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ORIGINAL ARTICLE

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Four-year growth dynamics of beech-spruce model ecosystems under CO_2 enrichment on two different forest soils

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Abstract To elucidate how atmospheric CO_2 enrichment, enhanced nutrient supply and soil quality interact to affect regrowth of temperate forests, young *Fagus sylvatica* and *Picea abies* trees were grown together in large model ecosystems. Identical communities were established on a nutrient-poor acidic and on a more fertile calcareous soil and tree growth, leaf area index, fine root density and soil respiration monitored over four complete growing seasons. Biomass responses to CO_2 enrichment and enhanced N supply at the end of the experiment reflected compound interest effects of growth stimulation during the first two to three seasons rather than persistent stimulation over the whole duration of the experiment. Whereas biomass of *Picea* was enhanced in elevated CO_2 on both soils, *Fagus* responded negatively to CO_2 on acidic but positively on calcareous soil. Biomass of both species profited from enhanced N supply on the poor acidic soil only. Leaf area index on both soils was greater in high N supply as a consequence of a stimulation early in the experiment, but was unaffected by CO_2 enrichment. Fine root density on acidic soil was increased in high N supply, but this did not stimulate soil respiration rate. In contrast, elevated CO_2 stimulated both fine root density and soil CO_2 efflux on calcareous soil, especially towards the end of the experiment. Our experiment suggests that future species dominance in beech-spruce forests is likely to change in response to CO_2 enrichment, but this response is subject to complex interactions with environmental factors other than CO_2, particularly soil type.

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Introduction

Due to fossil fuel burning and forest destruction, atmospheric CO_2 concentration is now rising at about 1.8 µl l^{-1} $year^{-1}$ (Mendelsohn and Rosenberg 1994) and is expected to double as compared to pre-industrial concentrations by the end of the 21st century (IPCC 1996). At the same time, an ever-increasing anthropogenic deposition of nitrogen (N) eliminates the clear dichotomy between pristine and human-altered ecosystems (Galloway et al. 1994; Vitousek 1994). Whether and how forest regrowth communities might respond to these environmental changes, alone or in combination, is the topic of this study. Knowledge in this field is particularly needed, since forests contain more than 80% of the total plant carbon (C) on Earth (Dixon et al. 1994; Olson et al. 1983).

There is more than ample evidence that growth in elevated CO_2 concentration can stimulate biomass gains of young trees (e.g. Ceulemans and Mousseau 1994; Norby et al. 1999; Saxe et al. 1998; Wullschleger et al. 1997). The majority of the older studies in these reviews has been conducted with seedlings or saplings, mostly growing isolated in limited rooting volumes and rarely lasting for more than 2 years. Scaling-up from such growth conditions to the real world is not straightforward (Eamus and Jarvis 1989; Körner 1995). Moreover, the overwhelming variability of biomass responses to CO_2 exposure (even within the same species) implies that interactions between environmental variables as well as between individuals of the same or of different species may play an important role in determining the outcome of such experiments (Körner 1996, 2000). In recent literature, an increasing number of longer-term experiments under more natural growth conditions is available, but our understanding of the interactions between the C and N cycles is still not sufficient (Ceulemans et al. 1999).

Further, we know of no attempt of testing such interactions on different types of forest soil and with tree species growing under intra- and interspecific competition.

Another matter, still unresolved, is whether growth responses of tree species to CO_2 enrichment will persist in the longer term or decline after an initial stimulation and return to growth rates of non-enriched plants. As discussed by Loehle (1995), CO_2-enriched trees might just exhibit an earlier approach to the same plateau of the sigmoidal growth curve than non-enriched plants. Hence, differences in biomass between ambient and elevated CO_2 grown trees at any stage of ontogeny might be due entirely to such phase shifts in phenology and therefore reflect compound interest effects of an early growth stimulation. At the same time, actual relative growth rates (RGR) may be indistinguishable experimentally, i.e. small initial differences in RGR that might propagate into large effects on absolute biomass may be hidden by experimental or biological variability (Gifford et al. 1996). Evidence of an initial CO_2 effect on the growth of tree species and subsequent convergence of RGRs over time has been found many times for seedlings or saplings growing in isolation (e.g. Bazzaz et al. 1993; Callaway et al. 1994; Centritto et al. 1999 and reviews by Bazzaz 1990; Gifford et al. 1996). Results from more natural experiments with model tree communities are sparse (e.g. Norby et al. 1995; Rey and Jarvis 1997; Tissue et al. 1996), but also do not indicate a sustained CO_2 effect on RGR.

The main objective addressed in this study is whether the greater biomass gains of trees grown in elevated CO_2 are the result of a persistent or transient stimulation of RGR, and how strongly the CO_2 response might depend on the soil type. We selected *Fagus sylvatica* L. and *Picea abies* Karst., two abundant and economically important European forest tree species (Kramer et al. 1988) which commonly occur in mature forests in Switzerland and particularly in regrowth sites. Trees were planted as saplings (2–4 years old) in large model ecosystems with nonlimiting rooting volumes, allowing trees to compete intra- and interspecifically for light, space and nutrients. This approach thus combines realistic growth conditions with the experimental feasibility to handle a complex factorial design. Communities were exposed for four complete growing seasons to atmospheric CO_2 enrichment and enhanced wet deposition of N, and, as a unique feature, the whole experiment was replicated on two different forest soils (an acidic sandy loam and a calcareous loamy sand). To our knowledge, this is the only experiment so far where soil effects and interactions between soils and CO_2 enrichment or enhanced N supply may be directly tested.

Rather than reporting responses at a given (necessarily random) point in time, the focus of this paper is on the temporal development of stands and of both tree species within stands over the 4-year experimental period (1995–1998). We use concepts of classical growth analysis and replicated measurements of key system parameters to address the following questions:

1. Do the effects of CO_2 enrichment and N fertilization on tree biomass in these 'forest gap-communities' persist over the whole duration of the experiment or are they transient (persistent stimulation vs compound-interest effects of an initial stimulation)?
2. Are biomass dynamics paralleled by corresponding effects in leaf canopy expansion (leaf area index, LAI)?
3. Do these trends correspond with soil exploration by fine roots and with overall belowground metabolism (soil respiration)?

Materials and methods

Experimental design and plant material

The interactive effects of atmospheric CO_2 enrichment, wet N deposition and two different soils on the growth of beech-spruce model ecosystems with herbaceous understorey were tested in a Latin square split-plot design in the open-top facility at Birmensdorf, Switzerland (Fig. 1). Factorial combinations of two CO_2 concentrations and two levels of wet N deposition (whole-plot treatment factors) were assigned randomly to 16 open top chambers (OTC) of 3 m diameter and height. The soil compartment of each OTC was split into two separate lysimeters (1.5 m depth and 3 m^2 net ground area each), occupying the northern and southern half of the OTC. In spring 1994, all lysimeters first received a 0.5 m bottom drainage layer of quartz sand (see Sonnleitner et al. 2001 for details). One of the lysimeters in each OTC was then filled with an acidic sandy loam (forest brown earth, derived from a Haplic Alisol on Riss moraine, classification FAO 1988), and consisted of a 0.4 m topsoil layer (pH 4.11 in 0.01 M $CaCl_2$; cation exchange capacity, extracted with 1 N NH_4Cl, 42 mmol kg^{-1} soil; N_{tot} 0.83 g kg^{-1} soil) and a 0.6 m subsoil layer (pH 3.8, CEC 60 mmol kg^{-1} soil; N_{tot} 0.30 g kg^{-1} soil). The other lysimeter was filled with a single layer of calcareous loamy sand, derived from a Calcaric Fluvisol (pH 7.16, CEC 127 mmol kg^{-1} soil; N_{tot} 0.76 g kg^{-1} soil). The calcareous soil was releasing more nutrients than the acidic soil, i.e. was more fertile. See Hagedorn et al. 2000 and Sonnleitner et al. 2001 for further details on soil properties. Both soils had been collected from natural Swiss forest sites at low altitude (350 m a.s.l.), where all experimental species co-occur naturally. The two soil types (split-plot treatment factor) were equally replicated within north- and south-oriented lysimeters within each CO_2×N treatment combination and will be referred to as 'acidic' and 'calcareous' respectively.

