Summary Elevated concentrations of carbon dioxide ([CO2]) and ozone ([O3]) affect primary metabolism of trees in opposite ways. We studied their potential interactions on carbohydrate concentrations and contents. Two hypotheses currently under debate were tested. (1) Stimulation of primary metabolism by prolonged exposure to elevated [CO2] does not compensate for the adverse effects of O3 on carbohydrate accumulation and biomass partitioning to the root. (2) Growth in a mixed-species planting will repress plant responses to elevated [O3] and [CO2] relative to conditions in a monoculture. To this end, European beech (Fagus sylvatica L.) and Norway spruce (Picea abies (L.) Karst.) saplings grown under conditions of intra- and interspecific competition were pre-acclimated for 1 year to ambient or elevated [CO2]. In the following 2-year phytotron study, trees were exposed to factorial combinations of ambient and elevated [O3] and [CO2]. The total carbohydrate content (sugar and starch) of spruce was greater in plants exposed to elevated [CO2] than in plants exposed to ambient [CO2]. In beech, the opposite response was observed, especially when this species was grown in combination with spruce. Overall, the data did not support Hypothesis 1, because the adverse effects of O3 were counteracted by elevated [CO2]. Support for Hypothesis 2 was species-dependent. In beech saplings, reduction of carbohydrates by elevated [O3] and stimulation by elevated [CO2] were repressed by competitive interaction with spruce. In contrast, in spruce, stimulation of carbohydrates by elevated [O3] was similar in monoculture but was largely repressed by interspecific competition. In contrast, the response of spruce to perturbations of atmospheric chemistry was not significantly affected by either intra- or interspecific competition.

Keywords: allocation, Fagus sylvatica, Picea abies, sugar and starch partitioning.

Introduction

Tropospheric ozone (O3) is a pollutant originating from photochemical reactions of volatile organic compounds with nitrogen oxides (NOx) released from anthropogenic and natural sources (Stockwell et al. 1997). During the past century, the concentration of O3 ([O3]) has increased in the northern hemisphere and is currently two to three times higher than in the early 1900s (Galloway 1998, Fowler et al. 1999). Furthermore, it is predicted that the tropospheric [O3] will remain high in the future (Elvingson 2001). The concentration of atmospheric carbon dioxide ([CO2]) has also increased from a pre-industrial concentration of 280 µl l−1 to the current value of 365 µl l−1, and is predicted to double during the 21st century as a result of anthropogenic combustion of fossil fuels, deforestation and biomass burning (Schimel et al. 1995, Wigley 1997). Hence, the growth and physiology of vegetation is currently being challenged by unprecedented coincident increases in both [CO2] and [O3] in the lower troposphere.

Ozone is considered to be one of the air pollutants most detrimental to plant growth and development in both urban and rural environments (Lefohn 1992, Skárby et al. 1998, Matyssek and Innes 1999). Beyond tolerable limits, O3 reduces the growth and yield of numerous agronomic crops as well as fruit and forest trees (Retzlaff et al. 1997, Fumagalli et al 2001, Matyssek and Sandermann 2003). Elevated [CO2] on the other hand, can stimulate carbohydrate production and growth of C3 plants, provided that other resources such as light, water and nutrients are not limiting (Ceulemans and Mousseau 1994, Norby et al. 1999, Stitt and Krapp 1999, Bruhn et al. 2000). Such a stimulation may derive from lowered photorespiration mediated by reduced oxygenase activity of Rubisco in response to elevated [CO2] (Stitt 1991, Conroy and Hocking 1993). The adverse effects of enhanced [O3] on carbohydrate
production may be moderated by elevated [CO2]; however, the physiological and biochemical bases for such compensation are unclear (Matyssek and Sandermann 2003).

