

Partitioning of remobilised N in young beech (*Fagus sylvatica* L.) is not affected by elevated [CO₂]

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Abstract – Effects of elevated CO₂ concentration ([CO₂]) on the remobilisation of tree internal nitrogen (N) of 3-year-old beech (*Fagus sylvatica* L.) was determined in a labeling experiment. Trees were pre-treated with ¹⁵N for 1 year and the remobilization of stored N was monitored in ambient (350 ppm) or elevated [CO₂] (700 ppm) in the subsequent year. N taken up during the pre-treatment made up 24.7% of total N at the start of the experiment. This value was almost halved after 24 weeks of growth for both CO₂-treatments. Significant differences in the partitioning of the remobilized N were only observed transiently after 6 weeks of growth but no CO₂-effect was observed at the end of the growing season.

elevated carbon-dioxide / N cycling / N partitioning / remobilization / stable isotope

Résumé – La partition de N remobilisé chez de jeunes hêtres (*Fagus sylvatica* L.) n'est pas affectée par une concentration élevée en CO₂. Les effets de concentrations élevées en CO₂ sur la remobilisation de l'azote interne de plants de hêtre (*Fagus sylvatica* L.) âgés de 3 ans ont été étudiés dans une expérimentation avec marquage. Les arbres ont été prétraités avec du ¹⁵N pendant un an et la remobilisation de l'azote stocké a été suivie à des concentrations de 350 ppm et de 700 ppm l'année suivante. L'azote fixé pendant le prétraitement correspond à 24,7 % de l'azote total au début de l'expérimentation. Cette valeur était presque diminuée de moitié après 24 semaines de croissance pour les deux traitements étudiés. Des différences significatives dans la partition de l'azote remobilisé ont été observées seulement de façon passagère après 6 semaines de croissance mais il n'a pas été observé d'effet du CO₂ à la fin de la période de croissance.

concentration élevée en gaz carbonique / cycle de N / partition de N / remobilisation / isotope stable

1. INTRODUCTION

Tree internal N cycling allows uncoupling of growth from N uptake; especially in spring, growth of deciduous trees relies to a great extent on the remobilisation of stored N [5, 9, 20]. Elevated [CO₂] has been shown to increase C uptake and growth in trees. However, especially in nutrient poor environments, the effect of elevated [CO₂] might be limited by N availability [11, 13, 17]. Many studies deal with the effects of elevated [CO₂] on the uptake of N from the soil (e.g. [1]) but there has been only little work on N remobilisation in trees under elevated [CO₂]. Temperton et al. [15] found for two year old *Pinus sylvestris* that N remobilisation was unaffected by elevated [CO₂].

The formation and remobilisation of internal N stores play an important role for tree growth [9] and thus probably for the long-term response to elevated [CO₂]. Generally, tissue N concentration in trees under elevated [CO₂] tends to decrease [2], indicating that store formation is not increased under elevated [CO₂]. It has been shown, that N stores formation in beech (*Fagus sylvatica* L.) was not increased under elevated [CO₂], but might even be decreased under unfavourable conditions [6].

The aim of the present study was to examine the effect of elevated [CO₂] on the partitioning of internal N remobilisation in young beech. Therefore, trees were pretreated with ¹⁵N for 1 year under ambient [CO₂] and the remobilization of stored ¹⁵N was monitored in the subsequent growing season under ambient and elevated [CO₂].

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2. MATERIALS AND METHODS

Three-year-old beech trees (*Fagus sylvatica* L.) from a tree nursery were examined in our experiment. To obtain trees with labelled N stores, the trees were grown on sand for one year and fertilized with a $^{15}\text{NH}_4^{15}\text{NO}_3$ (25 atom%) nutrient solution (pre-treatment). During the experiment in the following year, trees were placed into growth chambers (see below), supplied with 2 mM unlabelled NH_4NO_3 and grown at 350 or 700 ppm CO_2 in the chamber atmosphere. At the beginning of the CO_2 -experiment, trees had an average dry weight of 17 g which increased to 29 g at week 24 for both treatments.

For the experiment, beeches were planted on sand into cylinders of PVC (height 0.3 m, diameter 0.14 m). Irrigation was achieved by weekly feeding of 130 cm³ of a Hoagland-based nutrient solution (2 mM NH_4NO_3). The microcosms were installed in closed growth chambers at an atmospheric CO_2 concentration of 350 and 700 ppm CO_2 for the two treatments, respectively. During the CO_2 experiment, the chamber atmosphere was labelled in CO_2 to assess the C uptake during the experiment. The trees grew at a light level of 130 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for a 12 h day length. Temperatures varied between 13 °C in the night and 18 °C during daytime. Relative humidity was maintained at 75%. Details of the growth chamber system are given in Dyckmans et al. [4].