In order to reduce excess nutrient availability following initial soil disturbance, soils were allowed to rest for a full season with a mixed crop of oats and barley which was harvested in September 1994. In October 1994, beech-spruce model communities with understorey vegetation were established in each lysimeter. Each of these 32 model communities (Fig. 1) consisted of eight beech trees (*Fagus sylvatica* L.) and eight Norway spruce trees (*Picea abies* Karst.). Tree species will be referred to as *Fagus* and *Picea*. For the understorey, 5–6 individuals of *Carex sylvatica*, *Geum urbanum*, *Ranunculus ficaria*, *Viola sylvatica* and *Hedera helix* were planted in each model community. Such species assemblages were present at both lowland sites from where the soils were taken. All trees were similar in height at the time of planting (30–40 cm), so that there was no risk of tree height exerting any carry-over effects from pre-treatment periods. This also ensured that our treatments could interact with genotypes at equal starting states within communities. Tree saplings were transplanted directly from a common, unfertilized nursery bed into the model ecosystems, with root systems remaining intact. Individual trees within each tree species were selected to cover a wide range of genetic diversity. The *Fagus* trees had been grown from seeds collected from four Swiss low-elevation provenances, with each provenance repre-

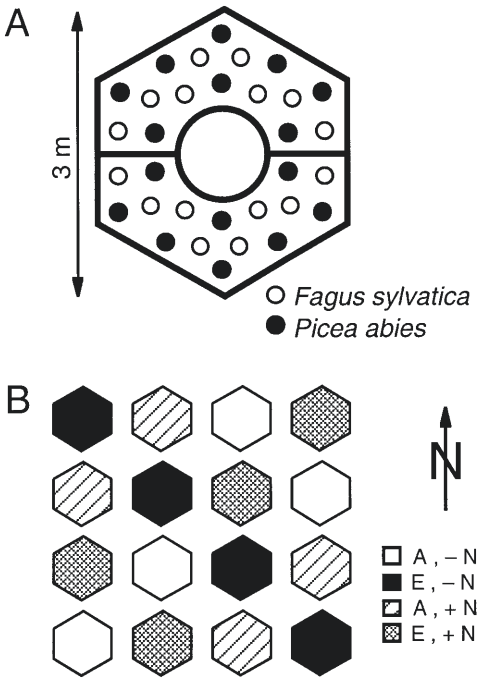

Fig. 1A, B Experimental layout. **A** Planting positions of beech and spruce trees in open-top chambers. **B** Assignment of CO_2×N treatment combinations (*A* ambient CO_2, *E* elevated CO_2, *–N* low N supply, *+N* high N supply) to the 16 chambers arranged in a Latin square array

senting a different population. Trees were either 2 or 3 years old at planting, and each of the four provenances was replicated twice per lysimeter. Two of the eight spruce trees in each lysimeter were grown from seeds and planted as 4-year-old saplings, representing two different Swiss populations. The other six individuals were well rooted clonal cuttings from different genotypes (three from Germany, two from Switzerland and one from Romania, all from low to moderate altitudes), and were 2 or 4 years old at planting. The 32 model communities were exact replicates in terms of species and provenance composition, with planting positions fixed for species but randomized for the different provenances within each species.

The CO_2 treatment was started in January 1995, with an ambient CO_2 concentration of ca. 370 µmol mol^{-1} and an elevated CO_2 concentration continually maintained at ca. 570 µmol mol^{-1} throughout the year. Natural precipitation was prevented by transparent roofs closing/opening automatically. The N treatment was applied by adding NH_4NO_3 to the irrigation water and started in June 1995 (frequent low concentration inputs). In 1995 and 1996, the amount of N deposited corresponded to 0.5 g m^{-2} year^{-1} ('low N' supply) and 5 g m^{-2} year^{-1} ('high N' supply); amounts were increased to 0.7 versus 7 g m^{-2} year^{-1} in 1997 and 1998. Our low N treatment may be close to preindustrial background supply and is clearly less than the wet N deposition rates currently experienced by forests in western Europe (1–10 g N m^{-2} year^{-1}, with 2–3 g m^{-2} year^{-1} found most commonly). Due to the wide range of current N deposition rates, it seemed reasonable to use preindustrial N deposition rates as the control treatment.

Table 1 summarizes air temperatures and simulated precipitation inside the chambers. In order to attain meaningful data on a land area basis, side light was diminished by a special coating on the glass walls of the chambers up to canopy height. For further information on the project see Landolt et al. (1997). In September 1998, after four complete growing seasons under experimental conditions, the experiment was terminated by harvesting above- and belowground plant parts.

Table 1 Climatic conditions during the 4-year experimental period: Simulated precipitation and air temperature measurements in rain sheltered open-top chambers (data from W. Landolt, WSL Birmensdorf)

	1995	1996	1997	1998
Precipitation (mm)				
Annual sum	519	694	808	744
Air temperature (°C) [a]				
Annual mean	10.6[b]	8.4	9.7	11.4[b]
Mean April – September	15.6	14.8	15.5	15.8
T_{min}	–2.7	–5.0	–4.7	–2.5
T_{max}	32.0	27.0	30.1	27.9

[a] Air temperature inside open-top chambers measured between February 1995 and September 1998. Data are based on half hourly means of readings taken every 3.3 s. T_{min} and T_{max} are the monthly means of the daily extremes of the coldest and warmest month
[b] Annual means for 1995 and 1998 include only part of the cold period and are therefore overestimates

Tree growth dynamics

Whole-tree dry mass (sum of aboveground plant parts and main root system) at the end of the experiment was available from final harvest in September 1998. Dry mass at the beginning of the experiment was determined through fresh weights measured on all saplings prior to planting (roots had been washed to remove dirt). Factors for conversion to dry weights were calculated as 0.45 for *Fagus* and 0.38 for *Picea* using dry/fresh weight ratios of surplus trees left over at planting. Tree masses in 1995, 1996 and 1997 were obtained biometrically from stem basal area. At final harvest, we cut a stem slice from each individual tree at 10 cm above ground and calculated (elliptical) basal area from two orthogonal diameters per tree ring. Strong correlations between dry mass and basal area for both species on both soils (correlation coefficients around 0.95 at final harvest and around 0.82 for planted saplings) indicated good predictability of dry mass from stem basal area irrespective of tree size. End-of-season dry masses in 1995, 1996 and 1997 were then calculated separately for each individual tree as the weighted means

$$M_i = B_i[w_i M_{1994}/B_{1994} + (1-w_i)M_{1998}/B_{1998}] \quad (1)$$

where M_i and B_i denote whole-tree mass and basal area respectively at the end of season i (i=1995, 1996 or 1997) and the weighting factors w_i were chosen arbitrarily as w_{1995}=0.75, w_{1996}=0.50 and w_{1997}=0.25.

Leaf canopy development

Leaf canopy development was studied non-destructively by measurements of light interception, well after completion of leaf development in early summer but prior to leaf senescence in autumn. The exact measurement dates were 11 August 1995, 31 July 1996, 15 October 1997 and 1 September 1998. Light levels above and below canopy were measured by means of a radiometer (CEP-80, Delta-T Devices, Burwell, UK) which integrates readings across an 80 cm horizontal line. Four such measurements near the centre of each lysimeter were averaged to account for small-scale variations. LAI was calculated from the Beer-Lambert model $I=I_0\ e^{-k\ LAI}$, where I_0 and I are light levels above and below the canopy respectively, and k is the extinction coefficient. The value of k was determined via calculating leaf area at final harvest from total leaf biomass and specific leaf area (M. Günthardt-Goerg, unpublished data) for both tree species. To these values we added estimates for the projected area of stems and branches, based on stem basal area and measurements of stem height. We found that the mean of this total light absorbing plant area (averaged across all treatments)

was matched by the mean LAI as obtained from light interception measurements if k=0.714. Any error in k (e.g. due to chamber influences) would cause the same proportional error in all treatments and hence not affect the outcome of the statistical analysis of the LAI data.

