Effects of Elevated CO_2, Increased Nitrogen Deposition and Soil on Evapotranspiration and Water use Efficiency of Spruce-Beech Model Ecosystems

By

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K e y w o r d s : Beech, ecosystem, elevated CO_2, evapotranspiration, nitrogen deposition, spruce, soil type, stomatal conductance, water relations, water use efficiency.

S u m m a r y

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Evapotranspiration (ET) of model ecosystems of young spruce and beech trees, exposed to either ambient or elevated CO_2 (ambient + 200 μmol mol^{-1}) and high or low (65 vs. 6.5 kg N ha^{-1} a^{-1}) wet nitrogen deposition for four years in open-top chambers was estimated from the water balance biweekly during the last growing season. The open-top chambers contained two lysimeter compartments, with two types of natural unfertilized forest soils taken from either an acidic or a calcareous site and were equipped with transparent roofs, which automatically closed at the onset of rain. After harvest the water use efficiency for the production of new leaf biomass (WUEp) was determined.

In the final year of the experiment, the CO_2 and N effects on water relations differed between the two soil types: on the acidic soil, elevated CO_2 reduced ET significantly by 7 % and increased soil moisture, whereas increased nitrogen deposition had opposite effects. In contrast, on the calcareous soil evapotranspiration was not significantly influenced by any treatment, but soil moisture and drainage water were reduced under elevated CO_2. WUEp was increased and ET per unit new foliage area decreased under elevated CO_2 on both soils. Under elevated CO_2 stomatal conductance was reduced in beech leaves, but not in spruce needles. Our results suggest that plants at high CO_2 either deplete the soil water more slowly at the same growth rate (as observed here under nutrient-poor conditions) or grow faster for the same rate of water 'consumption' (as we found under favourable growth conditions).

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Introduction

Water availability is assumed to be the major limiting factor for net primary production in several global terrestrial biospheric models (CHURKINA & al. 1999) and changes in evapotranspiration may have an influence on regional and global climate (HEATH 1998). Changes in the water balance will also have an effect on other ecosystem processes such as nutrient cycles (FIELD & al. 1995). Because of their large standing biomass and long life-span, such effects may be particularly critical in forests.

Effects of elevated atmospheric CO_2 concentrations on water relations of trees are well documented (review by SAXE & al. 1998). In many experiments, elevated CO_2 caused a reduction of leaf-level transpiration through reduced stomatal conductance (CENTRITTO & al. 1999b), which led to a lower whole-tree evapotranspiration per unit foliage area (CENTRITTO & al. 1999a). Such effects were assumed to increase soil moisture and improve the water economy of the tree. However, since exposure to elevated CO_2 is often reported to also enhance growth (CURTIS & WANG 1998) and increase leaf area (review by PRITCHARD & al. 1999), more water might be lost through increased whole-tree transpiration (cf. PATAKI & al. 1998, RUNION & al. 1999). Therefore total water consumption may even be increased in trees exposed to elevated CO_2 concentrations (EAMUS 1996, KRUIJT & al. 1999).

It has been criticized, that the water availability data used for global models of CO_2 effects on vegetation and climate have often been collected under unrealistic conditions (TOGNETTI & al. 1999). Most experiments on water relations under elevated CO_2 have been conducted with potted seedlings, often growing in an artificial substrate and without competition with other plants. Considering the wide variety and the great heterogeneity of forest soils and the crucial role of water and nutrients for plant growth, such experiments would have little relevance for predictions of water relations of forests in a future, CO_2-rich world. Further, in the few experiments conducted with trees larger than seedlings (LE THIEC & DIXON 1996, ELLSWORTH 1999), water relation estimates were mostly based on instantaneous water-use efficiency measurements probably unsuited to reveal small changes in water consumption over time. SAXE & al. 1998 states, that 'the simple question of whether rising concentrations of CO_2 will suppress or enhance evapotranspiration is far from clear', and points out, that for answering this question whole-canopy foliage areas and transpiration rates need to be calculated.

