

Nitrogen productivity and allocation responses of 12 important tree species to increased CO₂

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Abstract

Key message This paper provides responses in nitrogen productivities for 12 important tree species to elevated CO₂.

Abstract The increasing atmospheric carbon dioxide concentration is expected to increase plant productivity. However, the strength of the response depends on the interaction with other limiting factors, of which nitrogen has been identified as one of the most important. This study analyzed the effects of increasing the CO₂ concentration from 380 ppm (ambient) to 1000 ppm (elevated) on nitrogen productivity (incl. biomass allocation and nutrient concentration of plant organs) in nine deciduous and three conifer tree species. No clear effects on biomass allocation were observed, but leaf nitrogen concentration decreased. Nitrogen productivity increased by 28% over all species, with the strongest response in deciduous trees (34%) and the weakest in conifers (8%). Although these changes are statistically not significant, we conclude that nitrogen productivity provides an integrative and robust concept to

assess the effect CO₂ fertilization effects on tree growth under varying nitrogen availability, while more studies are required to firmly establish the magnitude of the response.

Keywords Nitrogen productivity · Carbon dioxide · Nitrogen · Allocation · Tree growth

Introduction

The increasing global atmospheric carbon dioxide concentration is expected to increase plant productivity. However, the strength of the response depends on the interaction with other limiting factors, of which nitrogen has been identified as one of the most important. This makes predictions of future plant responses difficult, as CO₂ and nitrogen will interact at several temporal and spatial scales (Reich et al. 2006). Therefore, it is of interest to find ways of expressing the interaction between CO₂ and nitrogen that simplify the description of this interaction. Most studies show that increasing CO₂ concentration increases nitrogen use efficiency (e.g., Drake et al. 1997; Curtis and Wang 1998; Taub and Wang 2008). However, the responses are not universal and seem to depend on species and growth conditions and involve both morphological and physiological changes (Field et al. 1992; Lou et al. 1994). Nitrogen use efficiency involves also the length of the retention time of nitrogen in the plant, making it difficult to apply to dynamic conditions. On the other hand, nitrogen productivity, the growth rate of plant biomass per unit nitrogen in the plant, is directly designed to handle plant growth under dynamic nitrogen conditions. For example, Lou et al. (1994) found in their literature review that the nitrogen productivity in elevated CO₂ could be from 5% less to 80% higher than at ambient CO₂ in different experiments with a decrease in only 1 out of

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12 observations. Nitrogen productivity here integrates carbon and nitrogen uptake and allocation to plant organs, and thus the impact of organs' nitrogen concentrations. Using nitrogen productivity, it is therefore possible to directly express the growth response to nitrogen uptake without having to follow the more complicated route through photosynthesis and respiration (Ågren 1996). This circumvents the problem of differences between photosynthetic and growth responses to CO₂ (Ainsworth and Long 2005). Temperature is another important control of plant growth and nitrogen productivity has previously been shown to be insensitive to temperature (Ladanai and Ågren 2004). For these reasons, it is of interest to use nitrogen productivity as an integrative concept of plant growth and to have quantitative estimates of how nitrogen productivity changes in response to increasing CO₂. An important aspect of the plant response to elevated CO₂ is a potential shift in biomass allocation, which would affect nitrogen productivity and ecosystem carbon cycling, if there were a shift between tissues of different nitrogen concentration and degradability. Increased CO₂ could also lead to higher allocation to fine roots to increase nutrient uptake, to balance the increased carbon availability (Finzi et al. 2007) although Hilbert et al. (1991) suggest that this response should be small. Ågren and Franklin (2003) demonstrated also that changes in nitrogen productivity would only have minor effects on root: shoot allocation. In this study, we examined how nitrogen productivity responds to an increase in CO₂ concentration for nine deciduous and three conifer tree species. In addition, we analyzed biomass allocation and leaf nitrogen concentration to disentangle their effect on nitrogen productivity.

