_2, and beech suffering from the enhanced O_3 regime. Although findings in juvenile and adult trees were consistent in that aboveground efficiencies in space occupation rather than space-related C gain determine competitiveness, extrapolations beyond the settings actually analyzed in field or phytotron studies must be viewed with caution (Connolly et al., 2001).

The analysis of physiological and structural principles in competitiveness was extended through investigations in monospecific stands of herbaceous species: sunflower *(Helianthus annuus)* and alfalfa (*Medicago sativa*; Klumpp, 2003; Lötscher et al., 2004). The primary focus was on aboveground interactions, and the stand systems used consisted of dense arrangements of individuals grown singly in pots. The exclusion of belowground interactions allowed targeted modification of fertilizer supply to individuals for studying their ensuing responses. C gains and losses of individuals in stands were assessed using new methodology (Lötscher et al., 2004): photosynthetic activity of individuals was determined by labelling, *via* swapping plants between (near-)identical communities growing in a controlled environment mesocosm facility using CO_2 with different ^{13}C content (Schnyder et al., 2003); and respiration of intact individuals was assessed through gas exchange measurement upon removal from stands. The relative growth rate (RGR, mol C mol C^{-1} d^{-1}) of individuals was obtained as RGR = RPR + RRR, where RPR is relative photosynthesis rate, and RRR is relative respiration rate (both in mol C mol C^{-1} d^{-1}). Experiments with sunflower (Klumpp, 2003) demonstrated that RGR of dominant individuals was higher than that of subordinates, reflecting a shifting balance between individuals (Anten and Hirose, 2003): the mass proportion of dominants increased at the expense of subordinates. The low or even negative RGR of subordinates was partly due to rather large respiratory losses: subordinates with adequate N supply lost the equivalent of 58% of their photosynthetic C gain in respiration, whereas respiratory losses in the dominants were equivalent to only 30% of photosynthesis. When subordinates also suffered from reduced N supply, the respiratory losses exceeded photosynthesis by > 200%. These results reveal (1) little scope for reducing respiratory costs in subordinates, and (2) the crucial importance of RPR as a determinant of RGR.

RPR can be factorised into light capture per unit mass (Φ_{mass}, mol photons mol^{-1} C d^{-1}) and light use efficiency (LUE, mol C mol^{-1} photons): RPR = Φ_{mass} × LUE (Hikosaka et al., 1999). Φ_{mass}

is a measure of the efficiency of plant C investments for capturing light – similar to the efficiency of space occupation (see above) – and was 6 to 12 times higher in the dominant individuals (Klumpp et al., unpubl.). Conversely, there was no significant difference in LUE among dominant and subordinate individuals, and between subordinate individuals with different access to N fertilizer. The higher Φ_{mass} of N-sufficient relative to N-deficient subordinates was related to increased leaf area and decreased root to shoot mass ratio. Taken together, these findings corroborate the conclusions from studies with woody species in that competitiveness was mainly determined by the efficiency of resource investment for light capture. The latter is primarily determined by space sequestration in the top, well-lit zone of the canopy.

Growth respiration in alfalfa and sunflower appeared to rely chiefly on currently fixed C (Lötscher et al., 2004). The actual role of different assimilate pools as substrates for leaf growth was explored in a C_3 (Lolium perenne) and a C_4 grass (Paspalum dilatatum) growing in a mixture at moderately low or high temperature (Lattanzi et al., 2005). These treatments led to C_3-dominated stands at low temperature, and C_4-dominated stands at high temperature (see Schnyder and Lattanzi, this issue). The analysis of substrate supply to leaf growth was based on compartmental modelling and $^{13}C/^{12}C$ and $^{15}N/^{14}N$ labelling. In all situations, leaf growth relied largely on currently fixed C delivered directly, or C derived from short-term storage pools (turnover rate = 1.6–3.3 d^{-1}). Conversely, short-term (turnover rate = 0.29–0.90 d^{-1}) and long-term (turnover rate < 0.04 d^{-1}) stores supplied most N to leaf growth. Irrespective of the species, subordinate individuals relied more on mobilization from long-term N stores.

Given the consistency in herbaceous and woody plants, regarding efficient space-related resource investment as a determinant of competitiveness in resource capture, the particular spatio-temporal dimension of forest systems provides a unique track of allometry and growth for scaling between individual plants and the stand level (Harper, 1977, p. 280). Allometry and growing space efficiency by species turn out to be key factors in understanding why the natural forest association at "Kranzberg Forest" would consist mainly of Fagus sylvatica and Quercus robur, although Picea abies is some 100% more efficient with respect to biomass production per unit area. Yoda et al. (1963), White (1981), West et al. (1997), and Enquist and Niklas (2001) propose general allometric laws, which assuage our propensity to reduce complexity. However, Zeide (1987) and Pretzsch (2005) stress that the pursuit of general laws engenders the risk of neglecting species peculiarities which are essential for assessing and understanding the dynamics of individuals, populations, and ecosystems, e.g., mixed spruce/ beech stands (Weller, 1987; Kozlowski and Konarzewski, 2004).

The allometric relationship $A_{p,w} = \ln(p_2/p_1)/\ln(w_2/w_1)$ between expansion of growing space p versus biomass increment w and the corresponding allometry between increments of height and biomass show that beech occupies 57 and 127% more growing space, respectively, per unit of biomass increment than spruce (Pretzsch and Schütze, 2005). However, size appears to be a conflicting achievement for a tree. It ensures privileged access to light and expels competitors from contested resources but raises energy demand for maintenance.

Hence, despite the superiority of beech in lateral and vertical expansion, Norway spruce is distinctly more efficient in area-related biomass production (see above) relative to other species under the same site conditions. This is one reason why foresters prefer spruce to beech and establish spruce monocultures or mixed spruce/beech stands (Körner, 2005; Pretzsch, 2004).

Spruce, as a strictly vertically orientated fast-grower, is far more efficient in space exploitation than beech at the stand level. Nevertheless, efficiency in space exploitation appears as a conclusive but not sufficient trait for success in stand and population dynamics. Beech, as an inefficient grower in terms of growing space efficiency at the stand level, can obviously make use of some ingenious traits to out-compete irksome fast-growers such as spruce, if stands are not tended by the forester. Through its superior efficiency of lateral crown expansion and space occupation, beech is able to maintain a multilayered veil-like canopy that suppresses understorey competitors and both readily and elastically fills gaps in the canopy after self-thinning or disturbance upon windthrow or bark beetle attacks. Beech can tightly encircle and deeply penetrate spruce's shade crowns (Leuschner, 1998; Pretzsch, 2002, p. 287). In addition, years with limiting precipitation hinder spruce more than beech in gaining privileged access to light (Pretzsch, 2004). Following Zeide's (1985) ratio r = $\Delta N/N / \Delta d/d$ between decrease in stem number N and increase in mean diameter d, beech is about 15% more rigorous in self-thinning (i.e., self-tolerance is lower) as compared to spruce in pure stands. Given alien thinning of mixed stands, however, the high expansion capacity of beech slows down its loss by 10% while accelerating loss of spruce by 50%.