At the beginning of the experiment (after the pre-treatment) and after 6, 12, 18 and 24 weeks of growth, five plants per treatment were harvested. The plants were divided into seven plant organs: buds, leaves, new branches, old branches, stem, coarse roots (> 2 mm) and fine roots (< 2 mm). Plant samples were dried at 65 °C and finely ground. To distinguish between the formation of new plant organs and the growth of old tissues the plant compartments were combined to new shoots (buds, leaves and new branches), old shoots (old branches, stem) and roots (coarse and fine roots) for the presentation in the results section.

The labelling of the N uptake during the pre-treatment allowed analysing the remobilization of stored N. The labelled N represents only a part of the total remobilised N during the CO_2 -experiment since N taken up during earlier seasons will also be remobilised.

The relative specific allocation (RSA) describes the fraction of labelled C or N in the tissue relative to total C or N in a given sample. The partitioning describes the proportion of the labelled element in a given plant organ relative to the total labelled element in the whole plant [3, 6].

The results were expressed as arithmetic means with standard deviation. The *t*-test was used to determine significant differences between the treatments in individual plant organs. Probabilities of less than 0.05 were considered to be significant whereas probabilities of $0.1 > P \geq 0.05$ were considered to indicate a trend.

3. RESULTS AND DISCUSSION

Carbon uptake during the experiment was significantly increased under elevated $[\text{CO}_2]$, as was indicated by the increase in RSA of new C in the elevated treatment by 27% from 30.5 ± 2.8 under ambient to $38.6 \pm 5.7\%$ under elevated $[\text{CO}_2]$, which is comparable to results we obtained earlier [6].

Labelled N made up 24.7% of total N before bud break (Fig. 1). As a result of N uptake from the soil, this value gradually decreased to 13.7 and 12.3% at Week 24 under ambient and elevated $[\text{CO}_2]$, and throughout the experiment, no CO_2 -effect was observed.

Before bud break, 75.4% of the labelled N was located in the root system. During the first 6 weeks after bud break, large quantities of N were allocated to the new shoot (which at that

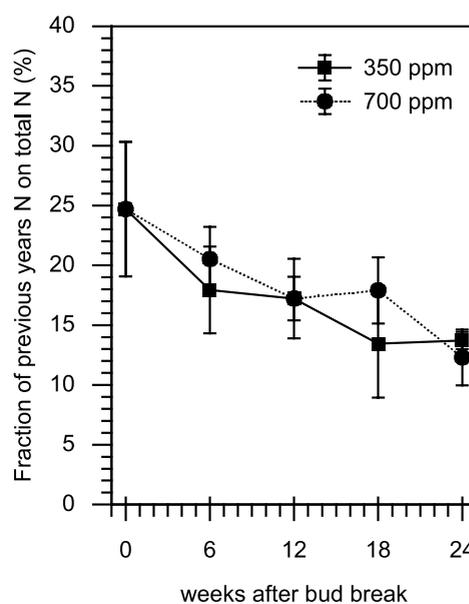


Figure 1. Fraction of labelled N (i.e. taken up during the previous year) on total N (RSA) on the whole plant level during the CO_2 experiment. Means and standard deviation ($n = 5$).

time consisted mainly of leaves) and at Week 6, 26.6 and 19.4% of labelled N were found in the new shoot for the 350 and 700 ppm treatment, respectively (Fig. 2). Both old shoot and coarse roots acted as a source of remobilised N during this period. The partitioning to the old shoot dropped from 23% to 10 and 7% in the ambient and elevated treatment (Fig. 2), the partitioning to coarse roots similarly decreased from 22 to 11% in both treatments (data not shown). It has been shown earlier that perennial organs (i.e. roots and stem) served as N stores for spring growth in deciduous trees, e.g. *Betula pendula* [10], *Juglans regia* [19] or *Prunus persica* [14]. Marmann et al. [8] showed that in *Fraxinus excelsior* N was mainly stored in the roots, whereas our data indicate that in beech N stocks in coarse roots and stem contributed about the same portion to new shoot growth.