Previous studies indicate that elevated [CO2] counteracts the adverse effects of O3 (Barnes and Wellburn 1998, Grams et al. 1999, Rudorff et al. 2000, Olszyk et al. 2002). Such compensatory effects have been found for photosynthesis at the leaf and canopy levels in both coniferous and broadleaf trees (Kellomäki and Wang 1997, Noormets et al. 2001). However, this compensatory interaction between elevated [O3] and [CO2] may not be sustained in the long term because of the potential acclimation of carboxylation capacity to elevated [CO2] (den Hartog et al. 1996, Makino et al. 1997, Moore et al. 1999, Karnosky et al. 2001). In general, it is uncertain to what extent perturbations in carbohydrate metabolism are expressed as changes in biomass production and partitioning (Bazzaz 1997, Matyssek et al. 2002).

Concentrations of soluble sugars in leaves and roots and in transport paths between those organs are important indicators of the extent to which photosynthesis exceeds the carbohydrate requirement for growth, development and storage (Körner 2003). Soluble sugars may also serve as an immediate carbohydrate supply in stress defense reactions pending mobilization of starch accumulated in various tissues (Heizmann et al. 2001).

Carbon relations may be altered as plants grow under conditions of intra- or interspecific competition rather than in isolation (Kolb and Matyssek 2001). Saxe et al. (1998) and Ceulemans et al. (1999) point out that tree responses to elevated [CO2] can be altered by competition. Recent studies indicate that competition also increases the O3 sensitivity of several species of herbaceous plants (Bender et al. 2003, Fuhrer et al. 2003) and of juvenile ponderosa pine when growing in competition with ryegrass (Andersen et al. 2001). McDonald et al. (2002) found that some aspen (Populus tremuloides Michx.) clones were more susceptible to O3 than others depending on how competitive they were with neighboring or interplanted clones. However, Grams et al. (2002) concluded that variations in CO2 and O3 regimes had only minor effects on the competitiveness of juvenile beech and spruce trees growing under conditions of intra- or interspecific competition.

In this study, we tested two hypotheses: (1) prolonged exposure to elevated [CO2] does not compensate for the limiting effects of O3 on carbohydrate (sugars, starch) accumulation and biomass partitioning to the root; and (2) growth in interspecific competition will repress the effects of atmospheric treatments (here elevated [CO2] and [O3]) relative to conditions under intraspecific competition.

Materials and methods

Plants and treatments

The study species, European beech (Fagus sylvatica L.) and Norway spruce (Picea abies (L.) Karst.) are both common in the forests of western Europe and often grow together on the same sites. European beech is highly responsive to elevated [CO2] and [O3] (Grams et al. 1999), but spruce often displays much lower sensitivity, especially to O3 (Skárby et al. 1998, Matyssek and Innes 1999). In May 1998, 2- and 3-year-old seedlings of beech (seed source 810-24 Freising) and spruce (seed source 840-27 Altötting), respectively, were selected for uniformity in height (about 0.2 m) and transplanted to containers (0.7 × 0.4 × 0.3 m, volume = 84 l) filled with untreated soil (dystric cambisol, Ah-B horizon, 540 m a.s.l.; see Kreutzer et al. 1991) from Höglwald forest near Augsburg, Germany. Twenty trees (arranged in rows of 4 × 5 individuals, equivalent to 71 plants per m2; Figure 1) were planted in each of 32 containers such that 16 containers had only one species (8 each of spruce and beech) and 16 containers had 1:1 beech:spruce mixtures. Canopy closure occurred early during the second growing season in 1999. To minimize the potential impact of edge effects, measurements for comparisons among treatments were only taken on the six central individuals in each container.

For 1 year prior to the phytotron study, the seedlings were held in two climate-controlled greenhouse chambers programmed to supply ambient or elevated (300 ppm) [CO2] and to track outside climate conditions. For the following two growing seasons, the containers were transferred to the four walk-in phytotrons (2.8 × 3.4 m) maintained by the GSF-National Research Center for Environment and Health in Neuherberg near Munich, Germany. Each phytotron contains four Plexiglas chambers (about 0.8 × 1.1 × 1.0 m) and adequate ventilation to allow for individual gaseous treatments (Figure 1). Irradiance in the phytotron, achieved by a combination of four lamp types, was 50% of natural light conditions. Soil temperature was regulated by independent cooling of each soil compartment (for details on phytotrons, see Payer et al. 1993, Thiel et al. 1996).