Classical growth parameters

Methods of classical growth analysis were applied to both tree species. Since RGR, the rate of dry mass increase per unit of dry mass present and per unit time, is only defined at instants of time, we used the concept of 'mean RGR' over an interval of time. According to Causton and Venus (1981), mean RGR between two consecutive determinations of biomass (M) at times t_1 and t_2 is calculated as

$$\text{Mean RGR} = [\ln(M_2) - \ln(M_1)] / (t_2 - t_1) \quad (2)$$

where the denominator simplifies to unity for annual time steps. Moreover, mean RGR in the last experimental season (1998) could be factored into LAR (leaf area ratio, the amount of leaf area per unit of whole-tree mass) and CPI (canopy productivity index, the annual production of whole-tree mass per unit of leaf area, see Norby 1996). LAR is generally regarded as the morphological component of RGR, indicating changes in allocation of biomass to the photosynthetic machinery and therefore describing the balance between the capacity for C assimilation and the respiratory load of the plant. In contrast, CPI is a functional parameter and serves as an analogue to the well-known net assimilation rate (the amount of dry mass produced per unit of leaf area and per unit time) which is not applicable to our annual time steps since it is defined at instants of time only.

Soil exploration by fine roots

Soil exploration by fine roots was monitored by the coring method. A first measurement of fine root density had been conducted in November 1995 (see Egli and Körner 1997 for details). Measurements were repeated in November 1997 and in late August 1998 by taking three soil cores (diameter 3.5 cm, length 42 cm) per lysimeter. Coring positions were chosen at a distance of at least 20 cm from tree stems. Coring holes were filled with spare soil and labelled to avoid re-coring. Soil cores were washed and tree roots collected by hand. Fine roots of trees in the 1998 cores were sorted into beech and spruce fractions. When classification of tree roots to either beech or spruce was doubtful, roots were categorized as 'not identified'. Dead roots (with dark brown to black colour and loss of integrity) and roots whose diameter exceeded 2 mm were removed from fine root samples. After oven-drying at 80°C for 24 h, the 'not identified' category (on average 23% of total fine root dry mass) was allocated to beech and spruce proportionally to the ratio of identified beech and spruce fractions in each of the eight soil×CO_2×N treatment combinations. Tests have shown that including or excluding the unidentified fine root category did not affect our conclusions.

Metabolic belowground activity

As an integrative measure of overall metabolic belowground activity, we measured CO_2 efflux from soils in situ at daytime. In November 1995 we took one and in September 1996 two measurements per lysimeter with the EGM-1 soil respiration system (PP-Systems, Hitchin, Herts, UK). In September 1997 and August 1998, three measurements per lysimeter were taken with a custom-built static system in order to avoid the well-known pressurization problems (Lund et al. 1999) of dynamic (flow-through) systems. Cuvettes (semi-transparent PVC, 10.4 cm diameter, 7.5 cm height) were placed on vegetation-free ground, paying special attention to minimal soil disturbance. CO_2 concentration in the cuvette headspace was determined by taking air samples through a diaphragm using 1-ml medical syringes. Samples were then injected into a closed system carrying air of ambient CO_2 concentration and consisting of an infrared gas analyser (Li 6252, Li-Cor, Lincoln, Neb., USA) and a small pump (50 ml min^{-1}). The soil respiration rate was calculated from the increase of the CO_2 concentration between two air samples taken immediately after sealing the cuvette and 4 min after sealing. Validation of this procedure has shown that the CO_2 concentration inside the cuvette headspace increased linearly for 5 min after sealing, with significant saturation effects emerging not before 6–7 min after sealing. Cross-calibration of the dynamic and the static system revealed that rates measured with the dynamic system were on average 28% higher. To make these rates comparable to those from the static system, we corrected the 1995 and 1996 data by dividing respiration rates through 1.28. This correction affects neither relative differences between treatments nor statistical data analysis.

Statistical analysis

As the experimental units in this study are the lysimeters, all data (individual tree masses, individual soil cores, single measurements of soil respiration) were averaged within lysimeters and statistical analyses conducted with these lysimeter means. Effects of CO_2 enrichment, enhanced N supply and their interaction were analysed separately for the acidic and the calcareous soil using 16 lysimeter means. In addition to these soil-specific analyses, effects of soil type and its interactions with CO_2 and N were tested in an overall analysis comprising the whole set of 32 lysimeter means. Latin square blocking factors (row, column) and orientation of lysimeters within chambers (north vs south) were removed from the models if they were not significant (P>0.1). Within this framework, series of annual measurements of whole-tree mass, LAI and soil CO_2 efflux were analysed by repeated measures analysis of variance (ANOVA), using procedure GLM of SAS (release 6.08, SAS Institute, Cary, N.C., USA) and type I sums of squares. Hence, overall treatment effects (between subjects effects) are tested by pooling across all temporal replicates for each subject. Interactions between treatments and year (within-subjects effects) are used to test for parallelism between the time courses of a trait under different treatment combinations. Following the test procedure outlined by Potvin et al. (1990), we tested within-subjects effects either by univariate or by multivariate repeated measures ANOVA, depending on whether the variance-covariance matrix was symmetric or not. The multivariate test has a lower statistical power but is more robust than its univariate counterpart because it makes less stringent assumptions about the correlation structure. If the within-subjects effects for biomass were statistically significant, we conducted single-degree-of-freedom contrasts to compare each measurement date with the first measurement date in the series. This allowed us to determine the point in time when treatments began to diverge. Other data (mean RGR, percentage increases of LAI, fine root density, LAR and CPI) were analysed by calculating separate ANOVAs for each (annual) measurement date (Genstat 5, Release 3.1, Lawes Agricultural Trust, Rothamsted Experimental Station, UK). As the residuals did not deviate substantially from normal distribution and homoscedasticity, all analyses were conducted with untransformed data.

Results

Dynamics of tree growth

Whole-tree mass (sum of aboveground plant parts and main root system) of both species on both soils increased exponentially during the first two to three experimental seasons, after which growth rates began to slow down (Fig. 2). Repeated measures analysis (Table 2) of growth curves has shown that CO_2×N interactions were statistically insignificant, suggesting that CO_2 enrichment and

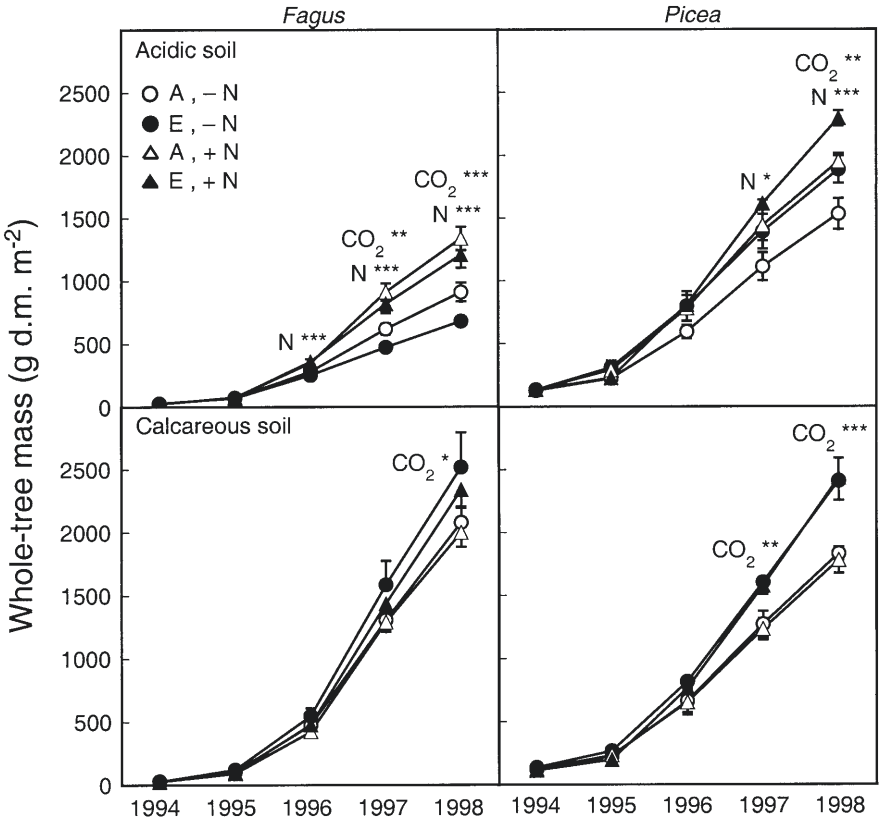

Fig. 2 Whole-tree mass per unit land area in beech-spruce model ecosystems from planting in 1994 to final harvest in 1998. Each *point* represents the mean (± 1 SE) of four model ecosystems in one of the four combinations of two CO_2 treatments (ambient, *A*, vs elevated, *E*) and two N treatments (*–N* vs *+N*). *Error bars* smaller than the symbols are not visible. Series were analysed by repeated measures analysis (see Table 2). *Stars* indicate statistical significance of CO_2 and N main effects in within-subject contrasts that compare each measurement date with the 1994 baseline: * (P<0.05), ** (P<0.01), *** (P<0.001). There were no significant CO_2×N interactions for these contrasts

enhanced N supply were additive in their effects on biomass. Hence, interpretation of main effects (between-subjects effects) is straightforward. However, as growth curves for individual treatments diverged progressively over time (significant year×treatment interactions, Table 2) these main effects are primarily due to the large differences in biomass that were observed between treatments in the last two experimental seasons.