Materials and methods

Experimental procedure

The experiment was conducted in the phytotron at the Justus Liebig University of Gießen in Rauschholzhausen (a detailed description is given in Kattge 2002). In brief, one individual of two-year old saplings of 12 tree species, selected to represent commercially and environmentally important species, were grown in vermiculite-filled pots in the phytotron in atmospheres of approximately 360 (ambient), 1000 (elevated), ppm CO₂ during 91–117 days (Table 1). The photosynthetically active radiation was 500 μmol quanta m⁻²s⁻¹, with a 18/6 h day/night period at 24/15 °C and relative humidity of 70/85% during two experimental periods. Four different nutrient treatments (N0, N1, N5, and N25) were combined with each CO₂ level, where N0 meant that no nitrogen was added, and N1, N5, and N25 contained 1, 5, and 25 mmol L⁻¹ nitrogen in a nutrient solution. Other nutrients were added in excess

relative to nitrogen, following recommendations by Ingestad and Lund (1986). Plants were watered daily in surplus with the respective nutrient solution. Three plants per species were harvested at the start and one for each combination of CO₂ level and nutrient treatment at the end of the experiment. All plants developed new leaves during the experiment. Plants were separated into leaves, stem, roots, and fine roots (diameter <2 mm), and dry masses and nitrogen concentrations determined for each fraction. As the experimental conditions have been identical in the two experimental periods, all results are pooled from them.

Estimating nitrogen productivity

To estimate the nitrogen productivity requires the temporal course of nitrogen uptake. From measurements of nitrogen content and dry weight on two observation occasions, nitrogen productivity was estimated as follows for each N and CO₂ level:

The amount of N in a plant was assumed to increase exponentially with time, t :

$$N(t) = N_0 e^{rt} \quad (1)$$

from which the parameter r was calculated. This is the simplest assumption and requires estimation of only one parameter. A more realistic assumption where the uptake rate declines with the size of the plant would have required an unavailable time series of plant nitrogen uptake. However, in this experimental setup it is a reasonable assumption that nitrogen uptake increases in proportion to plant size, which creates an exponential rate of uptake (Ågren 1985).

The growth of plant dry weight, W , was calculated from nitrogen productivity, P_N (Ågren 1985):

$$\frac{dW}{dt} = P_N N(t) = P_N N_0 e^{rt} \quad (2)$$

giving

$$W(t) - W_0 = \frac{P_N}{r} N_0 (e^{rt} - 1) \quad (3)$$

or

$$P_N = r \frac{W(t) - W_0}{N(t) - N_0}. \quad (4)$$

Results

Nitrogen productivity

Nitrogen productivity ranged between 0.20 and 3.79 g dw g⁻¹ N day⁻¹ in ambient CO₂ and between 0.22

Table 1 List of species, length of experimental period, and nitrogen productivities (average over N treatments) ($\text{g g}^{-1}\text{d}^{-1}$)

Species	Length of experiment (days)	Ambient P_N	Elevated	Other experiments
<i>Acacia dealbata</i> (Link)	91	0.58	0.58	
<i>Acacia melanoxylon</i> (R.Br.)	91	0.56	0.80 ^d	
<i>Eucalyptus debeuzevillei</i> (Sieber)	91	0.77	0.91	
<i>Eucalyptus niphophila</i> (L.)	91	0.37	0.56 ^c	
<i>Eucalyptus pauciflora</i> (Maiden)	91	0.77	0.91	1.20 ^a , 0.95 ^b
<i>Quercus ilex</i> (L.)				
Exposure period	91	0.89	0.98	
Exposure period	117	0.20	0.43	
<i>Quercus robur</i> (L.)	96	0.85	1.66 ^c	
<i>Fagus sylvatica</i> (L.)	117	1.20	1.19	1.25 ^a
<i>Alnus glutinosa</i> (L.)	87	1.56	1.64	
<i>Pinus sylvestris</i> (L.)	117	1.16	0.61	
<i>Picea abies</i> (Karst.)	117	1.08	1.64 ^d	
<i>Pseudotsuga menziesii</i> (Mirb.)	117	0.76	0.75	

Sources of other experiments. Other experiments show the ratio between P_N at elevated and ambient CO_2 in other experiments with the same species

^a Kirschbaum and Lambie (2015)

^b Lou et al. (1994)

^c Elevated P_N is significantly higher than ambient P_N ($p = 0.1$)