In the phytotrons, plants were exposed to ambient or elevated [CO2] in a factorial combination with treatments of ambient or elevated [O3] (i.e., twice ambient [O3]; restricted to < 150 ppb; Table 1) to provide four CO2/O3 regimes: (1) atmospheric control = ambient [CO2] + ambient [O3]; (2) + O3 = ambient [CO2] + elevated [O3]; (3) + CO2 = elevated [CO2] + ambient [O3]; and (4) + CO2/+ O3 = elevated [CO2] + elevated [O3]. Each phytotron (at either ambient or elevated [CO2]) contained four Plexiglas chambers for additional O3 fumigation (two at ambient [O3] and two at elevated [O3]; Figure 1). Two containers (either one beech and one spruce monoculture or two mixed cultures) were placed in each of the four Plexiglas chambers per phytotron. Six study plants per species, atmospheric treatment and type of competition (i.e., intra- or interspecific competition) were kept in one phytotron. This set-up was replicated in a parallel phytotron. We considered individual plants as experimental units, because no container effects on plant biomass development were observed (P > 0.05, data not shown).

Soil water content of each container was monitored continuously at a depth of 7 cm with tensiometers set to trigger irrigation with deionized water whenever soil water tension reached 350 hPa. Liquid fertilizer (partial strength Hoagland solution) was added regularly to ensure non-limiting nutrient supply.
Air temperature and relative humidity (RH) were measured in the phytotrons as described by Payer et al. (1993). Photosynthetic photon flux (PPF) was registered above the canopy, with one photodiode (Type G1118, Hamamatsu, Japan) above each container. All photodiodes were calibrated prior to installation against an LI-189 unit (LI-190 SA quantum sensor, Li-Cor, Lincoln, NE). Monthly mean day and night values for PPF, air temperature, RH and AOT40 (accumulated O3 exposure above a threshold of 40 nl l–1) are given in Table 1. During the winter months of 1998–1999 and 1999–2000, plants were placed into open-top chambers outdoors where corresponding CO2 regimes were maintained.

Analysis of plant biomass

The six central individuals of each container were harvested between August 28 and September 1, 2000 when terminal growth was > 95% completed. Mean height of trees was about 0.5 m. During harvest, temperature and relative humidity were set to 21 °C and 55%, respectively, and PPF was kept at values comparable with overcast days to minimize changes in sugars and starch concentrations during the course of the day. We separated each tree into the three organs: (1) foliage, (2) stems and branches (non-green aboveground biomass, hereafter referred to as shoot axes) and (3) roots (separated into fine roots (< 0.1 mm) and coarse roots). Total fresh mass was determined.
for each harvested tree organ and subsamples were frozen immediately in liquid nitrogen for subsequent carbohydrate assessment. The fresh/dry mass ratio was determined for additional subsamples. Carbohydrates and biomass of the aboveground organs were assessed in a total of six or 12 individuals (from one or two containers, respectively), whereas the corresponding root parameters were determined quantitatively in two randomly chosen trees per container. Because of the dense intermingling of roots it was not possible to harvest more than two root systems per container. For the two root systems, a customized metal cutter (0.115 × 0.115 m, area = 0.013 m²) was used to extract 0.004 m³ of soil. This soil volume underneath the tree was considered to contain the entire root mass of one plant, with the assumption that the amount of root tissue extending beyond this volume was similar to the amount intruding from neighboring plants of the same species (Bengough et al. 2000). Beech and spruce roots were separated from each other based on their characteristic diameters and branching patterns. Soil particles were removed by washing (Oliveira et al. 2000).

**Carbohydrate analysis**

To determine soluble sugar contents of individual plant organs, 30-mg subsamples of powdered tissue were extracted with 1 ml of double-distilled H₂O (using Milli-Q filter, Millipore, Schwalbach, Germany) at 100 °C for 5 min. The extracted soluble sugar was measured colorimetrically after derivatization with anthrone reagent at 578 nm (Carroll et al. 1966). Glucose was used as a standard. Starch content of the samples was determined colorimetrically after enzymatic hydrolysis (Bohringer, Mannheim, Germany).