Biomass of *Fagus* on acidic soil was decreased (!) in elevated CO_2. This effect was evident from the third season on (within-subjects contrasts, Fig. 2) and was more pronounced in low N (–24%) than in high N supply (–10%). In contrast, biomass of *Picea* on acidic soil was 17–20% greater due to CO_2 enrichment from the second season on, but only the 1998 data differed significantly from the 1994 baseline. Growth of both species on this nutrient-poor soil was strongly stimulated by enhanced N supply, with effects emerging after the first season and being stronger in *Fagus* (+5%, +32%, +58%, +60% in 1995–1998) than in *Picea* (–3%, +14%, +22%, +24% in 1995–1998). On calcareous soil, CO_2 enrichment affected biomass of *Fagus* only marginally (14–19% stimulation in every season), whereas *Picea* on the same soil was highly responsive to elevated CO_2, especially towards the end of the experiment (+2%, +20%, +27%, +34% in 1995–1998). On the other hand, enhanced N supply on this nutrient-rich soil did not affect biomass.

Growth on calcareous soil stimulated biomass of *Fagus* more than any other treatment factor (+39%,

Table 2 *P* values from repeated measures analysis conducted on series of whole-tree mass per unit land area in beech-spruce model ecosystems (M_{Fagus}, M_{Picea}, Fig. 2), leaf area index of stands (*LAI*, Fig. 4) and in situ soil CO_2 efflux rates (*R*, Fig. 6). *P*-values for the year main effect were always <0.001. *P*-values <0.05 are in bold

	M_{Fagus}	M_{Picea}	LAI	*R*
Acidic soil				
CO_2	**0.003**	**0.035**	0.110	0.206
N	**<0.001**	**0.022**	**<0.001**	0.105
CO_2×N	0.232	0.465	0.367	0.324
Year×CO_2	**0.014**	**0.040**	0.262	0.630
Year×N	**<0.001**	**0.008**	**<0.001**	0.814
Year×CO_2×N	0.151	**0.019**	0.267	0.858
Calcareous soil				
CO_2	0.060	**<0.001**	0.239	**0.001**
N	0.392	0.617	**0.003**	0.251
CO_2×N	0.708	0.907	0.136	**0.029**
Year×CO_2	**0.020**	**0.015**	0.648	**0.009**
Year×CO_2×N	0.533	0.487	0.082	**0.017**
Overall soil effects				
Soil	**<0.001**	0.325	**<0.001**	**0.002**
Soil×CO_2	**0.008**	0.260	0.128	0.332
Soil×N	**0.003**	**0.017**	0.754	0.168
Soil×CO_2×N	0.487	0.560	0.179	0.425
Year×soil	**<0.001**	0.063	**<0.001**	0.123
Year×soil×CO_2	**<0.001**	0.493	0.619	0.565
Year×soil×N	**<0.001**	0.125	**0.002**	0.694
Year×soil×CO_2×N	0.772	0.639	0.423	0.376

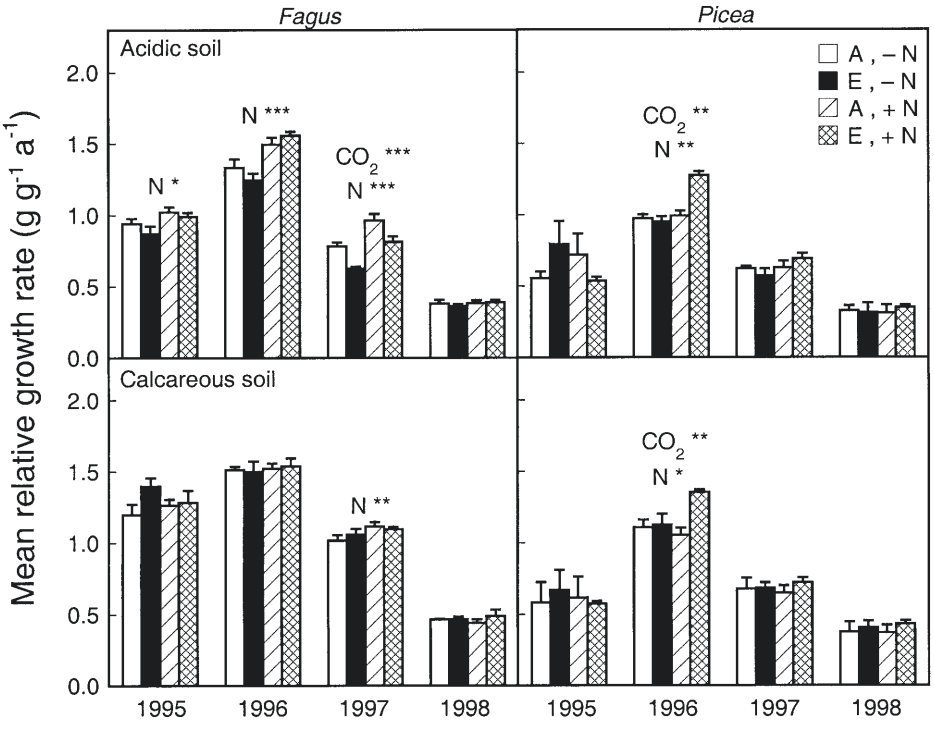

Fig. 3 Annual mean relative growth rates of whole-tree mass per unit land area in beech-spruce model ecosystems. Each *bar* shows the mean (+1 SE) of four model ecosystems in one of the four combinations of two CO_2 treatments (ambient, *A*, vs elevated, *E*) and two N treatments (*–N* vs *+N*). Stars indicate statistical significance of CO_2 and N main effects from separate ANOVAs for each yearly dataset: * ($P<0.05$), ** ($P<0.01$), *** ($P<0.001$). Except for *Fagus* on calcareous soil, all CO_2×N interactions in 1996 were significant

+54%, +99%, +116% in 1995–1998, relative to acidic soil). In the 4 years between planting and final harvest, biomass of *Fagus* increased 36-fold (from 29 to 1,036 g m^{-2}, averaged across CO_2 and N treatments) on acidic and 77-fold (from 29 to 2,236 g m^{-2}) on calcareous soil. This strong soil effect in *Fagus* contrasts to the minor and non-significant one in *Picea*. Over the whole duration of the experiment, biomass of *Picea* increased 14-fold (from 133 to 1,913 g m^{-2}) on acidic and 17-fold (from 121 to 2,114 g m^{-2}) on calcareous soil (the small initial difference between soils was purely accidental and did not affect the outcome of the experiment). Note that the difference between initial masses of *Fagus* and *Picea* was similar on both soils, suggesting that the substantially smaller 'final' mass attained by *Fagus* on acidic soil is not an artefact of its smaller initial mass. As direction and size of CO_2 and N effects in most cases differed between soils, the corresponding soil×CO_2 or soil×N interactions were statistically significant (Table 2).

Temporal pattern in mean RGR

Irrespective of CO_2 or N treatment, mean RGRs of both species on both soils peaked in the second season and then declined substantially (Fig. 3). Mean RGRs were lower in the first than in the second season, which most likely results from the planting shock when the 2- to 4-year-old tree saplings were transferred into the model ecosystems. Mean RGR was always higher in *Fagus* than in *Picea*, especially in the first three seasons, when canopy density had not yet reached its maximum. This difference between species was greater on calcareous soil, i.e. *Fagus* grew faster on calcareous than on acidic soil, whereas growth rate of *Picea* was similar on both soils.