^d Elevated P_N is significantly higher than ambient P_N ($p = 0.05$)

and 4.35 (*Pseudotsuga menziesii* at N5) $\text{g dw g}^{-1} \text{N day}^{-1}$ in the elevated CO_2 treatment (Table 1; Fig. 1, Supplementary information). Averaged over all species and all N levels, nitrogen productivity was 28% higher at the elevated CO_2 level. The increases in P_N were significant ($p < 0.1$) for four species (Table 1) but with clear differences between species; P_N increased with increased CO_2 at all N levels for *Picea abies* and *Eucalyptus pauciflora*, but in no case for *Pinus sylvestris*. An ANOVA analysis considering plant species, N supply and CO_2 , showed significant effects on P_N for species and N supply ($p < 0.05$), with a tendency for CO_2 ($p = 0.17$, Table 2). N levels also had an influence on whether P_N would increase with CO_2 ; at N0 and N1 only five and six species increased P_N , whereas at N5 and N25 eight species had increased P_N . All species except two (holm oak in the first exposure period and beech) increased their nitrogen productivity and pedunculated oak nearly doubled its productivity. The data suggest that nitrogen productivity of saplings of deciduous trees responded more strongly to CO_2 (average increase 34%) than conifers (average increase 8%).

Allocation and leaf nitrogen concentration

There were only small effects of the CO_2 treatment on allocation (Fig. 2) and no evidence of changes during the experiment. For example, under ambient CO_2 the

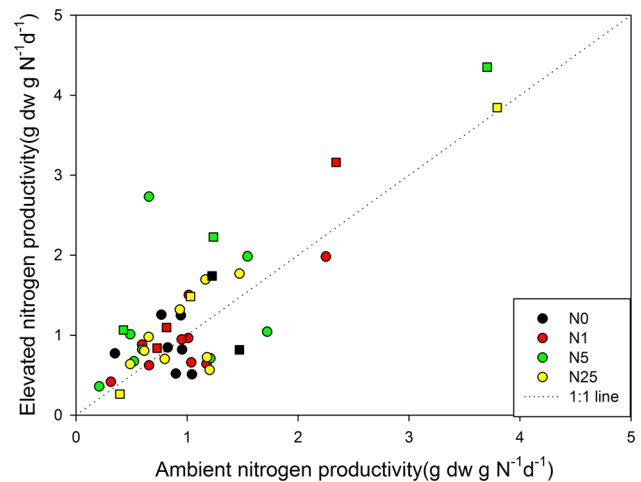
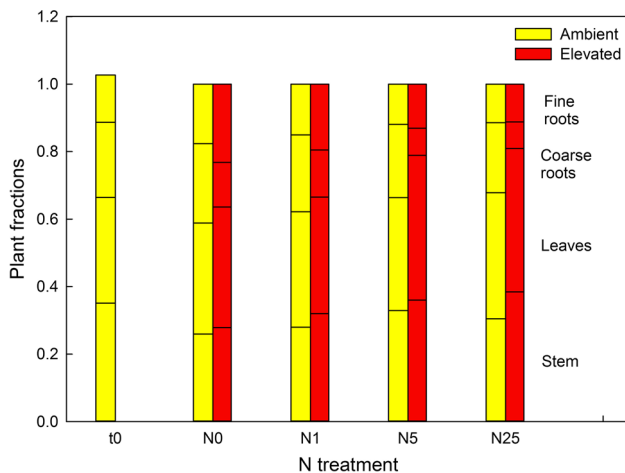


Fig. 1 Nitrogen productivities under ambient and elevated CO_2 . Circles deciduous species. Squares conifer species. Nitrogen treatments: black N0, red N1, green N5, yellow N25. The dotted line is the 1:1 line

allocation to leaves was 38% of total plant biomass, compared with 39% in the elevated treatment. Similarly, fine roots constituted 15 and 17% in the ambient and elevated CO_2 environments, respectively. The CO_2 treatments changed plant nitrogen concentrations (Fig. 3) although none of the changes were statistically significant. In the two highest N treatments (N5 and N25), contrary to expectations, the elevated CO_2 level actually increased

Table 2 Three-way ANOVA of treatment effects on nitrogen productivity

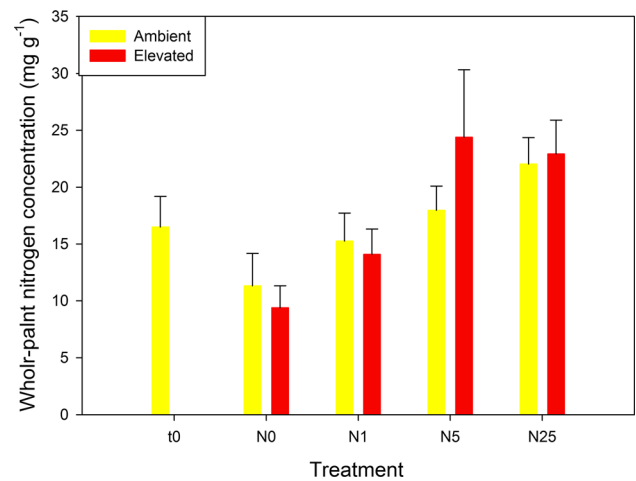
Effect	F value	p
CO ₂	1.94	0.1673
N	3.98	0.0109
Species	16.62	<0.0001
CO ₂ *N	1.25	0.2991
CO ₂ *species	0.60	0.8470