**Data analysis**

All statistical analyses were performed with the SPSS Version 10.0 software program (SPSS, Chicago, IL). Main effects of elevated [CO₂] and elevated [O₃] and their interactions were determined by 2-way analysis of variance (ANOVA), and interactions of atmospheric treatment (CO₂, O₃) with type of competition (i.e., intra- or interspecific competition) were tested by 3-way ANOVA. When a significant O₃ effect was indicated, Student’s t-test was used to determine whether elevated [CO₂] counteracted adverse O₃ effects. This was considered if data from the + CO₂/+ O₃ treatment were significantly different from the control. Differences were considered significant at \( P < 0.05 \).

**Results**

**Biomass production in beech and spruce**

When beech was grown in monoculture, total leaf biomass was about 25% less in the + CO₂ regime than in the atmospheric control regime (ambient [O₃] + ambient [CO₂], Table 2). Leaf biomass was about 15% less in plants in either O₃ treatment than in the atmospheric control. However, no significant CO₂ or O₃ main effect was found. Until late summer, enhanced [O₃] did not cause premature leaf loss. In the atmospheric control treatment, beech leaf production was about 60% less when the two species were grown together compared with the monoculture. Leaf production in the mixed culture was about 50% less in the + O₃, + CO₂, and + CO₂/+ O₃ treatments than in the atmospheric control; however, the only treatment to show a significant main effect on leaf production was the + O₃ treatment.

Fumigations had little effect on biomass production of shoot axes (sum of non-green aboveground biomass) of beech in monoculture. Growth of beech shoot axes in mixed culture was significantly reduced, with the smallest decrease occurring in the atmospheric control and the greatest decrease (about 70%) in the + CO₂/+ O₃ treatment. Treatment differences in biomass of fine roots paralleled those of the aboveground organs, whereas coarse root biomass was less affected. Overall, fine and coarse root biomass was not significantly different in any of the atmospheric treatments.

In monoculture, elevated [CO₂] increased the biomass of all spruce organs, but the increase was significant only for leaf biomass (Table 2). Spruce also benefited from the weak performance of beech when the two species were grown together. In mixed culture, the stimulatory effect of elevated [CO₂] on spruce biomass was significant for the leaves, shoot axes and fine roots. Ozone had no effect on biomass development of spruce.

**Soluble sugars in beech**

Concentrations of soluble sugars in beech leaves were unaffected by elevated [O₃], but elevated [CO₂] caused significant increases in soluble sugar concentrations in both mono- and mixed culture (Figure 2A). Sugar concentrations were about 50% lower in the shoots than in the leaves. In monoculture, there was a small but significant reduction in sugar concentration associated with elevated [O₃] (Figure 2B). The sugar concentration in coarse roots of beech in monoculture was significantly decreased by elevated [O₃] and significantly increased by elevated [CO₂]. This response was even more pronounced in fine roots. However, the atmospheric treatments had no significant effect in beech roots from the mixed culture (Figure 2D).

Elevated [O₃] and [CO₂] caused significant reductions and increases in sugar content, respectively, in the fine roots of beech plants grown in monoculture (Figures 2E–H). In contrast, sugar content was higher in shoot axes than in leaves (Figures 2E and 2F). When beech was grown in mixed culture, sugar content was markedly decreased by most atmospheric treatments compared with the corresponding treatments of plants in monoculture (Figures 2E–H). In mixed culture, [O₃] affected only the sugar content of the leaves, and elevated [CO₂] reduced sugar contents of roots. Regardless of the kind of competition or whether sugar concentration or sugar content was measured, significant [O₃] effects were always compensated for by elevated [CO₂]. Thus, exposure to elevated [O₃] and [CO₂] resulted in sugar concentrations and contents similar to those found in the control.
Table 2. Biomass of leaf, shoot axes, and coarse and fine roots (g) of beech and spruce under mono- and mixed culture. Data in parentheses are fresh mass/dry mass ratios. Plants were harvested after two growing seasons in the atmospheric treatments (end of August 2000). Values are means ± SD for 5–12 individuals (aboveground) and 2–4 individuals (belowground). Statistically significant main effects by elevated [CO2] or [O3] in either mono- or mixed culture are indicated by an asterisk (*P < 0.05; Fisher’s LSD test).