We tried to provide some of this missing information by way of a lysimeter experiment with 'realistic' model forest ecosystems consisting of two species of co-occurring forest trees and an understorey layer of five plant species growing on two different natural forest soils (a low-fertility acidic soil and a high-fertility calcareous soil). From the water balance, it was possible to calculate the actual evapotranspiration of the whole ecosystem weekly or bi-weekly during four growing seasons. Earlier (SONNLEITNER & al. in press), we reported on water-biomass relations, which were based on non-destructive estimations of leaf area and plant biomass in the third year of the experiment. Now at the end of the experiment, we

are able to relate the evapotranspiration to the transpiring foliage area and biomass as determined after harvest.

To account for possible interactions between nitrogen and CO_2 on growth and water relations, CO_2 and soil effects were also tested under low as well as increased wet deposition of nitrogen.

In this study we tested the following hypotheses: (i) the effects of elevated CO_2 on the water balance of forest ecosystems are dependent on soil type and N supply (ii) elevated CO_2 will increase water use efficiency of the ecosystem

Materials and Methods

Open-top chambers and lysimeter installations

16 hexagonal open-top chambers (height 3 m, diameter 3 m, depth 1.5 m), were divided below ground into two soil compartments of 3 m² surface area each. The compartments were used as non-weighable lysimeters. Underneath a 0.5 m deep of quartz sand filter layer, the drainage water of each compartment was collected in plastic containers.

Soils

On top of the quartz sand drainage packing, the two lysimeters of each chamber were filled with two natural unfertilized forest soils from the central plateau in Switzerland: one with a calcareous loamy sand originating from a Calcaric Fluvisol (referred to as 'calcareous soil'), the other with an acidic sandy loam taken from a Haplic Alisol ('acidic soil'). Corresponding to the absence of distinct soil horizons in the sampled Fluvisol, the calcareous soil was filled into the lysimeter as one layer, whereas a 0.4 m deep topsoil layer and a 0.6 m subsoil layer of the acidic soil were packed separately in accordance with the original layering of the material. The distribution (north vs. south) of soil type within the chambers was varied systematically from chamber to chamber (for more details on soil properties see SONNLEITNER & al. in press).

Vegetation

Eight 4-yr old saplings of Norway spruce (*Picea abies* Karst.), eight 2-3-yr-old saplings of beech (*Fagus sylvatica* L.) and a total of 30 individuals of five understorey species (*Carex sylvatica, Geum urbanum, Hedera helix, Ranunculum ficaria,* and *Viola sylvatica*), were planted into each lysimeter in autumn 1994. The trees were chosen to represent different genotypes (spruce) or provenances (beech, see EGLI & al. 1998 for further information on the plants used and planting design).

CO_2 and N treatments

The four combinations of CO_2 and nitrogen treatments applied in this experiment are denoted as 'control', 'CO_2', 'N' and 'CO_2xN'. Ambient air was supplied through wide porous tubes along the bottom of the chamber walls. In the CO_2 and CO_2xN treatments, approx. 200 ppm CO_2 was added to the ambient air. In the N and CO_2xN treatments, NH_4NO_3 was added to the irrigation water to represent an input of 25 (1995), 50 (1996), 70 (1997) and 65 (1998) kg N per ha and year. In the control and CO_2 treatments, we supplied 2.5 (1995), 5 (1996), 7 (1997) and 6.5 (1998) kg N per ha and year. The treatments were arranged in a Latin square with four replicates each, and the soil treatment was nested within each CO_2x N treatment.

Water regime

Uncontrolled input of water and wet deposition of nitrogen was prevented by automatic closure of transparent roofs at the onset of rain. Irrigation water (electro-osmotically purified tap water with ions added to imitate rain water) was supplied in equal amounts in all treatments by height-adjustable nozzles (7 per lysimeter) which were held just above the canopy. In 1998, the irrigation regime was adjusted to the actual water demand to avoid water stress.

The containers collecting the drainage water were usually emptied weekly and the amount of water measured volumetrically using plexiglass cylinders.