**Fig. 2** Relative allocation of plant biomass under ambient and elevated CO₂ and different N supply rates averaged over species. t0 is the allocation at the start of the experiment

plant nitrogen concentrations, whereas in the two low N treatments (N0 and N1) it lowered the concentrations. However, at the leaf level, there was a clear decrease in nitrogen concentration, from 28 to 23 mg g⁻¹ over all N treatments and species.

Discussion

We have demonstrated here that tree saplings response to elevated CO₂ can be described as an increase in nitrogen productivity although the evidences are not unequivocal as different statistics give different results, which is not surprising, given the factorial range of the experiment (2 CO₂ levels × 4 nutrient treatments × 12 species) and the limited number of plant individuals. The choice to not use replicates within species was a result of logistic restrictions and a desire to include as many species as possible in the study. To fully capture the growth response, we would also need information on the mean residence time of nitrogen in the plants, but measuring that was outside the scope of this study. Nevertheless, the estimated nitrogen productivities are in line with values reported previously (Ågren and

**Fig. 3** Whole-plant nitrogen concentration (mean and SE) under ambient and elevated CO₂ and different N doses (N0, N1, N5, N25) averaged over species. t0 is the concentration at the start of the experiment. The whiskers show the SE of the concentrations. None of the differences in concentrations between ambient and elevated CO₂ are statistically significant

Bosatta 1998) and the responses to CO₂ are in line with other studies (Table 1). The increase caused by increased CO₂ was higher than the 12% calculated in the DUKE FACE experiment (Finzi et al. 2002). However, in the latter experiment there was a steady decline from 20 to 4% in the response over the four years of the experiment. Our values are also higher than the 14% increase in relative growth rate, which is proportional to nitrogen productivity, under doubled CO₂ reported by Kirschbaum and Lambie (2015) for 78 experiments. The larger response in our study could be a result of a larger increase in CO₂ (from 380 to 1000 ppm) than in the cited studies and should probably be seen as an estimate of the maximal response. A response, with both increases and decreases in nitrogen and phosphorus productivity in response to increased CO₂, has been found by Huang et al. (2015). A critical aspect of our way of estimating nitrogen productivity is the assumption that the added N is taken up in an exponential fashion. However, to calculate the nitrogen productivity it is necessary to know the temporal pattern of nitrogen uptake and the assumption of an exponential uptake is the simplest, and deviations from this pattern are likely to be different between N levels, which should explain part of the differences between responses between N treatments. It has been shown that the temporal pattern of N uptake can greatly modify the growth pattern (Wikström 1994; Ågren and Bosatta 1998). However, as the level of N supply had limited effect on the estimated N productivity, this was probably not a major problem here. The constancy of allocation within the experiment (Fig. 2) is also an indication that growth should have followed an exponential pattern.

The observation that deciduous trees responded more strongly than conifers agrees with observations by Niinemets et al. (2011). The 20% decrease in leaf nitrogen concentration is similar to the value found by Ainsworth and Long (2005) in their meta-analysis of 12 FACE experiments.

Conclusions

Given the factorial range of the experiment and its limited number of plant individuals, our analysis confirms that nitrogen productivity is a robust concept to integrate the multiple components of growth responses to increasing atmospheric CO₂ concentrations. However, more studies are required to firmly establish the magnitude of the response. At the same time, the concept of nitrogen productivity provides a convenient tool for use at larger scales, as it bypasses some of the complex interactions between nitrogen and CO₂. The nitrogen productivity concept is also convenient to apply at the forest stand scale (Ågren 1983) and over longer time scales, bypassing some of the difficulties with spatial and temporal scaling (Way et al. 2015).

Author contribution statement JK performed the experiment. GÅ made the analyses. GÅ and JK wrote the manuscript.

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Compliance with ethical standards

Conflict of interest No conflict of interest.

