Abstract Elevated concentrations of atmospheric CO₂ increase plant biomass, net primary production (NPP) and plant demand for nitrogen (N). The demand for N set by rapid plant growth under elevated CO₂ could be met by increasing soil N availability or by greater efficiency of N uptake. Alternatively, plants could increase their nitrogen-use efficiency (NUE), thereby maintaining high rates of growth and NPP in the face of nutrient limitation. We quantified dry matter and N budgets for a young pine forest exposed to 4 years of elevated CO₂ using free-air CO₂ enrichment technology. We addressed three questions: Does elevated CO₂ increase forest NPP and the demand for N by vegetation? Is demand for N met by greater uptake from soils, a shift in the distribution of N between plants, microbes, and soils, or increases in NUE under elevated CO₂? Will soil N availability constrain the NPP response of this forest as CO₂ fumigation continues? A step-function increase in atmospheric CO₂ significantly increased NPP during the first 4 years of this study. Significant increases in NUE under elevated CO₂ modulated the average annual requirement for N by vegetation in the first and third growing seasons under elevated CO₂: the average stimulation of NPP in these years was 21% whereas the average annual stimulation of the N requirement was only 6%. In the second and fourth growing seasons, increases in NPP increased the annual requirement for N by 27–33%. Increases in the annual requirement for N were largely met by increases in N uptake from soils. Retranslocation of nutrients prior to senescence played only a minor role in supplying the additional N required by trees growing under elevated CO₂. NPP was highly correlated with between-plot variation in the annual rate of net N mineralization and CO₂ treatment. This demonstrates that NPP is co-limited by C availability, as CO₂ from the atmosphere, and N availability from soils. There is no evidence that soil N mineralization rates have increased under elevated CO₂. The correlation between NPP and N mineralization rates and the increase in the annual requirement for N in certain years imply that soil N availability may control the long-term productivity response of this ecosystem to elevated CO₂. Although we have no evidence suggesting that NPP is declining in response to >4 years of CO₂ fumigation, if the annual requirement of N continues to be stimulated by elevated CO₂, we predict that the productivity response of this forest ecosystem will decline over time.

Keywords Elevated CO₂ · Nitrogen · Net primary production · N limitation · Nutrient-use efficiency

Introduction

The atmospheric concentration of CO₂ has increased from ~280 µl/l to ~360 µl/l during the past 150 years and may double during this century (IPCC 2001). Tree biomass increases under elevated atmospheric CO₂ (Bazzaz and Miao 1993; Curtis and Wang 1998; Zak et al 2000a; Hamilton et al. 2002), and forest productivity may be enhanced by the projected increase in atmospheric CO₂ (Schimel et al. 2001). However, the magnitude of the CO₂ response in woody plants can be constrained by the availability of soil nutrients, notably nitrogen (N) (McMurtrie and Commins 1996; Pan et al. 1998; Luo and Reynolds 1999; Zak et al. 2000a; Oren et al. 2001).

Rapid tree growth under elevated CO₂ increases plant demand for N (Norby et al. 1999). Increases in soil N availability via fertilization maintain high rates of tree growth under elevated CO₂ (Johnson et al. 1997; Prior et al. 1997; Murray et al. 2000; Zak et al. 2000a). It is un-
clear, however, if endogenous processes of N cycling will increase N availability when natural ecosystems are exposed to high CO₂ (reviewed in Zak et al. 2000b). If the N-uptake potential of vegetation under elevated CO₂ exceeds the rate of N replenishment to the available pool via mineralization (Rastetter et al. 1997) or exogenous inputs (Schlesinger 1997), vegetation may not acquire sufficient N to sustain the pulse of growth seen with initial exposure to elevated CO₂. In the absence of increases in N mineralization or exogenous N inputs, biogeochemical models predict little or no enhanced C storage in woody biomass as atmospheric CO₂ concentrations rise (McMurtrie and Commins 1996; Rastetter et al. 1997; Luo and Reynolds 1999).

In the absence of an increase in soil N availability, there are two mechanisms that could maintain rapid rates of plant growth under elevated CO₂: increases in nitrogen-use efficiency (NUE) and increases in the efficiency by which plants acquire available soil N. Increases in NUE imply greater C fixation per unit N acquired from soil (Birk and Vitousek 1986; Pastor and Bridgham 1999) and the maintenance of a C sink in woody biomass in N-limited ecosystems. NUE is rare measured in elevated CO₂ studies. Following 2 years of CO₂ enrichment in a North Carolina pine forest, Finzi et al. (2001) found that NUE in aboveground litterfall increased ~5%, although this effect was not statistically significant.