A principal finding of our study was that both CO_2 enrichment and enhanced N supply affected mean RGR in one or several of the first two to three experimental seasons but not anymore in 1998, the fourth year of treatment (Fig. 3). It is important to recognize that due to compound interest effects even minor and statistically non-significant differences in mean RGR between treatments early in the experiment can generate major differences between absolute tree masses in later seasons. Effects on mean RGR thus are the more important the earlier they occur in the course of the experiment.

On acidic soil, the negative CO_2 and the positive N effect on the biomass of *Fagus* as observed at the end of the experiment were due to corresponding effects on mean RGR throughout the first three seasons. In contrast, mean RGR of *Picea* on acidic soil was stimulated by CO_2 and N in the first season only, i.e. in a very early phase of canopy development when there was ample space and light for each individual tree. When CO_2 enrichment was applied in combination with enhanced N supply, mean RGRs of both species were strongly stimulated in the second, but not in the first experimental season. Hence, there was a time-lag between the effects of the combined versus separate application of elevated CO_2 and high N supply. On the nutrient-rich calcareous soil, the greater biomass gains of both species in elevated CO_2 were caused by stimulation of mean RGRs in the first season only. In *Picea*, however, combined applica-

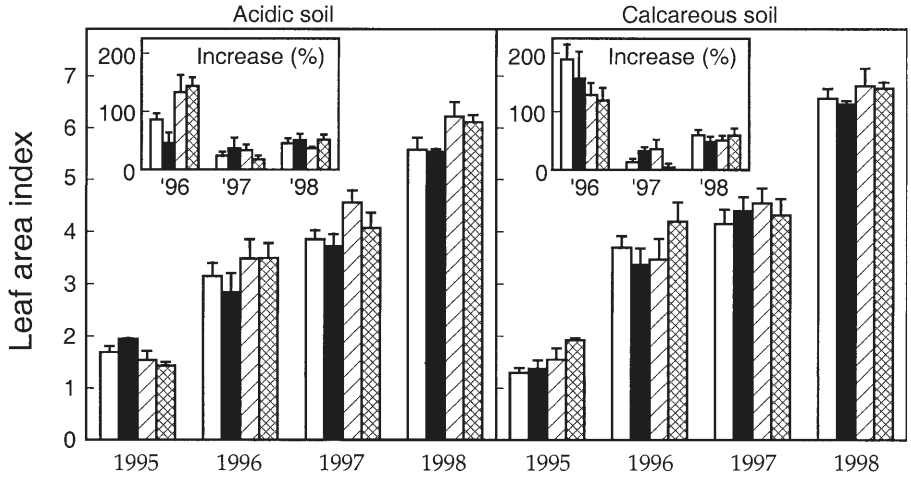

Fig. 4 Four-year trends in leaf area index (LAI) of beech-spruce model stands. Each *bar* shows the mean (+1 SE) of four model ecosystems, legend as in Fig. 3. Series were analysed by repeated measures analysis (see Table 2). Insert graphs show percentage increases of LAI in each year relative to the preceding year. For these %-increments the N main effect in 1996 on acidic soil was statistically significant (ANOVA, P=0.003)

Table 3 Leaf area index (*LAI*), leaf area ratio (*LAR*) and canopy productivity index (*CPI*) of *Fagus* and *Picea* in 1998, after 4 seasons growth under experimental conditions. Each number is the mean (±SE) of four model ecosystems in one of the four combinations of two CO_2 treatments (ambient, *A*, vs elevated, *E*) and two N treatments (*–N* vs *+N*). Statistical significance (*P* values) from ANOVA and percent main effects in italics (*n.s.* if P>0.05). CO_2×N and soil×CO_2×N interactions were never significant

	LAI (m^2 m^{-2})		LAR (m^2 kg^{-1})		CPI (g m^{-2} a^{-1})	
	Fagus	*Picea*	*Fagus*	*Picea*	*Fagus*	*Picea*
Acidic soil						
A, –N	2.3±0.2	3.4±0.3	21.1±1.8	17.9±0.6	15.4±2.5	16.6±1.3
E, –N	1.9±0.1	3.6±0.1	22.4±0.7	15.5±0.7	13.6±0.6	17.0±3.1
A, +N	2.9±0.2	3.3±0.1	17.2±0.7	13.8±0.4	18.5±0.5	19.1±2.5
E, +N	2.6±0.2	3.6±0.1	17.1±1.0	12.7±0.7	22.2±4.2	23.8±3.2
CO_2	*0.004 (–16%)*	*0.048 (+8%)*	*n.s.*	*0.015 (–8%)*	*n.s.*	*n.s.*
N	*<0.001 (+34%)*	*n.s.*	*<0.001 (–22%)*	*<0.001 (–19%)*	*0.005 (+30%)*	*n.s.*
Calcareous soil						
A, –N	3.6±0.1	2.9±0.2	14.1±0.3	12.7±0.4	26.5±0.7	24.1±4.1
E, –N	3.5±0.3	2.9±0.3	11.3±0.6	9.7±0.4	30.3±3.5	34.2±2.4
A, +N	4.0±0.2	2.9±0.2	16.0±1.1	12.8±0.5	22.7±2.1	23.7±2.3
E, +N	3.7±0.2	3.1±0.2	12.7±0.3	10.0±0.4	31.4±3.5	34.9±1.7
CO_2	*n.s.*	*n.s.*	*<0.001 (–20%)*	*<0.001 (–23%)*	*0.003 (+30%)*	*0.002 (+45%)*
N	*n.s.*	*n.s.*	*0.029 (+13%)*	*n.s.*	*n.s.*	*n.s.*
Soil effects						
Soil	*<0.001 (+53%)*	*<0.001 (–16%)*	*<0.001 (–31%)*	*<0.001 (–24%)*	*<0.001 (+71%)*	*<0.001 (+54%)*
Soil×CO_2	*n.s.*	*n.s.*	*0.002*	*0.022*	*0.002*	*<0.001*
Soil×N	*n.s.*	*n.s.*	*<0.001*	*<0.001*	*0.021*	*n.s.*

tion of CO_2 and N gave rise to the same time-lag phenomenon as on acidic soil, i.e. the two treatments cancelled each other in the first, but strongly stimulated mean RGR in the second season.

Development of the leaf canopy

By final harvest in late 1998 canopies had become very dense, with trees ca. 2 m high and exploiting all available chamber space. Light availability below canopies had decreased so strongly that most of the understorey species suffered badly or had died by the third or fourth experimental season (P Egli, unpublished data). The average amount of light transmitted through the canopies was 33% in 1995, 9% in 1996, 5% in 1997 and 1% in 1998, which comes close to the minimum in natural forests.

While LAI of tree stands (Fig. 4) on the nutrient-poor acidic soil was not affected by CO_2 enrichment, LAI responded positively to enhanced N supply from the second season on (–18%, +16%, +14%, +11% in 1995–1998). Across all seasons, the positive N main effect was highly significant (repeated measures analysis, Table 2). Due to the delayed initiation of the N treatment in 1995 at mid-season, i.e. well after leaf emergence, the N effect in the first season must be interpreted with caution. Between the first and the second season, the relative increase in LAI (inserts in Fig. 4) was significantly greater in high N supply (+138%) than in low N supply (+66%), whereas no such difference was found later on. The greater LAI in high N supply is thus the conse-

quence of a stimulation of leaf area in the second season. Species-specific LAI values were available for 1998, the last season, and show that the N effect on stand LAI was entirely due to a response in *Fagus* and that opposite CO_2 effects on LAI of *Fagus* and *Picea* completely cancelled each other (Table 3).

On calcareous soil, LAI was not affected by CO_2 enrichment (CO_2 main effect across all seasons not significant), but was greater in enhanced N supply, especially in the first season (+31%, +9%, +4%, +4% in 1995–1998). Across all seasons, the positive N main effect was significant (repeated measures analysis, Table 2). The relative increase in LAI from one season to the next never differed significantly between low and high N supply, indicating that the greater LAI in high N supply was due to a stimulation in the first season only.