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References

- Ågren GI (1983) Nitrogen productivity of some conifers. *Can J For Res* 13:494–500
- Ågren GI (1985) Theory for growth of plants derived from the nitrogen productivity concept. *Physiol Plant* 64:17–28
- Ågren GI (1996) Nitrogen productivity or photosynthesis minus respiration to calculate plant growth. *Oikos* 76:529–535
- Ågren GI, Bosatta E (1998) Theoretical ecosystem ecology- understanding element cycles. Cambridge University Press, Cambridge
- Ågren GI, Franklin O (2003) Root:shoot ratios, optimisation, and nitrogen productivity. *Ann Bot* 92:795–800
- Ainsworth EA, Long SP (2005) What have we learned from 15 years of free-air CO₂ enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO₂. *New Phytol* 165:351–372
- Curtis PS, Wang X (1998) A meta-analysis of elevated CO₂ effects on woody plant mass, form, and physiology. *Oecologia* 113:299–313
- Drake BG, González-Meler MA, Long SP (1997) More efficient plants: a consequence of rising atmospheric CO₂? *Annu Rev Plant Physiol Plant Mol Biol* 48:609–639
- Field CB, Chapin FS III, Matson PA, Mooney HA (1992) Responses to terrestrial ecosystems to the changing atmosphere: a resource-based approach. *Annu Rev Ecol Syst* 23:201–235
- Finzi AC, DeLucia EH, Hamilton JG, Richter DD, Schlesinger WH (2002) The nitrogen budget of a pine forest under free air CO₂ enrichment. *Oecologia* 132:567–578
- Finzi AC, Norby RJ, Calfapietra C, Gallet-Budynek A, Gielen B, Holmes WE, Hoosbeek MR, Iversen CM, Jackson RB, Kubiske ME, Ledford J, Liberloo M, Oren R, Polle A, Pritchardl S, Zak DR, Schlesinger WH, Ceulemans R (2007) Increases in nitrogen uptake rather than nitrogen-use efficiency support higher rates of temperate forest productivity under elevated CO₂. *Proc Nat Acad Sci USA* 104:14014–14019
- Hilbert DW, Larigauderie A, Reynolds JF (1991) The influence of carbon dioxide and daily photon-flux density on optimal leaf nitrogen concentration and root:shoot ratio. *Ann Bot* 68:365–376
- Huang W, Zhou G, Deng X, Liu J, Duan H, Zhang D, Chu G, Liu S (2015) Nitrogen and phosphorus productivities of five subtropical tree species in response to elevated CO₂ and N addition. *Eur J Forest Res* 134:845
- Ingestad T, Lund AB (1986) Theory and techniques for steady state mineral nutrition and growth of plants. *Scand J For Res* 1:439–453
- Kattge J (2002) Zur Bedeutung von Stickstoff für den CO₂—Düngeeffekt. Ph. D thesis, Justus-Liebig-University, Gießen
- Kirschbaum MUF, Lambie SM (2015) Re-analysis of plant CO₂ responses during the exponential growth phase: interactions with light, temperature, nutrients and water availability. *Funct Plant Biol* 10:989–1000
- Ladanai S, Ågren GI (2004) Temperature sensitivity of nitrogen productivity for Scots pine and Norway spruce. *Trees (Berlin)* 18:312–319
- Lou Y, Field CB, Mooney HA (1994) Predicting responses of photosynthesis and root fraction to elevated [CO₂]_a: interactions among carbon, nitrogen, and growth. *Plant Cell Environ* 17:1195–1204
- Niinemets Ü, Flexas J, Peñuelas J (2011) Evergreens favored by higher responsiveness to increased CO₂. *Trends Ecol Evol* 26:136–142
- Reich PB, Hobbie SE, Lee T, Ellsworth DS, West JB, Tilman D, Knops JMH, Naeem S, Trost J (2006) Nitrogen limitation constrains sustainability of ecosystem response to CO₂. *Nature* 440:922–925
- Taub DR, Wang X (2008) Why are nitrogen concentrations in plant tissues lower under elevated CO₂? A critical examination of the hypotheses. *J Integr Plant Biol* 50:1365–1374
- Way DA, Oren R, Kroner Y (2015) The space-time continuum: the effects of elevated CO₂ and temperature on trees and the importance of scaling. *Plant Cell Environ* 38:991–1007
- Wikström F (1994) A theoretical explanation of the Piper-Steenbjerg effect. *Plant Cell Environ* 17:1053–11060