Nevertheless, the comparison between cultivation of spruce and beech stands provides a classic example that superiority in the short term is not likely to be sustainable across prolonged times scales. Beech appears to obey a risk-spreading strategy, whereas the pillar-like crowns of spruce with high growing space efficiency but low efficiency in space occupation rather reflects risk concentration. Spruce is superior under steady-state growth conditions but rather susceptible to, and less adept in, overcoming disturbances than beech. We speculate that beech invented its successful allometry by co-evolution with gymnosperms which are evolutionarily older (Niklas, 1994, p. 164–174). A mixture of the two species lowers stand level production by 25%, however, due to stabilization and risk distribution, it may exceed production of pure spruce stands in the long run. Despite its superior growing space efficiency, Norway spruce would succumb to European beech over prolonged periods (Lüpke and Spellmann, 1999).

Species peculiarities in allometry should not be discarded in favour of disputable general allometry laws (Kozlowski and Konarzewski, 2004). Rather, it is a promising research perspective to reveal the species' competitive, allometry-based capacity at the tree level, as being linked with growing space and traceable to the stand level (Pretzsch, 2005; Weller, 1987). Nevertheless, general allometry laws may be suitable for scaling when evaluating principles in self-thinning of woody versus herbaceous plant systems for their extent of similarity. The question of whether unified rules of self-thinning for herbaceous and woody plants exist is still open to debate (Enquist and Niklas, 2001; Kozlowski and Konarzewski, 2004; Pretzsch,

2005). Unlike herbaceous plants, many tree species develop dead heartwood during ontogeny. Although physiologically inactive, this dead tissue is rarely excluded when self-thinning laws for herbaceous and woody plants are compared. As tree diameter, basal area, and volume are easier to measure than sapwood volume or living tissue biomass, they are often used as a surrogate for physiologically meaningful variables. However, relationships based on surrogate variables are always biased to some extent. The inert heartwood of trees is probably crucial for divergence from generalized self-thinning rules (Pretzsch, 2005; Weller, 1987; Zeide, 1987), whereas herbaceous plants tend to follow such rules (Harper, 1977; Yoda et al., 1963; West et al., 1997, 1999). Compensation for heartwood facilitates comparability of scaling rules between woody and herbaceous plants (Pretzsch, 2005) and straightens the path towards general usability of self-thinning slopes for density estimation, density control, and growth prediction.

With respect to evaluating the introduced hypothesis, mechanisms in competitiveness are the determinants of primary production and metabolism, which provide the internal resource pool of relevancy for feeding the trade-offs between the different kinds of competing resource demands within and between plants (cf. Fig. 2).

3   Allocation Related to "Plant-Pathogen" Interaction

The effect of elevated CO_2 concentration on the photosynthetic rate of woody and herbaceous plants has been investigated in many experiments. Most of these studies demonstrated that photosynthesis was increased by elevated CO_2 at the beginning of exposure (for days to weeks). However, during prolonged exposure (months to years), photosynthesis was down-regulated to initial activity levels (Lou and Baldwin, 2004). Acclimation to elevated CO_2 can be explained by starch accumulation in the chloroplast stroma upon vanishing C sinks in the plant. In the case of sucrose accumulation, sucrose phosphate synthase, the key enzyme in sucrose synthesis, is inhibited (Huber and Huber, 1992) and, because of this, affects C allocation in the plant. These findings were confirmed by Jach and Ceulemans (1999) who measured increased relative growth rates of 3-year-old *Pinus sylvestris* during the first season of exposure to elevated CO_2, however, growth rates similar to those of the control were recorded during the second season.

Any environmental conditions that change the resource balance between growth, storage demands, and assimilate supply can alter host-parasite interactions (cf. Fig. 2), however, research on the sensitivity of this interaction to elevated CO_2 is scarce. An excellent survey on this subject was presented by Manning and v. Tiedemann (1995). As early as 1930, Gassner and Straib reported on the effect of increasing CO_2 concentrations on various rust diseases of cereals. They showed that the different rust diseases were promoted within a range of 0.15 to 0.75% CO_2. A disadvantage of their experiment, however, was that, unlike field conditions, the exposure to elevated CO_2 was started only after plants had been inoculated with the pathogen.

Effects of elevated CO_2 have mainly been investigated on net photosynthesis rate, biomass, and yield of herbaceous plants. Increases in the root/shoot biomass ratio were found to be due to increased resource allocation to the roots (Dyckmans

et al., 2000; Saralabai et al., 1997), as long as such shifts were not size-dependent upon changed growth rates (see above). Recently, Norby et al. (2004) showed that annual production of fine roots in sweetgum *(Liquidambar styraciflua)* was more than doubled under 550 ppm CO_2 as compared to plants in ambient air. Such massive changes in fine root biomass might be conducive to a higher risk of infection by root rot pathogens of the genera *Phytophthora* and *Pythium* (Oßwald et al., 2004). Recently, Fleischmann et al. (2002) showed that beech plants *(Fagus sylvatica)* grown for three years under elevated CO_2 were more susceptible to the root rot pathogen *Phytophthora citricola* as compared to plants in ambient air. Shortly after infection, all plants in the elevated CO_2 regime showed a significant decrease in the net photosynthetic rate long before leaf wilt was induced. A comparable effect was reported by Stiling et al. (2003) who investigated the effect of elevated CO_2 on the herbivore density of species in a scrub-oak forest. They found decreased herbivore densities per 100 leaves for *Quercus myritifolia, Q. geminate, Q. chapmanii*, for the nitrogen-fixing vine *Galactia elliottii* and the shrub *Vaccinium myrsinites*, which were all grown under elevated CO_2, relative to plants grown in ambient air. The authors concluded that lowered nitrogen availability, in particular, in leaves of plants grown under elevated CO_2 might influence this decrease in herbivore density. Enhanced CO_2 levels are well known to lower plant N due to increased plant growth, which may result in a nitrogen dilution effect (Lincoln et al., 1993) and/or inhibit N uptake and assimilation (Rachmilevitch et al., 2004). Lowered plant nitrogen may become critical to the growth of herbivores (White, 1984).