Soil water content was measured bi-weekly during the growing season by time domain reflectometry (TDR). For the assessment of water storage changes, vertical TDR probes of 25 cm length were installed centering at 25, 50 and 75 cm depth. One lysimeter per CO_2xNxsoil treatment was equipped with 3 probes per sampling depth, while the other lysimeters were eqipped with one probe per sampling depth. TDR signals were calibrated and analyzed following the procedure of ROTH & al. 1990, taking account of soil temperature. Soil temperatures were measured in 4 lysimeters at 25, 50 and 75 cm depth. Temperature variations between lysimeters were negligible.

Soil water potentials were recorded manually every 14 days using the method of MARTHALER & al. 1983. The cups of the tensiometers centered at the same depths as the TDR probes, i.e. at 25, 50 and 75 cm (3 replicates per depth in all lysimeters).

Evapotranspiration (ET) was assessed biweekly during the growing season 1998 from the water balance: ET_{1998} = irrigation - drainage - water storage change (for more details on water measurements see SONNLEITNER & al. in press).

Leaf biomass and leaf area

At the end of the four-year experiment in autumn 1998, each tree was harvested separately, sorted into plant organ types and age, dried to constant mass and weighed. Specific leaf area (leaf area per leaf mass) of spruce was estimated as described in EGLI & al. 1998 on aliquots of representative needles (perimeter of microscopical cross cuttings, needle length and weight). From these measurements, the total leaf area and leaf dry mass production of the canopies in 1998 were calculated. Leaf areas refer to the stomata-covered areas, i.e. to one leaf side for beech leaves and total surface for the rhomboid spruce needles.

Since the understorey species were largely suppressed by the trees already in the third year, we only considered tree growth for the last year of the experiment. We chose total new foliage mass or area production per lysimeter in 1998 for the correlations with water consumption in 1998, because new wood biomass cannot be weighed separately from older woody parts.

Stomatal conductance

Instantaneous rates of gas exchange in beech leaves and spruce shoots were measured in situ with a portable CO_2/H_2O gas exchange measuring system (Li-Cor LI-6400, Li-Cor, Lincoln, NE, USA) in 1998 (beech was measured in June and spruce in August). Leaf gas exchange was based on total needle surface area in spruce and one-sided leaf area in beech. In beech, leaves from the well illuminated upper part as well as from the shaded part of the crown of two provenances were measured, one sun- and one shade-leaf per sampled provenance in each model ecosystem. In spruce, current-year and 1-yr old lateral shoots of branches from the second youngest whorl of trees from two genotypes were measured; one shoot per age class and sampled genotype in each model ecosystem. Gas exchange was measured on sunny days at treatment CO_2 concentrations and ambient air temperature and relative humidity under saturating quantum flux densities (QFD >1000 μmol m^{-2} s^{-1}) except for the shade leaves of beech, which were measured at average microsite light availability as determined for a sunny day in June (QFD 110 μmol quanta m^{-2} s^{-1}).

Statistical tests

Effects of treatments were tested statistically using cross-factorial ANOVA models. For more details of the statistical analyses see SONNLEITNER & al. in press.

R e s u l t s

Water balances

CO_2 and N had opposite effects on evapotranspiration (ET), soil moisture, and drainage water. The directions of these effects depended on soil type. On the

acidic soil, elevated CO_2 reduced the average daily evapotranspiration from April 1 until August 31 by 7 % ($P<0.05$, main effect of CO_2 pooled across N treatments, Fig. 1). As a consequence, under elevated CO_2 the soil remained wetter during the same period as shown by the 34 % difference in soil water potentials pooled across N treatments, soil depths and sampling dates, but this response was significant at 75 cm depth only ($P<0.05$, Fig. 2). Consistently, the whole-season total of drainage water was increased by 25 % under elevated CO_2 ($P<0.1$, Fig. 3). In contrast to CO_2, the high nitrogen treatment enhanced ET during the same period by 15 % ($P<0.001$, effect pooled across CO_2 treatments), reduced the amount of drainage water by 41 % ($P<0.001$) and resulted in drier soil (effect significant at 25 cm depth only). In the combined CO_2 and N treatment, ET was increased by 7 % while drainage water was decreased by 26 % as compared to the controls. Thus, the effects of CO_2 and N were approximately additive.