<table>
<thead>
<tr>
<th>Treatments</th>
<th>Beech</th>
<th></th>
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<th>Spruce</th>
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<td>Shoot axes</td>
<td>Coarse roots</td>
<td>Fine roots</td>
<td>Leaves</td>
<td>Shoot axes</td>
<td>Coarse roots</td>
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<td>9.42 ± 5.20</td>
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<td>16.33 ± 7.58</td>
<td>7.30 ± 4.23</td>
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<td>(2.27 ± 0.03)</td>
<td>(1.97 ± 0.02)</td>
<td>(3.60 ± 0.95)</td>
<td>(4.43 ± 0.03)</td>
<td>(2.31 ± 0.03)</td>
<td>(2.04 ± 0.02)</td>
<td>(3.06 ± 0.10)</td>
<td>(4.41 ± 0.00)</td>
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<td>12.32 ± 8.08</td>
<td>9.74 ± 3.87</td>
<td>3.78 ± 2.04</td>
<td>9.67 ± 2.78</td>
<td>18.67 ± 3.76</td>
<td>7.98 ± 2.31</td>
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<td>(2.20 ± 0.04)</td>
<td>(1.93 ± 0.02)</td>
<td>(2.95 ± 0.17)</td>
<td>(4.43 ± 0.03)</td>
<td>(2.30 ± 0.04)</td>
<td>(2.05 ± 0.02)</td>
<td>(3.49 ± 0.22)</td>
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<td>22.31 ± 10.34</td>
<td>12.13 ± 2.77</td>
<td>4.18 ± 0.20</td>
<td>8.21 ± 3.02</td>
<td>16.45 ± 6.45</td>
<td>6.44 ± 2.83</td>
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<td>(2.34 ± 0.74)</td>
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<td>7.59 ± 5.04</td>
<td>1.73 ± 0.61</td>
<td>11.32 ± 3.12</td>
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<td>(2.11 ± 0.07)</td>
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<td>(2.83 ± 0.15)</td>
<td>(4.46 ± 0.02)</td>
<td>(2.32 ± 0.02)</td>
<td>(2.04 ± 0.02)</td>
<td>(3.52 ± 0.29)</td>
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<td>Monoculture</td>
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<td>12.83 ± 1.51</td>
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<td>(3.09 ± 0.11)</td>
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<tr>
<td>Monoculture</td>
<td>4.55 ± 1.12</td>
<td>24.54 ± 7.23</td>
<td>13.27 ± 8.39</td>
<td>5.26 ± 0.19</td>
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<tr>
<td>(2.20 ± 0.03)</td>
<td>(1.93 ± 0.01)</td>
<td>(2.64 ± 0.06)</td>
<td>(4.42 ± 0.00)</td>
<td>(2.26 ± 0.04)</td>
<td>(2.03 ± 0.02)</td>
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<td>12.75 ± 5.21</td>
<td>24.07 ± 7.65</td>
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<td>(2.17 ± 0.06)</td>
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<td>(2.84 ± 0.11)</td>
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<td>–</td>
<td>CO2: *</td>
<td>CO2: *</td>
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</table>
Starch in beech

In beech grown in monoculture, elevated [CO₂] significantly increased starch concentration in shoot axes and roots, whereas elevated [O₃] caused reductions in starch concentrations (Figures 3A–D). In contrast, the atmospheric treatments had no significant effect on starch concentrations of beech grown in mixed culture. Starch concentrations were generally higher in shoot axes than in leaves and fine roots, but they were highest in coarse roots.

