

Resource Allocation in Plants – The Balance between Resource Sequestration and Retention

R. Matyssek¹, H. Schnyder², J.-C. Munch³, W. Oßwald⁴, H. Pretzsch⁵, and D. Treutter⁶

¹ Ecophysiology of Plants, Technische Universität München, Am Hochanger 13, 85354 Freising-Weihenstephan, Germany

² Grassland Science, Technische Universität München, Am Hochanger 1, 80638 Freising-Weihenstephan, Germany

³ Soil Ecology, Technische Universität München, Ingolstädter Landstraße 1, 85764 Neuherberg, Germany

⁴ Phytopathology of Woody Plants, Technische Universität München, Am Hochanger 13, 85354 Freising-Weihenstephan, Germany

⁵ Forest Growth and Yield Science, Technische Universität München, Am Hochanger 13, 85354 Freising-Weihenstephan, Germany

⁶ Fruit Science/Fruit Tree Physiology, Technische Universität München, Alte Akademie 16, 85350 Freising-Weihenstephan, Germany

In 2002, an “Acute View” was presented in this journal (vol. 4) on a key question regarding the understanding of resource allocation and partitioning within and between plants, namely, about the balance between resource sequestration and retention (Matyssek et al., 2002). The paper referred to the interdisciplinary research center of “Sonderforschungsbereich 607” (SFB 607), entitled “Growth and Parasite Defence – Competition for Resources in Economic Plants from Agronomy and Forestry”, which has been pursued – funded through the “Deutsche Forschungsgemeinschaft” (DFG) – by about 20 research teams since 1998 in the region of Munich and Freising-Weihenstephan (Germany). An overview was provided on the rationale and research concept of SFB 607, highlighting the positioning of this programme within the state of knowledge at that time. Focal points of the research in SFB 607 have been mechanisms that allocate energy, carbon, water, and nutrients between the demands of growth and defence, considering growth as a means of competitiveness while plants grow in stands. An inherent feature of the concept is analysis of functional “cost/benefit” relationships associated with the control of resource allocation. As, in this context, competitiveness and parasite defence represent the capacities for resource sequestration and retention, they reflect the essence of individual plant fitness. Trade-offs between growth and defence-related processes are being pursued through scaling approaches, from the molecular towards the stand level – as well as across plant ontogenetic stages, contrasting plant life forms (herbaceous versus woody) and growth conditions (controlled versus field). Response mechanisms in resource allocation are examined under biotic and abiotic stress scenarios, including competition, pathogen attack, elevated CO₂ and O₃ levels, as well as variable light and N supply, and drought. The scaling ranges allow examination of regulation in resource allocation, to the extent of general validity, not only relying on the synergism of expertise from basic and applied biological sciences, but also mathematics (modelling, informatics) and physics (climatology). The common focus within SFB 607 on resource allocation in economic plants is a novum in applied, biological research in agronomy and forestry.

The account published in volume 4 reflected the initial stage of SFB 607, as the “Acute View” by Matyssek et al. (2002) introduced a selection of original papers which originated from an international SFB 607 symposium held at that time (Fleischmann et al., 2002; Grams et al., 2002; Grote and Pretzsch 2002; Pretzsch, 2002; Reitmayer et al., 2002; Rühmann et al., 2002 and, as an invited, external keynote contribution, Ehleringer et al., 2002). About four years later, SFB 607 has amassed substantial evidence on the above highlighted research topic through experimentation, data analysis, and modelling, so that a special issue of this journal can now be filled with 19 original publications and two review articles, all of them originating from ongoing research from this programme.

Preview on the Publications in this Special Issue

The introductory review article by Matyssek et al. (2005, this issue) outlines overall progress in SFB 607 that has been achieved until now, in relation to the state of knowledge currently available in the addressed research area. This article is structured by the major domains of research within SFB 607, i.e., evidence on the involvement of “plant-plant” interactions (intra- and inter-specific competition), “plant-mycorrhizosphere” relationships (potentially conducive to competitiveness), “plant-parasite” interactions (adverse to competitiveness), and of the underlying, regulatory control of allocation at the physiological, biochemical, and molecular level in balancing resource sequestration versus retention across scaling levels. The account concludes by highlighting mechanistic modelling as an integrative tool that substantiates the concept of SFB 607 by locating “black boxes” in understanding, establishing “cost/benefit” balances in resource allocation, performing sensitivity analyses under factorial impacts and developing guiding hypotheses for the research programme.