In contrast to the acidic soil, the model ecosystems on the calcareous soil showed a trend towards increased ET fluxes in response to elevated CO_2 ($P=0.1$, Fig.1). In consequence, the calcareous soil was drier at all depths ($P<0.05$, effect pooled across N treatments and sampling dates) and the total amount of drainage water from this soil was reduced (-21 %, $P<0.01$) under elevated CO_2. The N treatment had no significant effects on the water relations of the systems on calcareous soil.
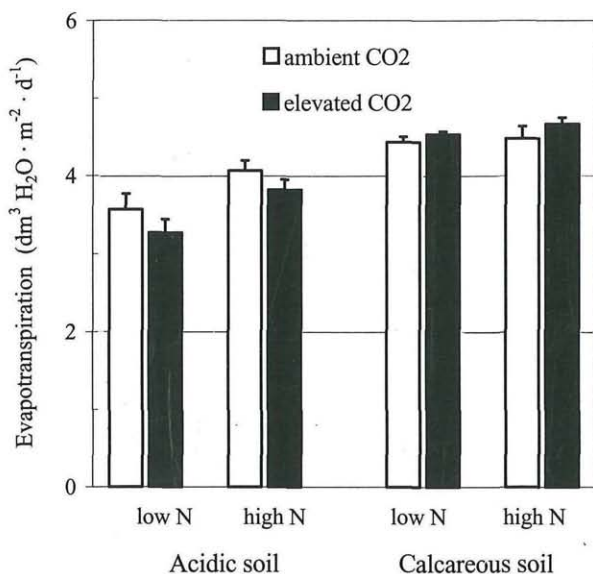