Starch content was significantly increased in shoot axes and roots of beech grown in elevated [CO₂] and limited by O₃ when grown in monoculture (Figures 3E–H). However, a significant reduction of starch content was found in leaves. For beech grown in mixed culture, elevated [O₃] did not significantly reduce starch content. Remarkably, the stimulation by elevated [CO₂] disappeared in the mixed culture and elevated [CO₂] seemed to lower starch content in coarse roots. Elevated [CO₂] compensated for the negative effects of O₃ on starch concentration and content.

Soluble sugars in spruce

Irrespective of the type of competition, elevated [CO₂] significantly increased sugar concentrations in leaves of spruce (Figure 4A). When spruce was grown in combination with beech, elevated [O₃] also increased leaf sugar concentrations. Sugar concentrations were generally lower in shoot axes than in leaves and stimulation by elevated [CO₂] was less in shoot axes than in leaves (Figure 4B). Neither elevated [CO₂] nor [O₃] affected sugar concentrations in coarse roots. In fine roots, growth in elevated [O₃] resulted in small reductions in sugar concentrations regardless of the type of competition (Figures 4C and 4D).

Sugar content in leaves and shoot axes was significantly increased by elevated [CO₂] in both mono- and mixed culture
Sugar content was somewhat lower in roots than in shoot axes and leaves. Elevated [CO₂] increased the sugar content in fine roots only in spruce grown in combination with beech (Figure 4H). There was no significant effect of O₃ on sugar content in spruce.

Starch in spruce

Growth of spruce in monocultures and elevated [CO₂] increased starch concentrations in leaves, shoot axes and fine roots (Figures 5A–D). In combination with beech, growth in elevated [CO₂] resulted in higher starch concentrations only in leaves and coarse roots.

Starch content and concentration in spruce organs were affected in the same way by the atmospheric treatments and types of competition (Figures 5E–H). In addition, higher starch contents were apparent in fine roots of spruce grown in combination with beech in elevated [CO₂]. Elevated ozone concentration had no significant effect on starch content.

Discussion

Our data did not support Hypothesis 1, that prolonged exposure to elevated [CO₂] does not compensate for the adverse O₃ effects on European beech or Norway spruce. In particular, for beech, all negative O₃ effects on carbohydrate concentrations and contents were counteracted by elevated [CO₂]. Hypothesis 2, which says that interspecific competition will repress the effects of atmospheric treatments, was supported in the case of beech, a species that is more sensitive to enhanced [O₃] and [CO₂] than spruce. However, the response of spruce to the atmospheric treatments was largely unaffected by inter- or intraspecific competition.

The roots of beech grown in monoculture had less sugar in elevated [O₃] and more sugar when [CO₂] was elevated (rela-
These results are consistent with numerous studies showing that assimilate translocation to the root is affected by elevated \([\text{O}_3]\) (Anderson 2003, Matyssek and Sandermann 2003) or \([\text{CO}_2]\) (Saxe et al. 1998, Blaschke et al. 2001, Schulte et al. 2002). All adverse \(\text{O}_3\) effects on carbohydrate concentrations and contents were compensated for by elevated \([\text{CO}_2]\) (Figures 2 and 3) and thus did not support Hypothesis 1. In contrast, elevated \([\text{O}_3]\) caused only minor reductions in sugar concentrations in fine roots of spruce (Figure 4D), confirming the frequently reported low sensitivity of this species to elevated \([\text{O}_3]\) (Skärby et al. 1998, Matyssek and Innes 1999). Again, all deleterious effects of \(\text{O}_3\) on carbohydrates in spruce were compensated for by elevated \([\text{CO}_2]\), thus contradicting Hypothesis 1.