From the second season on, LAI was always greater on calcareous than on acidic soil (-4%, +14%, +8%, +13% in 1995–1998). Averaged across all treatments, LAI values on the two soils were 5.9 and 6.6 by the end of the experiment. Species-specific LAIs also differed between soils, with *Fagus* contributing 41% to stand LAI on acidic and 56% to stand LAI on calcareous soil. N-effects were similar on both soils (no soil×N interaction).

LAR and CPI in 1998

Mean RGR of the last season (1998) was factored into LAR (the amount of leaf area per unit of whole-tree mass) and CPI (annual biomass increase per unit of leaf area; Table 3). On acidic soil, CO_2 enrichment slightly increased LAR of *Fagus* (+7%, not significant), but decreased LAR of *Picea* (–8%), whereas enhanced N supply decreased LAR of both species (*Fagus*: –22%, *Picea*: –19%). On calcareous soil, CO_2 enrichment decreased LAR of both species (*Fagus*: –20%, *Picea*: –23%), whereas high N supply stimulated LAR of *Fagus* only (+13%). Treatment effects in LAR were thus exactly opposite to the effects that had been observed in biomass (only *Fagus* on calcareous soil does not quite fit this scheme), indicating that trees that had grown larger due to any treatment, invested less biomass into the photosynthetic machinery. Since mean RGR was indistinguishable between CO_2 and N treatments in 1998, any effect in LAR was equilibrated by a corresponding (opposite) effect in CPI. Opposite responses of LAR and biomass were also observed with respect to soil, with LAR being smaller on calcareous than on acidic soil (*Fagus*: –31%, *Picea*: –24%), whereas CPI was greater on calcareous soil (*Fagus*: +71%, *Picea*: +54%).

Belowground development

Between the first and the last experimental season, fine root density in the upper 42 cm of the soil horizon had increased 5- to 6-fold on acidic and 2- to 4-fold on calcareous soil (Fig. 5). In the first season, Egli and Körner (1997) had found no fine roots below 20 cm depth, and by the end of the experiment most fine roots were still confined to the uppermost 20 cm of the soil horizon (ca. 70% on acidic and ca. 85% on calcareous soil, relative to the total fine root mass present in the upper 42 cm).

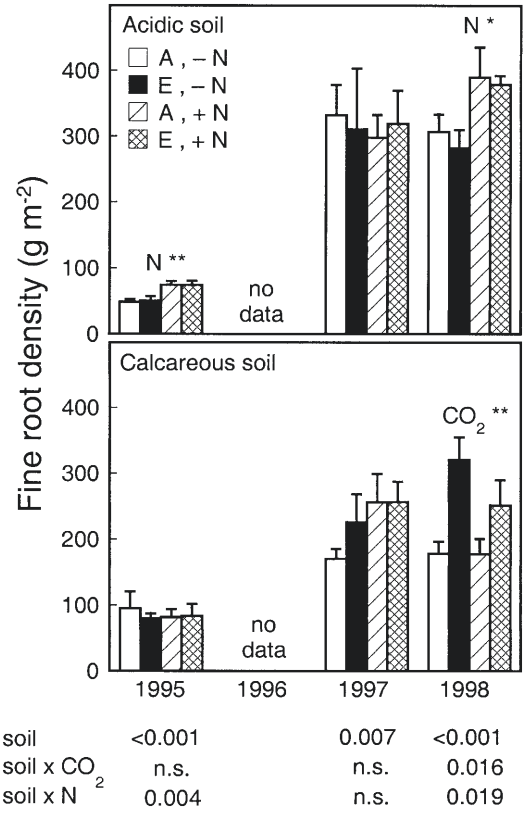

Fig. 5 Fine root density (fine roots <2 mm, g d.m. m^{-2}) in beech-spruce model ecosystems as measured by soil cores in November 1995 (Egli and Körner 1997), November 1997 and August 1998 (depth 42 cm). Each *bar* represents the mean (+1 SE) of four model ecosystems in one of the four combinations of two CO_2 treatments (ambient, *A*, vs elevated, *E*) and two N treatments (*–N* vs *+ N*). *Stars* indicate statistical significance of CO_2 and N main effects from separate ANOVAs for each annual dataset: * (P<0.05), ** (P<0.01). *P* values for soil effects are shown below graph ('n.s.' if P>0.05). Soil×CO_2×N interactions were never significant

Fine root density on the nutrient-poor acidic soil was not affected by CO_2 enrichment, but was strongly stimulated by enhanced N supply in the first and in the last experimental season (1995: +50%, 1998: +30%). There was no N effect in 1997. Separation of fine roots by species (data not shown) revealed that the N effect in 1998 was principally due to *Fagus* (+36%, P=0.012) and was statistically insignificant in *Picea*. On calcareous soil, a CO_2 effect on fine root density was emerging over the course of the experiment. The effect became apparent in the third season (+13%, not significant) and was significant in the fourth season (+61%). This CO_2 effect was caused mainly by *Picea* (+71%, P=0.004), but it was marginally significant (P<0.1) also for *Fagus* when sampling depth was extended from 42 cm to the whole pro-

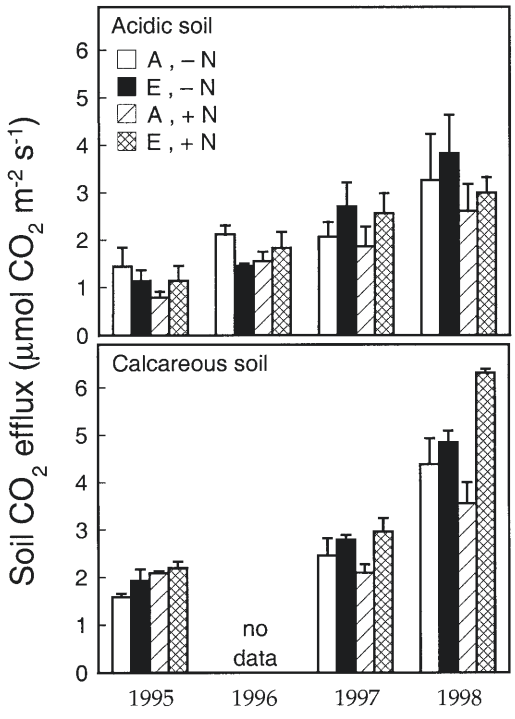

Fig. 6 In situ soil CO_2 efflux from beech-spruce model ecosystems. Measurements were taken at daytime near the end of the 1995–1998 seasons. Each *bar* shows the mean (+ 1 SE) of four model ecosystems in one of the four combinations of two CO_2 treatments (ambient, *A*, vs elevated, *E*) and two N treatments (*–N* vs *+N*). Series were analysed by repeated measures analysis (see Table 2)

file depth of 1 m (P. Egli, unpublished data). This is related to the fact that *Fagus* had grown substantially deeper roots than *Picea* (personal observation at final harvest). Enhanced N supply did not affect fine root density on this nutrient-rich calcareous soil.

Throughout the experiment, there was a statistically significant difference in fine root density between the two soils. But whereas fine root density in 1995 was greater on calcareous soil (+37%), the opposite was true in 1997 (–28%) and in 1998 (–32%). The latter effect was entirely caused by *Fagus*, whose fine root mass in the upper 42 cm was 77% smaller ($P<0.001$) on calcareous than on acidic soil. This effect did not disappear when sampling depth was extended to 1 m (P. Egli, unpublished data). In contrast, fine root density of *Picea* was similar on both soils.

In summary, responses of fine root density to CO_2 or N treatment in 1998 were similar to responses of whole-tree mass. However, only those treatment combinations which stimulated whole-tree mass most strongly also exerted statistically significant effects on fine root density (i.e. the N treatment on acidic soil and the CO_2 treatment on calcareous soil). The only major difference between responses of whole-tree mass and fine root density concerned the soil effect in *Fagus*, indicating that the fine root fraction (fine root mass/whole-tree mass) of *Fagus* was greater on acidic than on calcareous soil, whereas no such difference existed in *Picea*.