Consistently, the sequence of the subsequent papers in this volume, including the review article by Treutter (2005, this issue; see below), is structured by their contributions to the major research domains of SFB 607 and respective mechanisms. With respect to “plant-plant” interactions, Schnyder and Lattanzi (2005, this issue) focus on resource allocation as associated with competition in mixed systems of C₃ and C₄ grasses, making use of the analysis of natural ¹³C signatures in biomass and respired CO₂. In alfalfa, Lötscher and Gayler (2005, this issue) demonstrate, through ¹³CO₂ analysis, that 40% of root respiration is fuelled by currently assimilated C

(R_{new}) under high-light and N conditions, with a tendency to increase under low light, and to decrease under low N. R_{new} is apparently driven by the ratio of aboveground assimilatory capacity versus belowground maintenance costs, as short-term light limitation of photosynthesis is buffered in root respiration by the mobilization of reserves. In view of the disturbance to competition-related allocation in adult beech and spruce trees caused by ozone (O_3 , free-air canopy fumigation), Wipfler et al. (2005, this issue) report on a significant decline in radial stem growth in spruce (but not in beech), calculating the individual O_3 dose for up to 47 trees in each species, and analysing their stem increment across three consecutive years. Leuchner et al. (2005, this issue) present a novel multi-sensor system for measuring photon flux density between 360 and 1020 nm, with a resolution of 0.8 nm, within the beech/spruce stand, based on fibre optics technology and a diode array spectrometer. The system supports time series analyses of weather conditions, phenology, and stand development, all being of relevance for competition, and is able to quantify sunfleck events, light availability on the forest floor, and to identify periods of leaf flushing and leaf fall from changes in light quality. Pretzsch and Schütze (2005, this issue) evaluate the significance of crown allometry and growing space efficiency in beech and spruce at the stand level. Per unit of relative biomass increment, beech achieves a higher increase in crown projection area and height, and is superior in long-term space occupation to spruce, although ontogenetic drifts in competitiveness affect upscaling from tree to stand productivity.

The paper by Luedemann et al. (2005, this issue) provides a bridge between "plant-plant" and "plant-pathogen" interactions. Using ^{15}N labelling, they evaluate the hypothesis that belowground pathogen infestation, in combination with aboveground O_3 stress, reduce competitiveness for N acquisition, but that susceptibility to infestation is counteracted by preceding chronic O_3 exposure. They demonstrate contrasts between responses of juvenile beech and spruce in mixed plantations. The analysis by Fleischmann et al. (2005, this issue) indicates that disturbance of photosynthesis and water relations in beech upon root infestation is mediated through mobile signal triggering. However, the elicitor protein formed upon gene induction of the pathogen caused disturbance in leaves of tobacco (used as a reference) rather than beech. Colonization of leaves of adult beech by a fungal endophyte is shown by Bahnweg et al. (2005, this issue) to be favoured by light limitation but inhibited by drought, whereas inhibitory effects of enhanced O_3 exposure (through free-air canopy fumigation) were marginal. Endophyte-related necroses were found to be highly correlated with the occurrence of the stress metabolite 3,3',4,4'-tetramethoxybiphenyl. Olbrich et al. (2005, this issue) isolated cDNAs of genes that are differentially expressed in beech leaves upon O_3 exposure, showing expression patterns of selected ESTs (expressed sequence tags) which were confirmed by increased transcript levels. Strissel et al. (2005, this issue) address enzyme regulation of the trade-off between flavonoid concentration in leaves and growth performance of apple trees, in particular, under the influence of N nutrition. The latter is shown to inhibit flavonoid accumulation, because down-regulated PAL activity (phenylalanine ammonia-lyase) forms a "bottle neck" in flavonoid synthesis (this response being less distinct in resistant than susceptible cultivars). Treutter (2005, this issue), in his review paper, examines the significance of flavonoids in plant resis-

tance to biotic and abiotic stress, highlighting the plant-internal competition between growth- and defence-related metabolism. Ros et al. (2005, this issue) report stronger gene induction in potato cultivars susceptible to pathogen infestation than in those with moderate or high pathogen resistance. Pleßl et al. (2005, this issue) demonstrate, in barley, that elevated CO_2 levels diminish the inhibitory effect of enhanced O_3 exposure on pathogen resistance, although glucanase and chitinase activities were higher under enhanced than unchanged, ambient O_3 levels.