According to mass balance, an increase in the efficiency with which soil N is acquired by plants should cause a shift in the distribution of N within existing soil pools or decreased losses of N from an ecosystem under elevated CO₂. A decline in the N content of microbial-biomass is a likely, initial response because of the rapid turnover time of microbes (Paul and Clark 1986). However, a relatively limited number of studies have shown variable responses of soil microbial biomass to elevated CO₂ (Allen et al. 2000; Zak et al. 2000b) and no consistent changes in the size of the N pool in microbial biomass (Díaz et al. 1993; Hungate et al. 1999; Allen et al. 2000; Zak et al. 2000c; Hu et al. 2001). Thus there is equivocal evidence for a shift in N distribution away from soil microbial biomass to support plant uptake under elevated CO₂. A decrease in soil N content associated with the process of net mineralization could occur under elevated CO₂, but this would be very difficult to measure accurately because net mineralization constitutes a very small flux out of this very large pool (Binkley and Hart 1989).

More efficient retention of N within ecosystems exposed to elevated CO₂ could maintain N capital and lead to long-term increases in N cycling between plants and soils. There are very few reports of nutrient losses below the rooting zone of plants growing under elevated CO₂. Hungate et al. (1999) and Johnson et al. (2001) found a small decrease in N losses below the rooting zone of a scrub oak forest in Florida exposed to elevated CO₂, implying greater retention of available soil N. Similarly, there are few observations reporting gaseous losses of N under elevated CO₂. Hungate et al. (1997) found that elevated CO₂ and nutrient fertilization decreased emissions of NO following the onset of the rainy season in California grasslands. In contrast, Ambus and Robertson (1999) found no significant difference in N₂O fluxes in aspen stands exposed to elevated CO₂, and Smart et al. (1997) found higher gas fluxes of N in wheat systems exposed to elevated CO₂. Most studies do not place losses of N within the context of an overall ecosystem budget for N, making it difficult to interpret the importance of these losses as a mechanism maintaining or alleviating N limitation to net primary production (NPP) under elevated CO₂.

In this paper we present data on the pools and fluxes of dry matter and N for a young pine forest exposed to 4 years of elevated CO₂ using free-air CO₂ enrichment (FACE, Hendrey et al. 1999). With the dry matter and N budgets we address three questions: Does elevated CO₂ increase forest NPP and the demand for N by vegetation? Is demand for N met by greater uptake from soils, a shift in the distribution of N between plants, microbes, and soils, or increases in NUE under elevated CO₂? Will soil N availability constrain the NPP response of this forest as CO₂ fumigation continues?

Materials and methods

Site description

The FACE experiment in the Duke Forest (Orange County, N.C., USA) is composed of six 30-m-diameter plots. Three experimental plots are fumigated with CO₂ to maintain the atmospheric CO₂ concentration 200 µl l⁻¹ above ambient (i.e., 565 µl l⁻¹). Three control plots are fumigated with ambient air only (365 µl l⁻¹). The experiment began 27 August 1996 and is continuous (24 h day⁻¹; 365 days year⁻¹). Additional details on FACE operation can be found in Hendrey et al. (1999).

The forest is derived from 3-year-old loblolly pine (Pinus taeda) seedlings that were planted in 1983 in a 2.4×2.4-m spacing. In 1996, the 13-year-old pine trees were approximately 14 m tall and accounted for 98% of the basal area of the stand. Since planting, a deciduous understory layer has recruited from nearby hardwood forests and stump sprouts. The most abundant understory tree species is sweet gum (Liquidambar styraciflua), with admixtures of red maple (Acer rubrum), red bud (Cercis canadensis), and dogwood (Cornus florida). The 32-ha site contains an elevation gradient of 15 m between the highest and lowest points, but topographic relief is less than 1° throughout. Soils are classified as being from the Enon Series (fine, mixed, active, thermic Ultic Hapludalfs). Enon soils, derived from mafic bedrock, are slightly acidic (0.1 M CaCl₂ pH =5.75), and have well-developed soil horizons with mixed clay mineralogy. Additional site details can be found in Schlesinger and Lichter (2001) and Finzi et al. (2001).

Plant biomass pools, increments and turnover

During road construction at the FACE site, a small number of the 13-year-old loblolly pine trees were removed and used to develop allometric regressions between stem diameter and wood, bark, and coarse root mass (Naidu et al. 1996). Martin et al. (1998) and Whitaker and Marks (1975) published similar allometric relationships for several southern Appalachian hardwood species. In each of the six experimental plots all the woody vegetation was surveyed, including stem diameters, prior to the onset of CO₂ fumigation in August 1996. By using dendrometer bands to monitor di-