In contrast to its high responsiveness to the atmospheric treatments when grown in monoculture, beech grown in mixed culture was less sensitive to the atmospheric treatments (significant interaction between atmospheric treatment and type of competition, \(P < 0.05\); cf. Poorter and Navas 2003). Thus, the responsiveness of beech to perturbations of atmospheric chemistry is repressed by interspecific competition with spruce, supporting Hypothesis 2. This interaction of elevated \([\text{O}_3]\) with the type of competition (intra- and interspecific) is in accordance with previous observations on herbaceous plant populations (Bender et al. 2003, Fuhrer et al. 2003). Effects of atmospheric treatments on sugar concentrations of spruce were similar in both regimes (Figure 4), indicating that responsiveness of this species to perturbations of atmospheric chemistry was little affected by interspecific competition with beech (cf. Grams et al. 2002).

For beech, differences in starch concentrations between trees grown in ambient or elevated \([\text{CO}_2]\) or \([\text{O}_3]\) were only significant when plants were grown in monoculture (supporting Hypothesis 2). Elevated \([\text{O}_3]\) reduced the starch concentra-
tions of shoot axes and roots of beech trees (Spence et al. 1990, Lux et al. 1997), whereas elevated [CO₂] enhanced starch concentrations in the same organs (cf. Kubiske and Godbold 2001) and compensated for the adverse effects of O₃, again contradicting Hypothesis 1. In accordance with data for plants grown without competition (Barnes et al. 1995), we found that elevated [CO₂] increased starch concentration and content in nearly all spruce organs, whereas elevated [O₃] had no effect (cf. Lux et al. 1997). Therefore, in spruce, effects of atmospheric treatments were remarkably consistent between intraspecific and interspecific competition regimes, contradicting Hypothesis 2. In contrast, in beech, Hypothesis 2 was supported, because the measurable effects of elevated [O₃] and [CO₂] observed in monoculture did not persist in a mixed culture with spruce (Figures 2 and 3, cf. Poorter and Navas 2003). We conclude, therefore, that support for Hypothesis 2 is species-dependent.

In the case of sugar, the responsiveness to atmospheric treatments was inconsistent between concentration and content for both species. For beech, consistency was found only in the fine roots, although in general, organ biomass was unaffected by the atmospheric treatments (Table 2, cf. Grams et al. 2002). For spruce trees grown in elevated [CO₂], increased sugar contents persisted in interspecific competition with beech. This effect was paralleled by stimulated growth of the same organs in mixed culture (Saxe et al. 1998). A comparison of carbohydrates between trees growing in either monoculture or mixed culture in ambient [CO₂] + ambient [O₃] (atmospheric control) indicated that sugar contents of leaves and shoot axes of beech were less in mixed culture than in monoculture (consistent with Hypothesis 2). In the case of starch, atmospheric treatment effects were consistent between carbohydrate concentra-

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**Figure 5.** Effects of elevated concentrations of ozone ([O₃]) or carbon dioxide ([CO₂]), or both on starch concentrations and contents of spruce organs grown in intra- or interspecific competition. Open bars correspond to data for the atmospheric control regime (ambient [CO₂] + ambient [O₃]), grey bars to ambient [CO₂] and elevated [O₃] (+ O₃), hatched bars to elevated [CO₂] and ambient [O₃] (+ CO₂) and black bars to elevated [CO₂] + elevated [O₃] (+ CO₂/+ O₃); means ± SD; 5–12 individuals (aboveground) and 2–4 individuals (belowground). Elevated [CO₂] and [O₃] main effects are given by * and ** corresponding to P < 0.05 and P < 0.01, respectively. Molecular mass of glucose is 180.2 g mol⁻¹. Note different scaling of ordinates, in particular when comparing with Figures 3A and 3E.
Hypothesis 2, that growth in interspecific competition repressed plant response to the atmospheric treatments, was supported for beech. Nearly all significant effects of elevated \( \text{CO}_2 \) and \( \text{O}_3 \) on beech trees grown in monoculture, in particular effects on starch, disappeared under conditions of interspecific competition with spruce. In contrast, carbohydrate concentrations and contents of the stronger competitor spruce (Grams et al. 2002) were hardly affected by the type of competition. We conclude that responses of juvenile tree communities to perturbations of atmospheric chemistry cannot be predicted based on findings from plants grown without competition (e.g., one plant per pot) or in monoculture.

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