Besides CO_2, the effect of increased O_3 concentration on plant growth and development has been investigated intensively over recent decades. Nevertheless, information is scarce on how ozone might alter the ability of host plants to respond to viral, bacterial, and fungal pathogens. The review of Manning and v. Tiedemann (1995) summarized the effects of increased ozone levels on plant diseases. Unquestionably, ozone alters plant physiology (Matyssek and Sandermann, 2003) and, as a consequence, may affect susceptibility to fungal pathogens. In this regard, one has to distinguish between necrotrophic and obligate biotrophic fungi. The former kind of fungi prefer weakened or dead tissue, killed by their toxins, the latter kind is adapted to healthy living plant tissue. Research was concentrated on the necrotrophic fungi *Botrytis* and *Alternaria* on several crop species. In general, O_3 exposure favoured fungal growth and increased disease severity due to O_3-induced lesions that were considered to serve as infection sites for the pathogens. O_3 effects on the growth of obligate biotrophs have been studied extensively, mainly on aboveground plant parts, concentrating on rust fungi. In many cases, disease incidence and progress was inhibited (Dohmen, 1987; Coleman et al., 1987) by O_3 exposure. However, contrasting results were also reported. For example, growth of leaf rust on peach trees was enhanced during long-term O_3 fumigation in open top chambers (Badiani et al., 1992). The inhibition of pathogen growth and the reduction in disease incidence might be explained by the induction of several defence reactions, such as formation of phytoalexins which are known to be induced in host tissue by O_3 exposure via mitogen-activated protein kinases (Keen and Taylor, 1975; Rosemann et al., 1991; Sandermann et al., 1998; Zinser et al., 2000; Ahlfors et al., 2004). Many investigations have proved that O_3 stress reduces C allocation to roots

(Cooley and Manning, 1987; Andersen, 2003). However, several studies found an increase in mycorrhizal colonization of plants exposed to ozone, but the results were inconsistent (Andersen, 2003). One explanation for this phenomenon might be the mobilization of stored reserves that result in a transient increase in soluble sugars that are then available for mycorrhizal fungi (Kasurinen et al., 1999). Conclusions beyond the current state of knowledge require research into the effects of environmental change on plant disease incidence and severity as caused by necrotrophic and biotrophic pathogens.

Environmental stress (from air pollutants, pathogens, herbivores) often affects the secondary metabolism of plants, confirming its predominant but unspecific role in defence (Harborne, 1994; Feucht and Treutter, 1999). Common signalling pathways and comparable mechanisms of induction may be involved, under different stresses, in metabolite biosynthesis and accumulation. In the following, effects of CO_2 and N nutrition on the defence-related metabolism of plants will be highlighted, with special emphasis on phenolic compounds.

Elevated CO_2 increased condensed tannins and flavonol glycosides in birch seedlings (Kuokkanen et al., 2001) and total phenolics in *Pinus eliotti* (Saxon et al., 2004) under non-limiting nutrient and water supply. Similar findings exist in perennial grasses (Castells et al., 2002) and in *Plantago maritima* (Davey et al., 2004), as well as in several tropical trees (Coley et al., 2002). Other studies, however, failed to show effects of elevated CO_2 on phenolic compounds (Holton et al., 2003), moreover the above references do not provide information about the influence of phenolic contents on host-parasite interactions.

Nitrogen (N) as another growth-stimulating factor plays an integral role in the fertilization management of agricultural and horticultural crops, to improve vegetative growth and fruit yield. Impact of N nutrition on defence capacity, in particular against pathogens, has often been described and examined for general, underlying principles. Often there is an observed decrease in pest resistance in woody plants under high N nutrition, as reviewed by Herms (2002). Atmospheric N deposition is suggested to increase susceptibility of pines to beetle attack (Jones et al., 2004). High N supply increased susceptibility of wheat to the fungus *Septoria tritici* (Simon et al., 2003) and of maize to *Cercospora zeae-maydis* (Okori et al., 2004).

In contrast, it must be stated that low N nutrition may also severely constrain the formation of resistance-related compounds such as chitinase, chitosanase, and peroxidase (Dietrich et al., 2004). Their production is promoted under high N conditions. However, increased N fertilization of *Citrus aurantium* was found to increase herbivore performance, despite the presence of higher amounts of total proteins, including enzymes associated with defence (Borowicz et al., 2003). Such contradictory findings may be related to the effect of N supply on the forage quality of plant tissues (e.g., levels of resistance-related compounds) to herbivore insects and/or pathogens (Hoffland et al., 1999, 2000; Herms, 2002). The parabolic relationship between defence-related secondary metabolites and resource availability (nitrogen) according to the GDB hypothesis (Fig. 1) is widely accepted (Mattson et al., 2004). In *Solanum carolinense,* Cipollini et al. (2002) observed an increase in phenolics with increasing N supply. The authors stated that the "precision" in the plant's regulation of resource allocation to
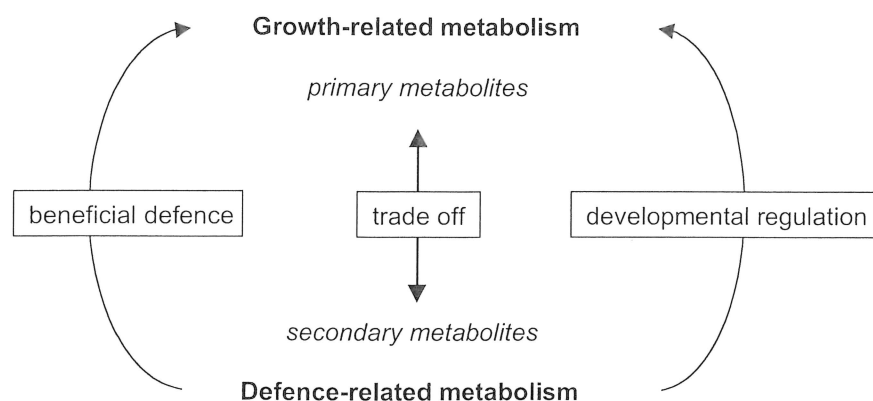
defence-related metabolites is determined by the "biology, history, and ecology" of the system being studied.

The accumulation of phenolic compounds in plant tissues is often negatively affected by high N nutrition, as recently described for barley (Nørbæk et al., 2003) and apricot fruits (Radi et al., 2003). This was also shown for red pine, which became more sensitive to *Sphaeropsis sapinea* (Blodgett et al., 2003), and for *Pinus elliotti* with reduced deterrence of a herbivore insect (Saxon et al., 2004). N fertilization reduced the concentration of individual phenolics in leaves of *Vaccinium myrtillus,* which may be linked to increased susceptibility to *Valdensia heterodoxa* (Witzell and Shevtsova, 2004). High N supply reduced the phenolic content in the leaves and bark of apple leading to increasing incidence of scab (Rühmann et al., 2002; Leser and Treutter, 2005).

With respect to defence, only distinct host-parasite interactions can be studied and, therefore, no conclusion can be drawn about the general defence status. In view of the variety of biotrophic and necrotrophic pathogens or even endophytes, it is to be expected that plants have a variety of mechanisms for assuring overall resistance. The secondary, defence-related, metabolism provides many "chemical tools" that are often based on small structural variations that reflect specific action against particular pathogens. Therefore, understanding needs to be fostered towards whether environmental factors influence, in terms of biosynthesis, the total pool of secondary compounds or act independently through a variation in subgroups. Increasing variation in subgroups may enhance general resistance.