Rates of in situ soil CO_2 efflux on acidic soil were not significantly affected by CO_2 or N (Fig. 6, Table 2), although there was a tendency towards higher rates in elevated CO_2 in the second half of the experiment. In contrast, soil respiration rates on calcareous soil were significantly enhanced in elevated CO_2, and this CO_2 effect increased over the course of the experiment. Throughout the experiment, soil respiration rates were significantly higher on calcareous than on acidic soil (+69% in 1995, +12% in 1997, +53% in 1998). On both soils and irrespective of CO_2 or N treatment, soil respiration rates were increasing over the course of the experiment, but this increase might be related in part to interannual differences in soil temperature.

Discussion

Temporal patterns in tree growth

In this 4-year study we aimed at documenting above- and belowground development of beech-spruce model ecosystems in an expansive phase of growth. The most striking feature in the temporal growth pattern of both tree species on both soils was that CO_2 enrichment affected mean RGRs in an early phase of the experiment only. Later on, as stands became increasingly dense and approached maximum natural LAI (see below), mean RGRs converged between ambient and elevated CO_2 and became virtually indistinguishable towards the end of the experiment. This transient nature of the CO_2 effect implies that any differences in whole-tree mass as observed at the end of the experiment reflect compound interest effects of a stimulation in a restricted period early in the experiment.

Further, and equally important, these temporal growth patterns varied between species and soils. For instance, on the nutrient-poor acidic soil, mean RGR of *Fagus* was decreased due to CO_2 enrichment, and this reduction was evident throughout the first three seasons. In the other three species×soil combinations tested, biomass got increasingly larger in CO_2 enriched trees from season to season, but this was due to first year stimulation only.

We suggest that the observed convergence of mean RGRs between ambient and elevated CO_2 over time is in part related to a more rapid progression of trees through early ontogenetic stages. If growth is accelerated due to any treatment, the fraction of photosynthetically active tissues declines faster than in untreated trees and proportionally more mass is sequestered into supporting and conducting tissues (Loehle 1995; Poorter 1993). Moreover, such acceleration of phenology leads to a faster increase in self-shading. As it is well known that CO_2 enrichment exerts the largest effect in deep shade due to the shift of the light compensation point, the increased self-shading and the observed decrease in mean RGR point at a decreasing CO_2 sensitivity of our trees. According to Gifford et al. (1996), early differences in RGR will disappear inevitably due to the mathematics of

growth that is departing from the initial exponential phase (even without any metabolic acclimation to CO_2 enrichment; see below). So in essence, what we see in our experiment is an initial out-of-phase phenomenon of sigmoid growth curves in ambient and elevated CO_2 which eventually may reach the same plateau.

The time span over which growth rates were affected by CO_2 enrichment was longest for *Fagus* on acidic soil, i.e. in the species×soil combination which had attained the smallest biomass at the end of the experiment. We suggest that this prolonged treatment effect on mean RGR is related to the substantially slower growth of these trees. Due to their less rapid progression through early growth stages, it can be expected that convergence of growth rates between ambient and elevated CO_2 is also delayed.

Indications of transient growth stimulation by elevated CO_2 have been found in several other experiments with tree species, and the time spans for which RGRs were stimulated by CO_2 enrichment varied considerably between experiments. In seedlings of *Pinus ponderosa* (Callaway et al. 1994) and *Prunus avium* (Centritto et al. 1999), differences in RGR between treatments occured only during the first 1–2 months of CO_2 exposure. In young *Quercus alba* (Norby et al. 1995), *Picea sitchensis* (Centritto et al. 1999) and *Pinus taeda* (Tissue et al. 1997) trees, CO_2 stimulation of RGR was evident during the first season only and not sustained later on. In an experiment with five different tree species grown from seedling stage in containers, Bazzaz et al. (1993) found that final biomass gains in elevated CO_2 grown plants were largely due to higher growth rates during the first year of CO_2 exposure. Moreover, species' growth enhancements declined at different rates, but had not disappeared completely even after 3 years of CO_2 exposure. A less rapid convergence of RGRs was observed in *Betula pendula* seedlings, where the CO_2-induced enhancement of RGR had vanished only after three growing seasons (Rey and Jarvis 1997). The only truly long-term study under field conditions available to date was conducted on mature *Quercus ilex* trees growing for 30 years around two natural CO_2 springs (Hättenschwiler et al. 1997b). The authors report that CO_2-induced growth enhancements were largely due to responses when trees were young and gradually disappeared over 25–30 years at both test sites.

Our experiment also has shown that growth of both *Fagus* and *Picea* was N-limited on the nutrient-poor acidic soil, whereas enhanced N supply did not stimulate tree growth on the richer calcareous soil. Temporal patterns of N-induced growth stimulation on acidic soil tightly matched those observed for the CO_2 treatment, i.e. differential effects of low or high N supply on mean RGR were restricted to the first three seasons (*Fagus*) or to the first season only (*Picea*). Later on, mean RGR in high N supply converged with that in low N supply. We suggest that the transient nature of the N stimulus on acidic soil is related to accelerated phenology and a concomitant increase in self-shading. This effect was further enhanced by accelerated canopy formation, as LAI was greater in high N supply from the second season on (see below). Since the N treatment had been started only by the end of June in the first season, it is likely that N-induced stimulation of mean RGR in the first season would have been even larger had the N treatment been initiated earlier in that season.

Any stimulation of mean RGR due to the combined application of elevated CO_2 and high N supply was restricted to the second experimental season, which was the first year with a full season N treatment. Hence, there was a time-lag between the effects of the separate application of CO_2 or N (as discussed above) and the effects of the combined application. We have no explanation for this phenomenon, except that it reflects an interaction between the two treatments which was strongest in the second year, after trees had overcome the initial planting shock. Later on, stimulation of mean RGRs also disappeared, a fact which is most likely due to accelerated development and increased self-shading of the stands. In the fourth year of treatment, Hagedorn et al. (2000) found that elevated CO_2 reduced the concentration of soil solution nitrate by increased N immobilization, as it had done in several other experiments (Diaz et al. 1993; Hättenschwiler and Körner 1998; Niklaus et al. 1998). This effect was observed on both soils, but it was greater when elevated CO_2 was combined with high N supply on acidic soil. We therefore speculate that such effects on soil N availability may have added to the negative effect of accelerated phenology and self-shading on mean RGR.

Canopy expansion

LAI is a major vegetation variable which influences important ecosystem-level processes such as transpiration and CO_2 gas exchange (e.g. Körner 1994). Any effects of CO_2 enrichment or enhanced N supply on LAI will therefore play a central role in future forest regrowth. A major objective of this study was to document leaf area expansion of beech-spruce model ecosystems over the entire duration of the experiment and relate LAI development to temporal growth patterns of trees.

Our results show that stand LAI on both soils was not affected by CO_2 enrichment but responded positively to enhanced N supply. Similar to the temporal pattern observed for whole-tree mass, the N effect on LAI was caused by stimulation in an early phase of the experiment (second season on acidic soil, first season on calcareous soil). However, there was no compound interest effect of this early stimulation, as the (relative) effect was getting progressively smaller towards the end of the experiment. It is beyond the scope of this experiment to decide whether the N effect still present in the last season represents greater steady-state LAI of stands receiving high N supply, or is merely due to accelerated canopy formation without affecting the ultimate state. LAI of stands had reached values of around 6 in the fourth sea-

son, and light transmittance through canopies had decreased to around 1% of above-canopy values, which is typical for dense natural forests. As it is unlikely that LAI could increase much further, we can reasonably assume that canopy density in the fourth season was close to steady state. For comparison, LAI of multi-species tropical model communities under relatively fertile growth conditions saturated at values between 6.5 and 7 (Körner and Arnone 1992), and nutrient-limited model communities of tropical plant species reached steady-state LAI at values around 4 (Arnone and Körner 1995), in both cases unaffected by CO_2.

There is only a small number of other studies reporting CO_2 effects on LAI of whole tree stands, but in none of these had LAI reached steady state. In a 4-year experiment with *Pinus taeda* on a highly fertile soil (Tissue et al. 1997), development of biomass as well as LAI in elevated CO_2 grown trees was always ahead of those in ambient CO_2, with largest relative differences early in the experiment. Later CO_2 effects on biomass are explained by compound interest effects of an early stimulation of LAI. In contrast, Hättenschwiler and Körner (1998) found LAI of *Picea abies* model communities to be reduced after 3 years in elevated CO_2, whereas ecosystem biomass was not affected. The authors attribute the lack of a growth response to CO_2 to CO_2-induced nutrient shortage and physiological down-regulation of the assimilation capacity. Similarly, LAI in model communities of tropical tree species was reduced after 6 months' growth in elevated CO_2, with no change in biomass (Lovelock et al. 1998).