Khalvati et al. (2005, this issue) further examine plant-fungus interactions in terms of mycorrhizae and their significance for leaf growth, photosynthesis, and water relations of barley under drought. Drought effects are buffered through hyphal water transfer to host plants and enhanced water uptake by increased hyphal growth. "Plant-mycorrhizosphere" interactions provide a bridge to plant competitiveness at the stand level, as Raidl et al. (2005, this issue) elaborate sensitive DNA-based quantification methods for the species-specific identification of mycorrhizal fungi. A direct correlation between ITS copies of ribosomal RNA and mycelial biomass (derived from structural assessments) was established, being of relevancy for quantitative competition analysis between mycorrhizal systems. Pritsch et al. (2005, this issue) report on functions in the mycorrhizosphere (MR) responsiveness to aboveground O_3 impact and belowground pathogen infestation in the same juvenile mixed beech/spruce systems as addressed above by Luedemann et al. (2005, this issue). Ozone stimulated extracellular enzyme activities, this effect being stronger in the MR of spruce than in beech, although pathogen effects were stronger in the MR of beech. The severity of stress suffered by the plant apparently determines MR enzyme activity. Schlöter et al. (2005, this issue) pursue O_3 effects on the plant-rhizosphere-bulk soil system through a novel outdoor lysimeter approach, reporting on structural and functional changes in the belowground microbial community upon aboveground O_3 impact.

Evaluation of the diverse information acquired in SFB 607 requires novel approaches in data analysis towards achieving integration. One example is given by zu Castell et al. (2005, this issue) for the assessment of water transport-related wood structure of entire tree trunks using computer tomography (CT). As demonstrated, three-dimensional reconstruction of stem volumes from stem slices requires an interpolation approach that accounts for the higher wood structural variability in the radial rather than the longitudinal direction.

References

- Bahnweg, G., Heller, W., Stich, S., Knappe, C., Betz, G., Heerdt, C., Kehr, R. D., Ernst, D., Langebartels, C., Nunn, A. J., Rothenburger, J., Schubert, R., Müller-Starck, G., Werner, H., Matyssek, R., and Sander-mann, H. Jr. (2005) Beech leaf colonization by the endophyte *Apiognomonia errabunda* dramatically depends on light exposure and climatic conditions. *Plant Biology* 7, 659–669.
- Castell zu, W., Schrödl, S., and Seifert, T. (2005) Volume interpolation of CT images from tree trunks. *Plant Biology* 7, 737–744.
- Ehleringer, J. R., Bowling, D. R., Flanagan, L. B., Fessenden, J., Helliker, B., Martinelli, L. A., and Ometto, J. P. (2002) Stable isotopes and carbon cycle processes in forests and grasslands. *Plant Biology* 4, 181–189.