No simultaneously regulated accumulation of the various subgroups of phenylpropanoids and flavonoids was found under varying N regimes in leaves of apple (Rühmann et al., 2002; Leser and Treutter, 2005), *Betula pubescens* (Keski-Saari and Julkunen-Tiitto, 2003), or *Vaccinium myrtillus* (Witzell and Shevtsova, 2004). The induced changes in the content of phenolics and terpenoids also differed in response to altered environmental conditions in birch (Mattson et al., 2004) and tobacco (Lou and Baldwin, 2004). Furthermore, ozone treatment of quaking aspen *(Populus tremuloides)* led to reduced accumulation of nitrogen and phenolic glycosides in the leaves but to increased concentrations of starch and condensed tannins (Holton et al., 2003). In a recent study on the influence of N supply on induced defences in *Nicotiana attenuata,* Lou and Baldwin (2004) observed that the effect of N supply on secondary metabolism differed, depending on the respective biosynthetic pathway and independent of whether the metabolites contain N or not. Moreover, they found a disconnect between the metabolite and transcript level in the accumulation of chlorogenic acid and rutin and their associated biosynthetic transcripts. The authors concluded that none of the current theories on resource limitations to secondary metabolism could account for all observed responses. They suggested that *"a more detailed physiological and biochemically informed model is required".*

Obviously, as a result of metabolic competition between growth-related and defence-related metabolism, reduced growth of spring wheat was found after activation of defence mechanisms (Heil et al., 2000), indicating some kind of trade-off. This corroborates existing theories. However, the lack of

Fig. 3   Possible feedback from defence-related secondary metabolites towards growth-related metabolism.

clear quantitative relationships between growth and defence or primary and secondary metabolites in plant tissues may be due to the fact that secondary compounds are integrated in differentiation programmes (Broun, 2005). The effect of environmental conditions on secondary metabolism is confounded by variations in leaf development and ageing (Covelo and Gallardo, 2001, Salminen et al., 2004; Leser and Treutter, 2005). Moreover, secondary plant metabolites may act as developmental regulators, which was recently reviewed for flavonoids (Taylor and Grotewold, 2005). Therefore, feedback from defence-related secondary metabolites towards growth-related metabolism has to be taken into account (Fig. **3**).

4   Allocation Related to Plant-Mycorrhizosphere Interaction

Trade-offs between growth and defence-related metabolism and associated resource allocation are inherently affected by *"third party trade-offs"* such as between plants, mycorrhizae, and other fungal and microbial organisms in the soil (Fig. **2**). Hence, understanding the plant's balancing act between growth (i.e., competitiveness) and defence intrinsically implies unravelling the drain which is exerted by the resource demand of the belowground interactions on the whole plant resource pool and adjustments in allocation. However, belowground biotic interactions, including effects by and on root functions, and their consequences for the plant's regulation of resource allocation are complex.

Besides providing physical support in the soil, roots together with their associated mutualistic fungi, as well as the other microorganisms, supply plants with water and are bioreactors that transform mineral and organic compounds into nutrients available to plants for growth and other beneficial functions in metabolism. Plant roots are also, via their ectomycorrhizae, in chemical and biological contact with the soil matrix and actively create a special soil space of biological interaction, the rhizosphere (Bowen and Rovira, 1991; defined as the zone influenced by root metabolism). In this surrounding area, adherent soil volume (i.e., the rhizoplane, mycorrhizoplane), roots influence and support microbial activity and growth. In addition, symbiosis may arise between roots and bacteria, and fungi. Bacterial symbiosis can induce new structures and activities in the roots, whereas the fungal symbiosis, i.e., mycorrhiza, extends the root-influenced zone to beyond the rhizosphere, establishing the "mycorrhizosphere". Within the latter, fungal

hyphae arising from within root cells or the intercellular space may reach, at least, a scale of metres, depending on the fungus and class of mycorrhiza (Smith and Read, 1997). The induced structural and functional changes are inherently associated with varying cost/benefit relationships between the involved organisms, including the plant.

The rhizosphere is a nutrient-enriched habitat of microorganisms provided through root exudation of compounds (Lynch, 1990) and rhizodeposition from root cap cells and decaying root tissue and root hairs (Lynch and Whipps, 1991). The microorganisms of the rhizosphere maintain intense activity upon the release of root exudates (Bowen and Rovira, 1999), which are of complex and varying composition (organic acids, amino acids, vitamins, polymeric carbohydrates: Neumann and Römheld, 2001). Exudates vary between plant species, e.g., oil rape and maize (Schilling et al., 1998), grass species (Morse et al., 2000), pea and tomato (Whipps, 1987). Furthermore, symbionts such as mycorrhizal fungi represent a significant demand and proportion within the resource allocation of plants.

The microbial colonization of the rhizosphere is highly influenced by plant species (Smalla et al., 2001; Kowalchuk et al., 2002; Garbeva et al., 2004) but can still depend on plant age (Baudoin et al., 2002), root effects on rhizospheric pH (Hackl et al., 2000), or plant nutrition (Yang and Crowley, 2000). Also, the transgenic status may directly or indirectly affect microbial activity (Milling et al., 2004). The specific physical and nutritional conditions of the rhizosphere, mycorrhizosphere, and mycorrhizosplane may favour microbial organisms and can be selective on microbial communities, as the latter differ in composition from those in bulk soil. Even the genetic structure of populations and communities may be altered, as became evident in comparisons of *Burkholderia* or *Paenibacillus* between bulk soil, soil adhering to roots and the rhizoplane (Seldin et al., 1998; Chiarini et al., 2000; Marilley and Aragno, 1999). In addition, gene transfer between organisms appears to be a common phenomenon in functional adaptation (Knudsen et al., 1988). The rhizobial microorganisms, populations, and communities fulfil important ecological functions in nutrient cycling and availability as well as in influencing plant growth and plant health (Sørensen, 1997). In view of this latter aspect, interactions may be beneficial or pathogenic (Whipps, 2001). Rhizo-microorganisms can produce antibiotics against pathogenic bacteria and fungi (Fravel, 1988; Raaijmakers et

al., 2002; Weller et al., 2002) and develop antagonistic populations that exhibit anti-fungal and anti-bacterial activities (Berg et al., 2002, 2005; Hagn et al., 2003). Beneficial effects against pathogens may also result from direct influences of rhizobacteria on roots (Hartmann et al., 2004). The rise in the atmospheric CO_2 level, aside from effects on plant growth, directly influences the rhizosphere through root exudation, and indirectly through litter fall of altered chemical composition (Aneja et al., 2004; Zak et al., 2000). Soil respiration may distinctly rise upon elevated CO_2 supply (Sowerby et al., 1999; Lin et al., 2001), although deficits in knowledge exist about effects on microbial communities, regarding their composition as well as activity in nutrient turnover and beneficial, antagonistic effects against pathogens.