For the last experimental season, stand LAI could be separated by species and mean RGR factorized into LAR and a CPI. Except for *Fagus* on acidic soil, LAR (leaf area per unit whole-tree mass) was reduced in elevated CO_2, suggesting some degree of downward adjustment of leaf area. The same effect also occurred between soils, with LAR being smaller on the nutrient-rich calcareous soil. These morphological adjustments were equilibrated by increases in CPI (greater annual biomass accumulation per unit leaf area), so that mean RGR in the fourth experimental season did not differ measurably between treatments.

In a compilation of all available experiments with tree species (including growth chamber experiments with potted seedlings), Wullschleger et al. (1997) found responses of LAR to be fairly consistent across studies, with an average decrease of 15% in elevated CO_2. In a study with eight woody species LAR was on average 13% lower in elevated CO_2 (Cornelissen et al. 1999). The only long-term data on mature forest trees were collected near natural CO_2 vents in Italy and indicate a 24% reduction of the ratio of leaf area to branch biomass, pointing in the same direction (Hättenschwiler et al. 1997a). LAI in that study was similar at both CO_2 enriched and nearby control sites (Hättenschwiler et al. 1997b), as it had been in our own experiment. We therefore believe that our study offers a realistic forecast for a future CO_2-rich world, namely that leaf area of tree stands in an expansive growth phase (i.e. forest regrowth) will be reduced relative to tree mass, but without affecting stand LAI.

Another likely explanation for the convergence of mean RGRs between ambient and elevated CO_2 is downward adjustment of the assimilation capacity. Photosynthetic rates in our model communities were increased in elevated CO_2 both at the leaf and canopy level (Egli et al. 1998; Maurer et al. 1999), but Egli et al. (1998, 2001) also detected partial downward adjustment of photosynthesis throughout the experiment. This effect was more pronounced on the nutrient-poor acidic soil and stronger for *Fagus* than for *Picea*. By the fourth season of our experiment, downward adjustment had become complete in *Fagus*, but disappeared in *Picea*. Photosynthetic downward adjustment was accompanied by concomitantly higher carbohydrate contents and lower Rubisco activity in elevated CO_2 grown leaves, particularly on acidic soil (Landolt and Pfenninger 1997; W. Landolt, personal communication). The decrease in Rubisco activity was stronger in *Fagus* than in *Picea*, confirming that physiological downward adjustment was stronger in *Fagus*.

We conclude from these complementary studies that the observed convergence of mean RGRs between treatments is in part the result of photosynthetic downward adjustment. Many other studies have yielded similar results, supporting that initial CO_2 stimulation of photosynthesis is not maintained in the long run (e.g. reviews by Curtis 1996; Drake et al. 1997). This adjustment is often more pronounced when plants are subject to nutrient limitation (meta-analysis by Curtis 1996), similar to what occurred in our systems on the nutrient-poor acidic soil.

Belowground development

The third focus of this study, complementing temporal development of whole-tree mass and canopy expansion, was the dynamics of soil exploration by fine roots and associated metabolic below-ground activity. Fine roots on the nutrient-poor acidic soil showed a pronounced response to enhanced N supply at two out of three measurement dates, whereas CO_2 enrichment had no effect. On calcareous soil, fine roots responded only to CO_2 enrichment, with the effect emerging in the third season and becoming significant at the end of the experiment. A separation of fine roots by species in the last experimental season revealed that fine root responses approximately paralleled whole-tree mass responses, but the statistical power of detecting effects was only about 25% (post hoc power analysis) because of the required cautious sampling intensity. The only treatment which induced contrasting responses of fine root density and whole-tree mass was the type of soil in *Fagus*. On the poor acidic soil, the fine root fraction (fine root mass/whole-tree mass) of *Fagus* was significantly enhanced, a difference not seen in *Picea*. It seems that *Fagus* on acidic soil was forced to invest more biomass in roots, perhaps because

of either the poorer nutrient supply itself or limited mycorrhizal support.

The dramatic divergence of whole-tree mass of *Fagus* on acidic versus calcareous soil is in accordance with results of classical forestry studies on mixed stands of *Fagus* and *Picea* (Assmann 1961; Kramer et al. 1988). The effect is likely to be related to the different rooting patterns of the two species. *Picea* had developed a more dense and shallow root system than *Fagus* on both soils (personal observation at final harvest). Since nitrate concentrations on acidic soil were highest in the uppermost horizons (Hagedorn et al. 2000), there may have been an advantage for *Picea* in exploiting nutrients on this poor soil. This effect may have been enhanced by the fact that nutrients were recycled in these systems largely through litterfall. Moreover, CO_2 enrichment decreased soil solution nitrate on both soils (Hagedorn et al. 2000), and this apparently affected trees, *Fagus* in particular, much more on the nutrient-poor acidic soil. Differences in mycorrhization may also have strongly affected tree growth.

Similar to our findings on calcareous soil, many other studies with conifers and deciduous tree species report a greater fine root production in elevated CO_2 (e.g. Crookshanks et al. 1998; Janssens et al. 1998; Tingey et al. 1997). In a recent review of experiments with tree species grown in open top chambers in the field, fine root densities are reported to increase between 60% and 140% (Norby et al. 1999), but it remained open whether such an acceleration of soil exploration would persist in a forest in the long run, a conclusion which also applies to our own findings.

In situ rates of soil CO_2 efflux might be expected to parallel fine root responses to CO_2 or N treatment. On acidic soil, however, such correspondence was not seen. In particular, the N effect that was observed in fine root density was not reflected in soil CO_2 efflux, a phenomenon for which we have no explanation. In contrast, the CO_2 effect on fine root density on calcareous soil was associated with higher rates of soil CO_2 efflux in elevated CO_2. But whereas fine roots responded only towards the end of the experiment, soil CO_2 efflux was increased in elevated CO_2 throughout the whole experiment. Increased soil CO_2 efflux in response to CO_2 enrichment was also found in other studies, both in the field and in model ecosystems (Hättenschwiler and Körner 1996; Janssens et al. 1998; Körner and Arnone 1992; Norby et al. 1992). In summary then, respiratory C release from the soils in our experiment was not uniformly enhanced, and the size of the signal in response to CO_2 enrichment did not reveal trends reflecting canopy maturation.

Conclusions

Temporal growth patterns clearly demonstrate that CO_2 enrichment and enhanced N supply affected growth of young *Fagus* and *Picea* trees primarily during the first season of this 4-year experiment. Later on, differences in tree biomass between treatments increased largely due to compound interest effects of this early stimulation. Trees which gained such an initial advantage due to elevated CO_2 or high N supply underwent accelerated development with a concomitant increase in self shading and greater allocation of biomass to heterotrophic tissues. Consequently, initial differences in RGR between treatments were progressively reduced. Partial downward adjustment of photosynthesis, greater fine root mass and soil CO_2 efflux (at least on calcareous soil) added to the transient nature of the CO_2 stimulation.

Our experiment has demonstrated that the type of soil can represent a major determinant of plant responses to CO_2 enrichment and enhanced N supply. Since these soil-dependent responses were already apparent very early in the experiment, they are likely to reflect direct soil effects rather than consequences of interactions between individual plants. In view of the size of the soil effect it is evident that rather different conclusions would have been reached had we chosen to work with only one soil.

Both the strong soil influence and the transient nature of CO_2 and N effects point at the difficulty of extrapolating from initial growth responses of very young trees to later life stages or even mature forests. Reliability of forecasts of vegetation responses to future environmental changes is certainly enhanced by using experimental test systems that are allowed to come close to steady state (e.g. canopy closure). We therefore believe that our model ecosystems allow for reliable predictions with respect to future forest regrowth stands. Given that experimental periods and funding will always be limited, studying the dynamics of responses over the whole duration of an experiment seems more instructive than assessing responses at some single random point in time, such as final harvest.

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