- Fleischmann, F., Koehl, J., Portz, R., Beltrame, A. B., and Oßwald, W. (2005) Physiological changes of *Fagus sylvatica* seedlings infected with *Phytophthora citricola* and the contribution of its elicitor "citricolin" to pathogenesis. *Plant Biology* 7, 650–658.
- Fleischmann, F., Schneider, D., Matyssek, R., and Oßwald, W. (2002) Investigations on net CO₂ assimilation, transpiration and root growth of *Fagus sylvatica* infested with four different *Phytophthora* species. *Plant Biology* 4, 144–152.
- Grams, T. E. E., Kozovits, A. R., Reiter, I. M., Winkler, J. B., Sommerkorn, M., Blaschke, H., Häberle, K.-H., and Matyssek, R. (2002) Quantifying competitiveness in woody plants. *Plant Biology* 4, 153–158.
- Grote, R. and Pretzsch, H. (2002) A model for individual tree development based on physiological processes. *Plant Biology* 4, 167–180.
- Khalvati, M. A., Hu, Y., Mozafar, A., and Schmidhalter, U. (2005) Quantification of water uptake by arbuscular mycorrhizal hyphae and its significance for leaf growth, water relations, and gas exchange of barley subjected to drought stress. *Plant Biology* 7, 706–712.
- Leuchner, M., Fabian, P., and Werner, H. (2005) Spectral multichannel monitoring of radiation within a mature mixed forest. *Plant Biology* 7, 619–627.
- Lötscher, M. and Gayler, S. (2005) Contribution of current photosynthates to root respiration of non-nodulated *Medicago sativa*: effects of light and nitrogen supply. *Plant Biology* 7, 601–610.
- Luedemann, G., Matyssek, R., Fleischmann, F., and Grams, T. E. E. (2005) Acclimation to ozone affects host/pathogen interactions and competitiveness for nitrogen in juvenile *Fagus sylvatica* and *Picea abies* trees infested with *Phytophthora citricola*. *Plant Biology* 7, 640–649.
- Matyssek, R., Agerer, R., Ernst, D., Munch, J.-C., Oßwald, W., Pretzsch, H., Priesack, E., Schnyder, H., and Treutter, D. (2005) The plant's capacity in regulating resource demand. *Plant Biology* 7, 560–580.
- Matyssek, R., Schnyder, H., Elstner, E.-F., Munch, J.-C., Pretzsch, H., and Sandermann, H. (2002) Growth and parasite defence in plants: the balance between resource sequestration and retention. *Plant Biology* 4, 133–136.
- Olbrich, M., Betz, G., Gerstner, E., Langebartels, C., and Ernst, D. (2005) Transcriptome analysis of ozone-responsive genes in leaves of European beech (*Fagus sylvatica* L.). *Plant Biology* 7, 670–676.
- Pleßl, M., Heller, W., Payer, H. D., Elstner, E.-F., Habermeyer, J., and Heiser, J. (2005) Growth parameters and resistance against *Drechslera teres* of spring barley (*Hordeum vulgare* L. cv. Scarlett) grown at elevated ozone and carbon dioxide concentrations. *Plant Biology* 7, 694–705.
- Pretzsch, H. (2002) A unified law of spatial allometry for woody and herbaceous plants. *Plant Biology* 4, 159–166.
- Pretzsch, H. and Schütze, G. (2005) Crown allometry and growing space efficiency of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* L.) in pure and mixed stands. *Plant Biology* 7, 628–640.
- Pritsch, K., Luedemann, G., Matyssek, R., Hartmann, A., Schloter, M., Scherb, H., and Grams, T. E. E. (2005) Mycorrhizosphere responsiveness to atmospheric ozone and inoculation with *Phytophthora citricola* in a phytotron experiment with spruce/beech mixed cultures. *Plant Biology* 7, 718–727.
- Raidl, S., Bonfigli, R., and Agerer, R. (2005) Calibration of quantitative real-time TaqMan PCR by correlation of hyphal biomass and ITS copies in mycelia of *Piloderma croceum*. *Plant Biology* 7, 713–717.
- Reitmayer, H., Werner, H., and Fabian, P. (2002) A novel system for spectral analysis of solar radiation within a mixed beech-spruce stand. *Plant Biology* 4, 228–233.
- Ros, B., Thümmel, F., and Wenzel, G. (2005) Comparative analysis of *Phytophthora infestans* induced gene expression in potato cultivars with different levels of resistance. *Plant Biology* 7, 686–693.
- Rühmann, S., Leser, C., Bannert, M., and Treutter, D., (2002) Relationship between growth, secondary metabolism, and resistance of apple. *Plant Biology* 4, 137–143.
- Schloter, M., Winkler, B., Aneja, M. Koch, N., Fleischmann, F., Pritsch, K., Heller, W., Stein, S., Grams, T. E. E., Göttlein, A., Matyssek, R., and Munch J. C. (2005) Short time effects of ozone on the plant-rhizosphere-bulk soil system of young beech trees. *Plant Biology* 7, 728–736.
- Schnyder, H. and Lattanzi, F. A. (2005) Partitioning respiration of C3-C4 mixed communities using the natural abundance ¹³C approach – testing assumptions in a controlled environment. *Plant Biology* 7, 592–600.
- Strissel, T., Halbwirth, H., Hoyer, U., Zistler, C., Stich, K., and Treutter, D. (2005) Growth promoting nitrogen nutrition affects flavonoid biosynthesis in young apple (*Malus domestica* Borkh.) leaves. *Plant Biology* 7, 677–685.
- Treutter, D. (2005) Significance of flavonoids in plant resistance and enhancement of their biosynthesis. *Plant Biology* 7, 581–591.
- Wipfler, P., Seifert, T., Heerdt, C., Werner, H., and Pretzsch, H. (2005) Growth of adult Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* L.) under free-air ozone fumigation. *Plant Biology* 7, 611–618.

R. Matyssek

Ecophysiology of Plants
Technische Universität München
Am Hochanger 13
85354 Freising-Weihenstephan
Germany

E-mail: matyssek@wzw.tum.de