Within these interactions, mycorrhizae are critically positioned in influencing the exchanges of carbon and nutrients between the sources and sinks of fungi and plants (Read et al., 2004). Studies on carbon and nutrient allocation in plants and – at a higher level – in grassland and forest ecosystems have consequently to focus on the interference of these mutualistic fungi with dead and living soil compartments and, at the same time, on the aboveground influences on carbon availability, as the heterotrophic fungal partner is dependent on the plant's photosynthetic capacity. Most important for this mutualistic symbiosis are, amongst several potentially influencing factors, increased atmospheric CO_2 and ozone levels, as well as changes in soil nutrient status (e.g., Perez-Soba et al., 1995; Wallenda and Kottke, 1998; Andersen, 2003; Brunner, 2004; Fransson et al., 2005).

Mycorrhizal fungi are not the only soil organisms that influence the trees' performance. Saprotrophic fungi can interact with ectomycorrhizal mycelia and can take over or mobilize nutrients, e.g., phosphate (Lindahl et al., 2001). And a great diversity of phylogenetically different bacteria are frequently associated with mycorrhizae, particularly with ectomycorrhizae, and seem to create ectomycorrhiza-specific bacterial communities (Poole et al., 2001; Frey-Klett et al., 2005; Kellermann, Schmidt, Hartmann and Agerer, unpubl.). Other N_2-fixing symbionts and rhizospheric bacteria are well known. Nevertheless, ectomycorrhizae themselves can form various communities that are composed of different ecological strategists (Agerer, 2001). Moreover, different fungal species can be associated with or appear to be excluded from the vicinity of others (Agerer et al., 2002; Koide et al., 2005) and confined in soil micro-habitats (Agerer and Göttlein, 2003). Even different plant individuals and species can be connected through mycorrhizal mycelia, suggesting a transport of nutrients and carbohydrates from plant to plant via common hyphal networks (Simard et al., 2004). Invertebrates can live with or feed on mycorrhizae and, therefore, influence the nutrient absorbing capacity and the carbohydrate pool necessary for establishment of hyphal systems (Hiol Hiol et al., 1994; Jentschke et al., 1996). Altogether, mycorrhizae are, at the same time, object and subject of alterations in nutrient availability and carbon allocation. The mycelial networks they develop within the soil are a crucial factor for mycorrhizal functioning and for the ecosystem as a whole. A recent review of mycelial networks focuses particularly on these structures (Leake et al., 2004) and points out that modern approaches are urgently needed for studying this fugal compartment.

One major focus of SFB 607 is on the extramatrical mycelium of ectomycorrhizae, regarding quantification, distribution patterns, and impact on carbohydrate sink (Agerer and Raidl, 2004; Raidl et al., this volume). The investigations are in line with Leake et al. (2004), who claim that the extra-radical mycelium of mycorrhizal fungi deserves attention in influencing plant community composition and ecosystem functioning. Ectomycorrhizae can be categorized into different exploration types with respect to abundance, organization, and distance that the extramatrical mycelium grows from the ectomycorrhizal surface through the soil (Agerer, 2001; Agerer and Raidl, 2004).

Quantifications of extramatrical mycelia suggest some 700–900 kg ha^{-1} are produced in forest soils (Wallander et al., 2001), and conservative estimation results in a proportion of ectomycorrhizae of approximately one third within the total microbial biomass of forest soils (Leake et al., 2004; Högberg and Högberg, 2002). The total length of extramatrical mycelium ranges between 30–8000 m hyphae m $root^{-1}$ and 3–600 m g $soil^{-1}$ (Leake et al., 2004). In conclusion, from the few available studies, it appears that up to 30% of the trees' net fixation is allocated to the extramatrical mycelium (Ek, 1997; Leake et al., 2004; Rillig et al., 2002).

Nutrient acquisition and uptake considerably depends on the surface area that extramatrical hyphae provide. According to an investigation by Rousseau et al. (1994), the ectomycorrhizal mycelium comprised 75% of the surface area, while roots were only 25%. Comparing structural costs per unit of absorptive area between roots, root hairs and hyphae indicates mycorrhizal hyphae to be approximately 10 times more efficient than root hairs and roughly 100 times more efficient than roots (Leake et al., 2004; Read, 1999). Unlike plant roots, ectomycorrhizae are able to take up organically fixed nitrogen in the form of amino acids, thus the costs for nitrogen uptake by roots as nitrate (20 mol ATP) or ammonium (5 mol ATP) can be saved through the mediation of ectomycorrhizal mycelia (Leake et al., 2004); this is another advantage of extramatrical mycelia.

One difficulty in estimating extramatrical mycorrhizal mycelia is the distinction between mycelia of mycorrhizae and that of saprotrophs, which grow in an inherently intermingled way. Although ergosterol and phospholipid fatty acid (PLFA) have been applied to quantify the mycelia, these methods can only distinguish between the two types of mycelia when subtractive methods are used (Wallander et al., 2001). A recently developed method used quantitative PCR to compare changes in relative quantities of hyphae when growth conditions are altered. A determination of the biomass of mycelia, however, was still impossible (Schubert et al., 2003). Recently, a calibration of DNA signals became available with respect to hyphal length and in relation to hyphal biomass (Raidl et al., 2005). Although access to mineral nitrogen and exposure to elevated levels of ozone and CO_2 have been accepted to influence abundance of ectomycorrhizae, the species composition and the amount of extramatrical mycelium, the evidence for such a reaction is still limited (Andersen, 2003; Erland and Taylor, 2002; Gorissen and Kuyper, 2000; Rillig et al., 2002).

As the extramatrical mycelium of mycorrhizae is apparently the most important part for plant community composition and ecosystem functioning (Leake et al., 2004), focus in the

following will be on the response of this mycelial network to environmental changes. Irrespective of additional mineral N nutrition or exposure to elevated CO_2 (700 ppm), an almost constant relationship between the lengths of extramatrical mycelia and *Piloderma croceum* ectomycorrhizae was found relative to the control (Raidl et al., unpubl.), although the total length of ectomycorrhizae decreased under high nitrogen or CO_2 supply. Only a combination of the latter treatments increased the length of ectomycorrhizae and, even more, of extramatrical mycelium. A three-fold increase in the total fungal biomass (ectomycorrhizae including extramatrical hyphae), and a two-fold increase in extramatrical hyphae alone were observed with ectomycorrhizae of *Hebeloma crustuliniforme* on *Pinus sylvestris* seedlings under elevated CO_2 (700 ppm), whereas *Paxillus involutus* did not show significant differences (Fransson et al., 2005). Similarly, *Pisolithus tinctorius* showed a doubling of biomass under elevated CO_2 (600 $\mu mol\ mol^{-1}$; Ineichen et al., 1995). These studies confirm earlier findings that ectomycorrhizal species with a higher incidence of extramatrical mycelia increased in abundance under high CO_2 levels (Godbold and Berntson, 1997). As the carbohydrate availability decreases under ozone exposure (Andersen, 2003), a decrease in extramatrical mycelia may be expected, although the database is scarce. On these grounds, considerable influences of changing soil conditions or CO_2 or ozone levels are imaginable. As the absorptive area may be altered, together with the ectomycorrhizal carbon sink strength, plant growth and nutrition appear to be prone to impacts of changing environmental conditions.