Fig. 1. Daily evapotranspiration for the period April 1 – August 31, 1998 of spruce-beech model ecosystems growing on two different soils in the fourth year of exposure to elevated CO_2 and increased N deposition (treatment means + S.E.). Significance levels of the main effects on the acidic soil: $P_{CO_2} < 0.05$, $P_N < 0.001$, on the calcareous soil: no significant effects ($P_{CO_2} = 0.1$).
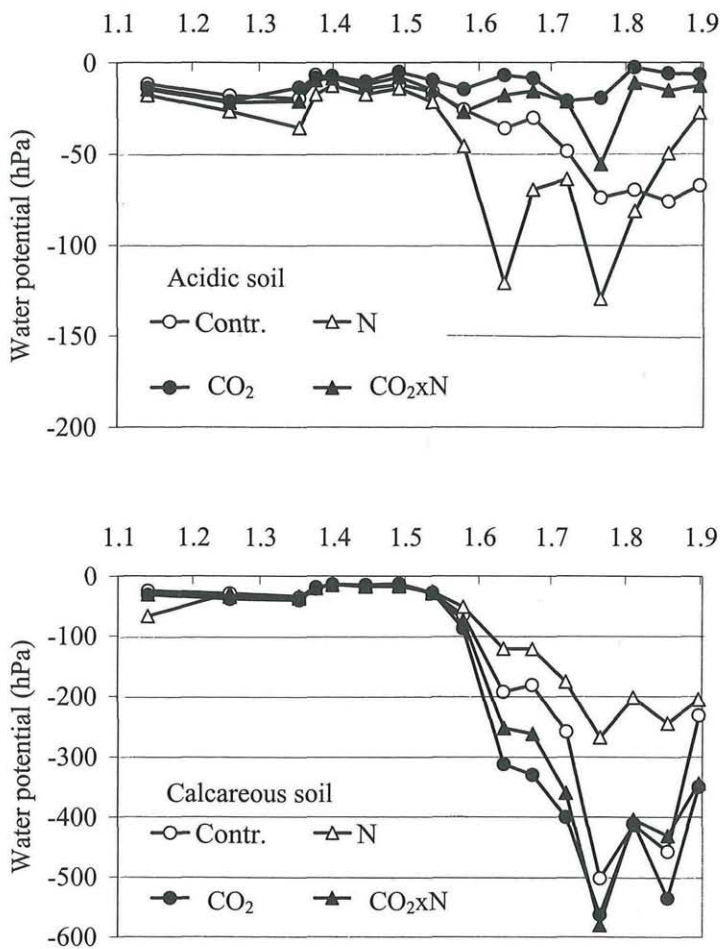
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Fig. 2. Tensiometric soil water potentials during 1998 for the acidic soil (top) and for the calcareous soil (bottom) at 75 cm depth. Significance levels of the main effects for the period April 1 – August 31 on the acidic soil: P_{CO_2} <0.05 (significant only at 75 cm depth), P_N <0.05 (significant only at 25 cm depth), on the calcareous soil: P_{CO_2} <0.05 (at all depths), P_N not significant.
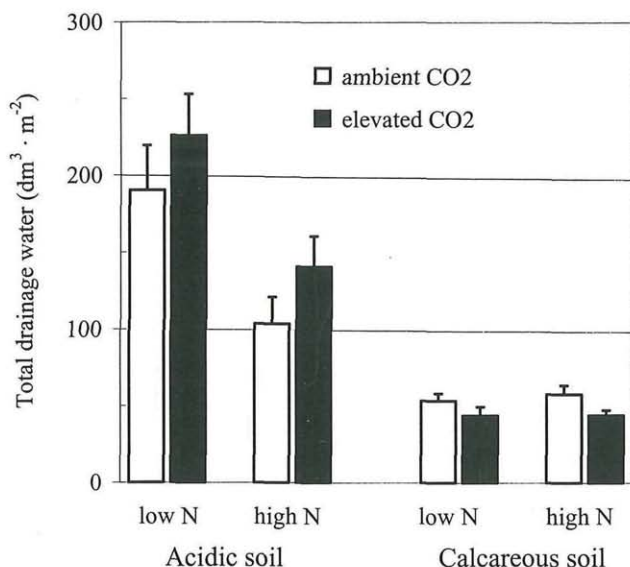
Fig. 3. Total drainage water for the period April 1 – August 31 1998 from the two soils (treatment means + S.E.). Significance levels of the main effects on the acidic soil: $P_{CO_2} < 0.1$, P_N <0.001, on the calcareous soil: $P_{CO_2} < 0.01$, P_N not significant.

Treatment effects on ecosystem foliage production, water-use efficiency and total ET per unit foliage area

As could be expected from the higher fertility of the calcareous soil, both new foliage biomass and new foliage area were considerably higher on this soil than on the acidic soil in all CO_2xN treatment combinations. As evapotranspiration differed less than growth between the soils, water use efficiency (WUEp) was 65 % higher on the calcareous than on the acidic soil. The total ET per unit new foliage area was 39 % lower (Table 1). Elevated CO_2 and increased nitrogen both had positive effects on growth, expressed as new leaf biomass or new leaf area. However, the CO_2 effects were significant only on the calcareous, nutrient-rich soil, whereas the nitrogen effects were significant only on the acidic nutrient-poor soil.

On both soils, water use efficiency (WUEp), expressed as unit new foliage biomass produced per unit water ‚consumed‘ by the system, was significantly increased by elevated CO_2 (+16 % on acidic soil, +21 % on calcareous soil, pooled across N treatments). On the acidic soil, not only CO_2 but also nitrogen had a positive effect on WUEp (+26 %, pooled across CO_2 treatments). On this soil, the effect of the combined CO_2xN treatment on foliage biomass production (+61 %) and WUEp (+47 %) corresponded approximately to the sum of the single CO_2 and N effects as compared with the control (Table 1).

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Table 1. New foliage growth, water-use efficiency, evapotranspiration (ET) per unit leaf area and stomatal conductance for the period April 1 – August 31, 1998 of spruce-beech model ecosystems growing on two different soils in the fourth year of exposure to elevated CO_2, and increased N deposition (treatment means ± S.E.). Levels of significance: (*) P<0.1, * P<0.05, ** P<0.01, *** P<0.001.