Significant differences in the partitioning of labelled N between the ambient and elevated treatment were only observed at Week 6: The partitioning to roots was higher under elevated $[\text{CO}_2]$, while partitioning to new shoot was significantly decreased (Fig. 2), combined with a trend of decreased partitioning to old shoots under elevated $[\text{CO}_2]$. This was associated with a significant decrease in N concentration in the aboveground compartments under elevated $[\text{CO}_2]$ (data not shown). These data might indicate that N demand was increased for root growth to increase N uptake and as a consequence less N was allocated to the aboveground compartments under elevated $[\text{CO}_2]$ as compared to ambient. During the following weeks, however, partitioning of labelled N increased in the shoots and decreased in the roots in the elevated treatment, and at Week 12, no difference in the partitioning of labelled N was observed between the two treatments, nor were there differences in N concentration.

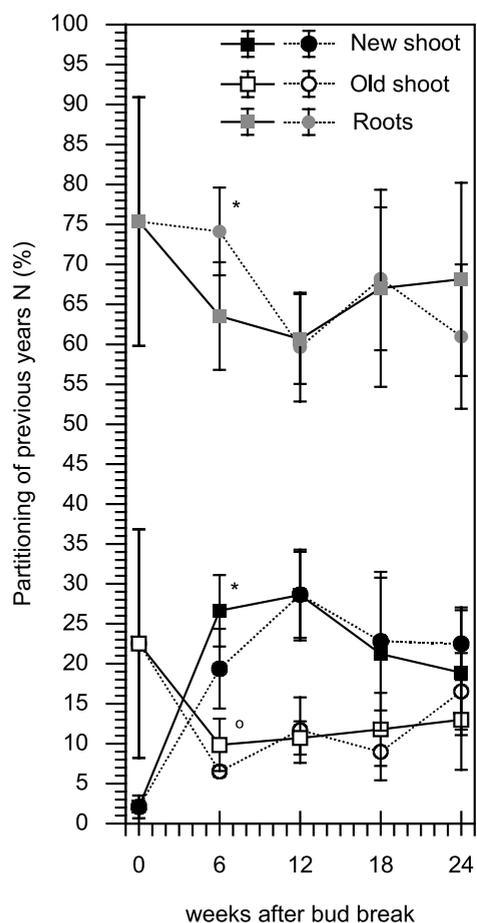


Figure 2. Partitioning of labelled N (i.e. taken up during the previous year) in different plant compartments during the CO₂ experiment under ambient (squares, solid lines) and elevated [CO₂] (dots, broken lines). Means and standard deviation ($n = 5$). An asterisk indicates significant differences between treatments ($P < 0.05$) and ° indicates a trend ($P < 0.1$).

In both treatments, partitioning of remobilised N in the old shoot increased after Week 6, while partitioning to new shoot decreased after Week 12. The partitioning to roots did not alter significantly after Week 12. At Week 24, 68.1 and 61.0% of remobilised N was found in the roots for the 350 and 700 ppm treatment, respectively.

Our data indicate that the partitioning of remobilised N is largely unaffected by the atmospheric [CO₂]. In an earlier study this was also found for the partitioning and amount of new N uptake although the partitioning of new C to roots and root respiration was increased under elevated [CO₂] as compared to ambient [6]. In this latter study, we could also show that no increased N store formation was observed under elevated [CO₂]. Temperton et al. [15] reported similar results for *Pinus sylvestris*, where N store formation and the partitioning of remobilised N were not altered under elevated [CO₂]. For the N₂ fixing *Alnus glutinosa*, however, they reported an increased N store formation in winter and increased N remobilisation for leaf growth in spring under elevated [CO₂]. Similar results of

increased N stores formation have been reported earlier for *Alnus glutinosa* [18] but also for *Robinia pseudoacacia* [7, 12], and the tropical tree species *Gliricidia sepium* [16].

Taken together these data suggest that young non-fixing tree species are less responsive to increased C assimilation in terms of increasing N uptake than N₂-fixing trees. Ultimately, this might indicate that the effect of elevated [CO₂] on tree growth in non-fixing species will be limited by N availability. The tree internal cycling of N might help to overcome this N deficiency under elevated [CO₂]. Nevertheless, our results give no evidence for a response of internal N cycling to elevated [CO₂] in young beech.

However, it should be taken into account that our results only reflect the short-term response to elevated [CO₂] and so far there are no results on the long-term CO₂-effect on internal C cycling in trees.

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