Being crucial in ecosystem functioning (Leake et al., 2004), mycorrhizae need to be considered in ecosystem modelling. However, even the most recent models of carbon allocation between herbaceous plants and the soil ignore interactions with mycorrhizae and their mycelia (Toal et al., 2000). The models within SFB 607 are the first to address the substantial amounts of carbohydrates being allocated to mycorrhizae and the soil (see 6).

5 Molecular Mechanisms

Functional genomics is revolutionizing understanding of the complex interactions between plants and symbiotic ectomycorrhizal or endomycorrhizal fungi (Martin, 2001). Suppressive subtractive hybridization has resulted in the isolation of unique ESTs (expressed sequence tags) of mycorrhiza-regulated genes during arbuscular mycorrhizal development in pea (Liu et al., 2003; Grunwald et al., 2004). An enhanced expression level of a pea chalcone synthase was found in roots at the stage of first fungal contact, indicating the induction of a defence pathway (Mohr et al., 1998; Bonanomi et al., 2001). However, other plant defence genes were not induced in the symbiotic interaction, but were induced in a pathogenic interaction (Mohr et al., 1998). During colonization of pine roots by ectomycorrhizal fungi, an auxin up-regulated pine gene was characterized, indicating the involvement of this hormone during the colonization process (Charvet-Candela et al., 2002). The carbohydrate flow from the plant to the ectomycorrhiza is an important process for this symbiosis. A fungal monosaccharide transporter was up-regulated in ectomycorrhizas by a monosaccharide-controlled mechanism (Nehls et al., 1998). In addition, a fungal phenylalanine ammonia-lyase transcript was induced, indicating that monosaccharides not only serve as

fungal nutrients, but might also be involved in gene expression (Nehls et al., 2001). Therefore gene expression profiling and analysis of relevant genes at the plant, as well as at the fungal level will help in understanding this important ecological symbiosis (Franken and Requena, 2001).

Regarding the other kind of biotic interaction with respect to plant internal resources, i.e., that between plants and pathogens (Fig. **2**), plants have evolved a set of defence mechanisms to protect themselves against pathogenic, fungal, and microbial attack. This phenomenon has been called systemic acquired resistance (SAR in Fig. **2**; Maleck and Dietrich, 1999). Endogenous signal molecules, such as salicylic acid, jasmonic acid or ethylene, play a key role in signalling for resistance and cross-talk between different signalling pathways are known (Maleck and Dietrich, 1999; Schenk et al., 2000). Defence-related genes are induced resulting in defence-orientated transcriptional reprogramming of the cell (Hahlbrock et al., 2003). Among the well-known genes encoding pathogenesis-related proteins, genes of the antioxidative system and of secondary metabolism are also induced (Hahlbrock et al., 2003). The transcriptome of *Arabidopsis thaliana* during systemic acquired resistance has been studied in detail and regulatory networks and new genes were identified (Maleck et al., 2000; Schenk et al., 2000). In addition, *cis* elements that are recognized by structurally related DNA binding proteins have been characterized (Eulgem et al., 2000; Maleck et al., 2000; Hahlbrock et al., 2003; Ernst and Aarts, 2004).

Plants respond to abiotic stresses such as ozone and to pathogens by increasing the production of reactive oxygen species (ROS) that activate local programmed cell death and systemic induction of pathogen and stress resistance (Sandermann, 2000; Langebartels et al., 2002; Mahalingam and Federoff, 2003). ROS then trigger the activation of signalling cascades such as the mitogen-activated protein kinase cascade and accumulation of ethylene, jasmonic acid, and salicylic acid (Zhang and Klessig, 2001; Mahalingam and Federoff, 2003; Overmyer et al., 2003). Transcription factors, binding to specific *cis* elements, then create an efficient transcription initiation complex that finally results in balanced gene regulation. Distinct promoter motifs for ozone and pathogen stress have been summarized by Ernst and Aarts (2004).

Environmental impact at the gene level results not only in the up- or down-regulation of several different genes, but also to an influence on gene cascades that are involved in the regulation of primary and secondary metabolism. In recent years, most work at the transcriptional level has been carried out by applying a single stress. The air pollutant ozone has been found to be an abiotic elicitor of plant defence reactions and a cross-induction of two distinct defensive pathways by ozone was found in parsley (Eckey-Kaltenbach et al., 1994; Sandermann et al., 1998). Transcripts from the shikimate pathway, which has a dual involvement in primary and secondary metabolism, are up-regulated by pathogens (Weaver and Herrmann, 1997), and recently an ozone-induced accumulation of shikimate pathway genes in European beech was found (Betz and Ernst, unpubl.). This indicates the importance of this pathway for growth and defence processes (cf. Siemens et al., 2002, 2003).

Using Affymetrix microarray technologies, the stress/defence transcriptome of *Arabidopsis* has been studied in detail (Craigon et al., 2004; http://affymetrix.arabidopsis.info/). A crosstalk and differential response to abiotic and biotic stressors was found at the transcriptional level of effector genes from secondary metabolism, including P450 monooxygenases, glycosyltransferases, and ABC transporters; and principal component analysis affirmed common and separate response reactions (Glombitza et al., 2004). Similarly, clustering of P450 genes showed crosstalk from various treatments, e.g., pathogen attack, wounding, paraquat and hormone treatment (Narusaka et al., 2004). Moreover, most genes induced by both abiotic and biotic stress contained defined identical *cis* elements in their promoter region, and are known to participate in the regulation of plant defence. This indicates that the response of each gene to multiple stresses is highly regulated (Narusaka et al., 2004). Screening a pathogen- and ozone-induced subtracted cDNA library of *Arabidopsis thaliana* resulted in about 48 differentially expressed genes (Mahalingam et al., 2003). Shifts in gene expression in response to abiotic stressors, such as drought, temperature, and UV-B, were distinct from those in response to ozone (Tamaoki et al., 2004). This also indicates differences in gene expression upon treatment with different stress factors.