Parameter	Ambient CO_2		Elevated CO_2		Significance levels		
	low N	high N	low N	high N	CO_2[1]	N[2]	CO_2xN
Total new leaf biomass (g·m^{-2} ground area)							
Acidic soil	214 ± 22	321 ± 14	238 ± 10	344 ± 20		***	
Calcareous soil	446 ± 11	453 ± 20	535 ± 12	580 ± 23	***		
Total new area (m^2 leaf area ·m^{-2} ground area)							
Acidic soil	4.38 ± 0.38	7.02 ± 0.27	4.63 ± 0.18	6.68 ± 0.35		***	
Calcareous soil	9.13 ± 0.53	10.05 ± 0.50	10.65 ± 0.46	11.46 ± 0.10	**	(*)	
WUEp (g new leaf biomass 98 ·dm^{-3} H$_2$O)							
Acidic soil	0.398 ± 0.014	0.516 ± 0.005	0.477 ± 0.011	0.587 ± 0.010	***	***	
Calcareous soil	0.657 ± 0.010	0.661 ± 0.027	0.772 ± 0.023	0.826 ± 0.044	***		
Total ET April-August/New leaf area (dm^3 H$_2$O·m^{-2} leaf area)							
Acidic soil	122.5 ± 2.7	89.0 ± 4.2	107.9 ± 3.3	88.2 ± 4.0		***	(*)
Calcareous soil	74.9 ± 3.8	68.8 ± 4.5	65.6 ± 3.2	61.4 ± 1.2			
Stomatal conductance (mmol H$_2$O m^{-2} s^{-1})							
Beech sun leaves (June)							
Acidic soil	226 ± 40	254 ± 25	128 ± 23	151 ± 45	***	(*)	
Calcareous soil	176 ± 75	130 ± 30	177 ± 23	159 ± 40	*		*
Beech shade leaves (June)							
Acidic soil	212 ± 30	134 ± 31	100 ± 31	95 ± 16	**	(*)	(*)
Calcareous soil	91 ± 28	72 ± 30	63 ± 13	87 ± 20			
Spruce current-year needles (August)							
Acidic soil	33 ± 6	50 ± 9	55 ± 9	38 ± 7			
Calcareous soil	37 ± 10	33 ± 10	42 ± 9	48 ± 6			*
Spruce one-year needles (August)							
Acidic soil	21 ± 4	32 ± 4	28 ± 7	32 ± 6			
Calcareous soil	25 ± 8	25 ± 2	29 ± 5	29 ± 10			

[1] effect pooled across N treatments   [2] effect pooled across CO_2 treatments

Over the period from April–August 1998, elevated CO_2 significantly reduced the total ET per unit new leaf area in all soil type x N combinations except on the acidic soil under high N deposition (Table 1). Increased N deposition reduced the total ET per unit leaf area by 23 % on the acidic soil (P<0.001), but not significantly on the calcareous soil (-7 %, effects pooled across CO_2 treatments).

Stomatal conductance

Stomatal conductance (g_s) of sun and shade leaves of beech as measured in June was significantly lower on the calcareous soil (-31 % pooled across CO_2- and N-treatments and leaf types; P<0.01) than on the acidic soil (Table 1). CO_2 enrichment reduced stomatal conductance of beech on both soils, but the effect was stronger on the acidic than on the calcareous soil (P_{CO2}xsoil<0.05). The CO_2 effect did not differ significantly between the N treatments on the acidic soil (approx. – 40 % pooled across N levels for both leaf types), whereas on the calcareous soil the CO_2 response was negative (approx. –30 %) under low N deposition, but positive (approx. +20 %) under increased N deposition, irrespective of leaf type (Table 1).

In contrast to the earlier years when g_s of spruce had been significantly reduced at elevated CO_2 (EGLI & al. 1998), the current and 1-yr old needles as measured in August in the fourth and last year of treatments showed a positive (but not significant) response to CO_2 on both soils (current: +21 %, 1-yr: +15 %).

