Competition in mixed stands of beech and spruce: effects of climate and ozone

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The “Growth-Differentiation Balance Theory” assumes a trade-off between parasite defense and increases in growth and competitiveness (Herms and Mattson 1992). Accordingly, increasing resource availability would induce a decrease in secondary metabolites, and hence defense capacity, relative to primary production. Since 1998, about 20 research teams have examined this theory in the interdisciplinary research center “Sonderforschungsbereich 607” (SFB 607), being conducted in Munich and Freising-Weihenstephan (Germany; Matyssek et al. 2005). In this issue, they present results from studies focusing on the effects of ozone and drought stress on beech and spruce competing in mixed stands.

The mature stand as one research object of the reported studies is “Kranzberger Forst”, a 55-year-old Norway spruce stand near Freising/Germany with groups of 62-year-old beech. From the year 2000 on, a group of beech and spruce trees has been exposed to experimentally enhanced free-air ozone fumigation (Karnosky et al. 2001). Ozone was applied, through a novel methodological approach, via more than 100 PTFE tubes into the stand canopy in such a way that five spruce and five beech trees were exposed to a twice-ambient ozone regime, with ozone levels being restricted to below 150 nl l^{-1} (Nunn et al. 2002; Werner and Fabian 2002; Karnosky et al. 2007).

The first paper introduces a novel approach to study the hydraulic architecture of coarse roots. Nikolova et al. (2008b, this issue) combined computer tomography, light

microscopy, and sap flow measurements in order to anatomically and functionally compare the conductive sapwood area of coarse roots between beech and spruce. Cumulative sapwood lumen area was 12% of the total coarse root cross-sectional area in both species. Normalized by that parameter, sap flow rate increased with root diameter.

Häberle et al. (2008, this issue) tested a conceptual approach to assess the amount of carbon available for trade-offs between defense and growth. They monitored the variation in levels of nine defense-related metabolite groups within and between four consecutive growing seasons in mature beech and spruce trees. The difference between minimum and maximum metabolite levels was assumed to be dispensable between growth and defense-related metabolism, ranging between 2 and 5% of gross primary production.

A set of papers describes the effects of ozone and drought, especially during the extreme summer of 2003. Betz et al. (2008, this issue) investigating the shikimate pathway in the greenhouse and in the field, caution against uncritical comparisons between greenhouse-grown saplings and mature forest trees. Rodenkirchen et al. (2008, this issue) studied the effects of ozone and CO_2 on the competitiveness of beech and spruce saplings under standardized phytotron conditions. Ozone stress reduced nutrient efficiencies in beech, suggesting a higher demand for N and P in defense at the expense of competitiveness. Elevated CO_2 counteracted the effects of ozone. In mature ozone-fumigated trees, the extreme summer of 2003 had no effect on the concentrations of P and K in the leaves, whereas the control trees had significantly lower levels of these nutrients in 2004 (Göttlein et al. 2008, this issue). Although ozone fumigation reduced absolute tree diameter increment at breast height in spruce, there was no such effect in beech

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(Wipfler et al. 2009, this issue). In beech and spruce, fumigation with ozone affected onset and end of intra-annual diameter increment. In both species, the drought of 2003 reduced autotrophic soil respiration underneath mature trees, much more so in spruce (by 70%) than in beech (by 50%, Nikolova et al. 2008a, this issue). Although in 2003 fine-root production declined in spruce to less than a fifth of the level during 2002, production remained unchanged in beech.

Seifert and Müller-Starck (2008, this issue) monitored the influence of fructification on growth of individual mature spruce trees, accessing the crown by use of the canopy crane at the site (Häberle et al. 2003). They did not find any reduction in vegetative growth when comparing diameter increment of coning and not-coning trees, neither during the year of fructification nor in the following year.

Rötzer et al. (2008, this issue) present results from a modeling study analyzing the impact of different climate change scenarios on carbon allocation in mixed stands of spruce and beech. In both species, total biomass increment decreased along with increasing severity of the scenarios. In spruce, however, increment decreased more above than belowground, whereas in beech it was the belowground biomass increment that decreased to a greater extent.

Pretzsch and Schütze (2008, this issue) studied the aboveground biomass development in a range of mixed and pure stands of beech and spruce. In both species, individuals grew faster and larger in mixture than in pure stands. The authors explain the effect by facilitation of spruce and reduced intra-specific competition in beech.

The results of these studies lead to the conclusion that increasing levels of stress, such as through climate change, will change the pattern of carbon allocation in mixed stands of beech and spruce and the outcome of competition.

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