Few reports exist on the transcriptional regulation of a changed balance between growth and defence upon multiple stress responses. A well-known system is the crosstalk of UV light and pathogen defence in parsley. UV light and elicitor treatment selectively co-induces pathways from primary metabolism, shikimate pathway, and secondary metabolism (Logemann et al., 2000). A UV light mediated acyl-CoA oxidase and chalcone synthase transcript induction was rapidly reversed by subsequent addition of an elicitor (Logemann et al., 2000). Furthermore, it was shown that this reversion was caused by an inversely regulated light-responsive promoter element (Logemann and Hahlbrock, 2002). This indicates an extensive reprogramming and interplay of primary and secondary metabolism and a broad spectrum of flexible metabolic adaptiveness to environmental hazards. In poplar, wounding and subsequent viral infection resulted in additive as well as antagonistic effects on host transcript accumulation (Smith et al., 2004). Hiercharchical cluster analysis showed an additive increase in transcript abundance for genes coding for cell rescue and metabolism, whereas antagonistic effects were found for genes belonging to pathogen defence. This indicates again a flexible transcriptional adaptiveness of plants to environmental stress factors. A similar complex reorganization of transcriptional changes was also found for pathogen and herbivore resistance in plants (Felton and Korth, 2000; Baldwin et al., 2001). Ozone is known to induce five major defence systems in plants and is thus predicted to strengthen plant defence against pathogens, in addition to its well-known detrimental effects (Sandermann, 1996). However, at the transcriptional level, no reports are available when plants are treated with ozone and a subsequent pathogen infection of leaves. Expression profiling using micro-array technologies will identify transcripts that are involved in the plant's answer following environmental challenges.

A major aspect of integration and validation of findings for plant life in the field is scaling of responses from laboratory to field conditions (Sandermann and Matyssek, 2004). Miyazaki et al. (2004) analyzed transcript expression profiles of *Arabidopsis thaliana* grown under controlled conditions and in open air elevated concentrations of CO_2 and ozone. Most changes in gene expression were found between ambient field and growth chamber conditions. The number of up- and down-regulated transcripts was up to four times higher between controlled chamber and field conditions as compared with high versus low CO_2 or ozone levels. Therefore, molecular biological studies must not be restricted to laboratory experiments but also need to be carried out in the field.

6   Modelling Resource Allocation in Plants

To support experimentation on mechanisms of whole plant resource allocation, mechanistic plant growth models provide thoroughly defined conceptual frameworks, representing complex hierarchies of mutually coupled assumptions and hypotheses (Thornley and Johnson, 1990). These hypotheses are often based, in part, only on well established knowledge and can bridge knowledge gaps by providing alternative built-in modelling approaches. The conceptual framework of a plant resource allocation and growth model expresses ecophysiological processes in plant performance that are subject to the investigated environmental scenarios. Since plant internal cause-effect relationships that control resource allocation are only scantly known, in many plant or crop growth models effects of changing environmental state variables (such as temperature or soil water and nitrogen supply) are mostly modelled at the whole plant or canopy level but rarely directly related to specific processes in plant organs or compartments (Jones et al., 2003; van Ittersum et al., 2003; Gayler et al., 2002). Exceptions are simulations of photosynthesis in individual tree growth models, where light interception is assessed for each individual leaf, but leaf water or nutritional status is neglected (Le Roux et al., 2001). The difficulties in determining a model structure that describes the relevant plant internal mechanisms are illustrated by Passioura (1996) for plant responses to water shortage. In the case of drying soil, the leaf water potential falls, which induces stomatal closure and photosynthetic decline that limit growth. The respective model structure can be defined in a way that the total photosynthesis rate, as integrated over each single leaf, determines the growth rate of the whole plant (source-limited). Alternatively, a scenario can be conceived where the plant senses that its environment has deteriorated and in turn reduces growth, i.e., such that the overall growth rate determines photosynthesis in the single leaves (sink-limited).

Since knowledge of plant internal mechanisms and systemic responses that regulate resource allocation is far from being complete, very different approaches exist to model carbon and nutrient allocation (Tiktak and van Grinsven, 1995; Lacointe, 2000; Le Roux, 2001; Yang and Midmore, 2005): Allocation models may be based on (i) fixed allocation fractions using empirical or hypothetical allometric relations that are affected by or independent of environmental conditions (Aber and Federer, 1992; Mohren and van de Veen, 1995; Valentine, 1999; Mäkelä, 1997; Berninger and Nikinmaa, 1997; van Ittersum et al., 2003; King, 2005); (ii) systems of priorities, phenology, and nutrient status (Grossman and DeJong, 1994; Weinstein and Yanai, 1994; Jones et al., 2003); (iii) transport resistance approaches for sugar transport (Thornley, 1991; Luan et al., 1996; Thornley, 1997); or (iv) teleonomic approaches that

optimize goal functions for maximal resource uptake (Rastetter et al., 1991; Sekimura et al., 2000).

Our modelling approach (Gayler and Priesack, 2003; Grote and Pretzsch, 2002), used as an interpolation and extrapolation tool in clarifying mechanisms of "plant-plant", "plant-pathogen", and "plant-mycorrhizosphere" interactions and their interrelationships in growth and defence dynamics (cf. Fig. **2**), is mainly a combination of approaches according to (i)–(ii). Effects of environmental conditions are simulated, following sink-limited modelling that describes plant responses at the whole plant level rather than integrating responses of single plant organs. This approach eventually has to be complemented by source-limited models, if corresponding mechanisms or processes are identified. Such a complementation was achieved for the apple tree model, where the dependence on nitrogen supply for investment in defensive compounds was characterized (Gayler et al., 2004).

Another focus in plant modelling is the interaction between plants. Especially for forest trees, a long history exists of such models. Early approaches modelled forest stands by aggregated sums and mean values of, e.g., volume of growing crop or diameter (Schwappach, 1890; Wiedemann, 1937; Assmann and Franz, 1965; Schober, 1967), or by diameter frequency distributions (Clutter, 1963; von Gadow, 1987). Present models pursue the individual tree approach when aiming at application and prediction in practice (Monserud, 1975; Sterba, 1983; Pretzsch, 2000, 2001), or they are based on ecophysiological knowledge when focusing on research (Le Dizès et al., 1997; Perttunen et al., 1998; Gayler et al., 2004; Grote and Pretzsch, 2002). Mechanisms of internal coupling between structure and function in trees have hardly been revealed (Kurth, 1999), but forest science holds a considerable set of time series in support of empirical modelling approaches. In contrast to herbaceous plants, the morphology of individual trees and their growth response to competition has spatio-temporally been documented in explicit ways on some hundred experimental plots and over about one century. For example, recordings of individual tree development (tree height, crown width, crown length, shift of the crown base) are available for pure and mixed stands of Norway spruce and European beech, and the competition structure is documented for the same trees (distance to neighbours, height, crown dimensions of adjacent trees).