For the trees from the control treatment, g_s was reduced by 22 % in sun-exposed and by 57 % in shaded beech leaves on the calcareous as compared with the acidic soil, while spruce did not respond significantly to soil type (and also to the N treatment). The stomatal conductance of 1-yr-old spruce needles on average was 36 % (acidic soil) and 32 % (calcareous soil) lower than that of the current-year needles.

Discussion

In our four-year experiment with spruce-beech model ecosystems, we measured a slight but significant reduction of evapotranspiration (ET) in response to atmospheric CO_2 enrichment only in those systems that exhibited no significant CO_2 stimulation of tree growth, i.e. those on the nutrient-poor acidic soil. When nitrogen was added to this soil, both growth and ET increased significantly – since the positive effect of nitrogen on ET exceeded the negative effect of elevated CO_2, ET was slightly increased in the CO_2xN treatment as compared to the control. In contrast to the acidic soil, there were no significant CO_2 effects on ET from the calcareous soil. This soil was actually drier under elevated CO_2 than under ambient CO_2. Hence, the increase in WUEp of the systems on acidic soil was mainly due to reduced ET (while growth was rather unresponsive to CO_2), whereas that of the systems on calcareous soil was attributable to increased foliage production, but not decreased ET under elevated CO_2. Under water-limiting conditions, increased WUEp can be associated with more growth for a given rate of water supply, as has been shown for two crop species (HUNSAKER & al. 1994, PINTER & al. 1996), or a

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prolongation of the growing period in plant communities that are subjected to periodic droughts (JACKSON & al. 1994, OWENSBY & al. 1997).

The above results suggest that plants under high CO_2 either deplete the soil water more slowly at the same growth rate (as observed here in the nutrient-poor soil and for longleaf pine under low N conditions (RUNION & al. 1999)) or grow faster at the same rate of water 'consumption' (as found here under favourable growth conditions and also by CENTRITTO & al. 1999a for cherry seedlings) – or exhibit intermediate responses between these two 'extremes'. The latter was reported for model ecosystems with beech saplings, where daily evapotranspiration rates were reduced although CO_2 enrichment increased the leaf area index (OVER-DIECK & FORSTREUTER 1994). Similarly, STOCKER & al. 1997 observed a trend for reduced ET despite a significant increase in above-ground biomass at elevated CO_2 in their in situ study of a calcareous grassland.

We found decreased evapotranspiration per unit foliage area in response to elevated CO_2 on both soils. This whole-canopy effect may have been associated with the CO_2-induced reduction in the stomatal conductance (g_s) of beech leaves as measured in June. However, in contrast to the earlier years of the experiment (EGLI & al. 1998), g_s of spruce did not significantly respond to CO_2 in the final year. Overall, our results do not support the hypothesis, that ecosystem level ET is often relatively insensitive to CO_2-induced changes in g_s (FIELD & al. 1995, see also STOCKER & al. 1999). Responses in g_s were in line with the overall trend (SAXE & al. 1998), that tree species with low intrinsic stomatal conductance, i.e. conifers, are less responsive to CO_2 (cf. PATAKI & al. 1998, ROBERNTZ & STOCKFORS 1998, ELLSWORTH 1999) than many deciduous tree species with higher intrinsic g_s (cf. Table 1). Reduced plant transpiration per unit foliage area at elevated CO_2 may not only have been associated with reduced g_s at the single-leaf level, but could also have been a result of a change in the two tree species' contribution to the total foliage area of the canopy. Any increase of spruce relative to beech foliage area could have reduced the average g_s in our canopies. Actually, the proportion of beech leaf area to total foliage area was decreased by 22 % (pooled across N treatments, data not shown; see also EGLI & al. 1998) under elevated CO_2 on the acidic soil, which might have contributed to the CO_2-induced reduction of ET on that soil.

The restricted scale of our experiment does not allow to test whether or not reduced evapotranspiration, on a landscape level, could increase the water vapour deficit of the air, which in turn could act as a negative feedback on the decline in ET under elevated CO_2. At any rate, if ET will in fact respond to atmospheric CO_2 enrichment, such a response is likely to depend on soil fertility and N supply.

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