Such datasets provide valuable information for empirical modelling of relationships between competition and biomass allocation of trees. Practically oriented modelling approaches are based on the concept of growing space and predict tree growth as a whole, especially tree form development as depending on available space by means of competition indices (Hasenauer, 1994; Pretzsch et al., 2002; Nagel, 1985). Mechanistic approaches choose a more refined approach and allocate biomass to different tree organs, being based on detailed characterization of the competitive state in terms of resource availability and intrinsic physio-morphological relationships. However, in most cases, allocation processes are based on empirically validated allocation functions (Mäkelä et al., 1997; Seifert, 2003). The solid empirical database from long-term plots, however, is used in several cases for the evaluation and calibration of more sophisticated mechanistic approaches. For example, the model BALANCE (Grote and Pretzsch, 2002) pre-

dicts crown growth and branch expansion as depending on the spatially explicit detection of resource supply at the respective canopy position. To ensure plausible model behaviour over prolonged simulation periods, empirically derived stem form and crown functions are used to provide realistic starting conditions; in addition, empirically deduced potential maxima limit growth to realistic boundaries. The suitablility for scrutiny of the hypotheses of SFB 607 have provided a modelling approach which links the tree's allometry with its competitive constellation. This mechanistic approach embedded into a frame of empirical boundaries was appropriate to revealing dependences between allocation, growth, and competition, as addressed by the hypotheses of the research programme. Evaluations are underway which consider such interrelationships as affected by the stand structure and the genetic traits of trees.

7   Conclusions: The Whole Plant Perspective

As is becoming evident from the findings of SFB 607 and the literature, there is no simple answer to the hypothesis posed at the beginning of this paper, and indeed, a simple answer is not to be expected. Apart from aspects of science theory (see "Introduction"), effects of internal and external factors interacting in resource allocation are complex, in particular, under field conditions, and may cause intricate responses.

The rationale for SFB 607 and the presented account did focus on three central kinds of factorial interactions, i.e., the biotic ones between (competition) and within plants (interrelationships with pathogens and mycorrhizae as well as associated soil micro-organisms), as influenced by abiotic scenarios. As demonstrated, responses in the host-pathogen interaction are driven – again in a complex way – by external (resource supply) and internal factors; in the latter case, e.g., by the extent of primary production and, hence, the plant's competitiveness (representing the core of the above hypothesis and the trade-off visualized in Fig. **1**). However, primary production and pathogen defence are determined, at the same time, by the plant's interaction with the mycorrhizosphere, so that the processes in the latter, although not being part of the hypothesis, modify the outcome of hypothesis evaluation. This underlines common principles in the control of resource allocation, fed from one common, internal resource pool, between the three highlighted types of biotic interaction (cf. Fig. **2**). In other words, understanding regulation in resource allocation and the mechanisms "behind" the above hypothesis means viewing these types of biotic interaction as one "unity" in the control of allocation. In view of the rationale of Fig. **2**, it is tempting to examine plant-pathogen and plant-mycorrhizosphere interactions for similarities in the competition for plant internal resources. The ecological significance of biotic interaction also became apparent in the finding that interspecific competition (between e.g., woody plants) mediates effects of abiotic stress (by CO_2, O_3) on allocation. Nevertheless, it must be cautioned that changes in allocation may not necessarily be the consequence of metabolic re-adjustment under stress, but obey allometric rules as occurring during ontogeny (Weiner, 2004) – a phenomenon which has often been overlooked in the analysis of resource allocation.

Given the limitation of general hypotheses, such as that posed at the beginning, in covering the full potential range of plant performance and biology, the more the unravelling of the underlying mechanisms in resource allocation becomes mandatory. Such a mechanistic basis can resolve conflicts in hypothesis evaluation. Process-based interpretations require mechanisms to be pursued across the relevant range of spatio-temporal scaling levels (Sandermann and Matyssek, 2004), e.g., up to the stand level, following the rationale of Fig. **2**. When viewing findings in the context of the published knowledge, deficits are still apparent in understanding factorial impact on host-pathogen relationships as exerted by e.g., varying levels in CO_2 or O_3 exposure, N supply or competition with neighbouring plants, including mycorrhization. On such grounds, modelling represents a tool not only to integrate findings, but also to position them within the context of the current state of knowledge, to examine mechanisms for plausibility, to probe the system response under scenarios that are not presently investigated, and to generate more refined hypotheses. In addition, mechanisms need to be explored "downwards" to the gene level to ensure thorough understanding of allocation (Figs. **1,2**). Expression profiling through micro-array technologies needs to identify transcriptional networks that are involved in the plant's capacity to regulate growth and defence upon environmental challenges. A prerequisite is the knowledge of sufficient ESTs. Subtracted libraries and analysis of selected metabolic pathways (e.g., shikimate, phenylpropanoid metabolism) will provide insights into host-pathogen interactions, because ozone behaves, in signalling, as a kind of "abiotic pathogen" (Sandermann, 1996).

Unravelling mechanisms in resource allocation implies the consideration of cost/benefit relationships involved in regulation, although such relationships (as reflected in the core of the above hypothesis, Fig. **1**) may be modified by "third party trade-offs" and associated "ecological costs" in view of the multi-factorial demands which are directed towards the resource pool. A "full cost analysis" is the ultimate goal and needs to remain a perspective in concept design and experimentation but, given restrictions in knowledge and methodology, it can hardly be achieved at the present time (see "Introduction"). To some extent, at least, cost/benefit relationships turned out to be assessable and fundamental in quantifying competitiveness. In balancing resource investments versus gains per unit of above- and belowground space that is subject to competitive resource exploitation amongst neighbouring plants, a mechanistic basis – as postulated long ago – becomes accessible in the conceptual understanding of competition. Relation to space also provides the basis in linking allocation with allometry, which appears crucial not only in distinguishing effects of metabolic regulation from those of ontogenetic control (see above), but also in pursuing population dynamics (self-thinning) at the stand level. Perhaps, relating resource turnover to the space relevant in competition can create a common platform for comparing the three kinds of biotic interaction addressed in this paper. This is obvious in quantifying competitiveness and, hence, also appears to be appropriate in interpreting plant-mycorrhizosphere interactions, but it may be rewarding as well to ensure functional understanding of parasite defence and associated costs. As space-related resource turnover is the key in quantifying competitiveness, then the plant's efforts in making proficient use of space in competition implies prevention of loss of occupied space

through pathogens (cf. Siemens et al., 2002), and hence, may imply a space-related view of defence. Such a perspective on defence may provide a new dimension to evaluating the central hypothesis and in distinguishing its crucial mechanisms. At the same time, the conversion of resource turnover may be fostered across the different kinds of biotic interaction, stressing their capacity in jointly controlling whole plant resource allocation.

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