Abstract

Rising atmospheric CO₂ may stimulate future forest productivity, possibly increasing carbon storage in terrestrial ecosystems, but how tropospheric ozone will modify this response is unknown. Because of the importance of fine roots to the belowground C cycle, we monitored fine-root biomass and associated C fluxes in regenerating stands of trembling aspen, and mixed stands of trembling aspen and paper birch at FACTS-II, the Aspen FACE project in Rhinelander, Wisconsin. Free-air CO₂ enrichment (FACE) was used to elevate concentrations of CO₂ (average enrichment concentration 535 µl l⁻¹) and O₃ (53 nl l⁻¹) in developing forest stands in 1998 and 1999. Soil respiration, soil pCO₂, and dissolved organic carbon in soil solution (DOC) were monitored biweekly. Soil respiration was measured with a portable infrared gas analyzer. Soil pCO₂ and DOC samples were collected from soil gas wells and tension lysimeters, respectively, at depths of 15, 30, and 125 cm. Fine-root biomass averaged 263 g m⁻² in control plots and increased 96% under elevated CO₂. The increased root biomass was accompanied by a 39% increase in soil respiration and a 27% increase in soil pCO₂. Both soil respiration and pCO₂ exhibited a strong seasonal signal, which was positively correlated with soil temperature. DOC concentrations in soil solution averaged ~12 mg l⁻¹ in surface horizons, declined with depth, and were little affected by the treatments. A simplified belowground C budget for the site indicated that native soil organic matter still dominated the system, and that soil respiration was by far the largest flux. Ozone decreased the above responses to elevated CO₂, but effects were rarely statistically significant. We conclude that regenerating stands of northern hardwoods have the potential for substantially greater C input to soil due to greater fine-root production under elevated CO₂. Greater fine-root biomass will be accompanied by greater soil C efflux as soil respiration, but leaching losses of C will probably be unaffected.

Keywords: Northern forests · Global change · Carbon sequestration · Soil respiration · Dissolved organic carbon · Soil pCO₂

Introduction

Decades of experimentation using growth chambers, glasshouses, and open-top chambers (OTCs) have provided evidence that rising atmospheric CO₂ will increase tree productivity in the absence of strong limitation by other resources (Ceulemans and Mousseau 1994; Curtis 1996; Wulfschlegel et al. 1997; Curtis and Wang 1998; Ceulemans et al. 1999). Productivity may be further stimulated by nitrogen (N) deposition (Galloway et al. 1995; Vitousek et al. 1997), warmer global temperatures, and a more vigorous hydrologic cycle (Houghton et al. 1996). Less attention has been given to gaseous pollutants that may dampen or even reverse the stimulating effect of elevated CO₂.
Coincident with the rise in atmospheric CO$_2$ over the past 150 years, ambient levels of O$_3$ have risen from <10 nl l$^{-1}$ to the current 30–40 nl l$^{-1}$ background levels today (Hough and Derwent 1990; Levy et al. 1997; Crutzen 1998; Percy et al. 2000). Elevated O$_3$ experiments using charcoal-filtered air as a treatment have repeatedly demonstrated that plant growth is currently constrained by ambient levels of ozone (Pye 1988; Baker et al. 1994; Taylor et al. 1994; Karnosky et al. 1996), and atmospheric O$_3$ concentrations are expected to continue to rise (Hough and Derwent 1990). Highly reactive O$_3$ binds to plasma membranes resulting in poor regulation of stomatal aperatures and damage to thylakoids, thereby inhibiting photosynthesis (Taiz and Zeiger 1991). These effects are directly antagonistic to those of elevated CO$_2$. Therefore, experiments (and models) that seek to provide insight into future forest productivity should explicitly examine the influence of these interacting gases.

Extending results from previous research in controlled environments to actual field conditions is a challenging but necessary advancement in ecology. Recently, investigators working at the FACTS-I project free-air carbon dioxide enrichment (FACE) experiment reported a 25% stimulation of total net primary production in a young loblolly pine stand after 2 years of fumigation with elevated CO$_2$ (Delucia et al. 1999). This degree of stimulation falls within the 16–31% increase in total biomass summarized from over 500 studies performed in growth chambers, glasshouses, and OTCs in a recent meta-analysis of the CO$_2$ literature (Curtis and Wang 1998). The consistency of results from different experimental scales lends confidence to our interpretation of tree responses to elevated CO$_2$, but knowledge of how rising tropospheric O$_3$ will affect the CO$_2$ growth response is still limited. In an earlier review of the literature, Pye (1988) reported reductions in growth from 2 to 69% (average 23%) for a variety of coniferous and deciduous tree species exposed to elevated O$_3$, although most studies were of seedlings and of short duration. More recently, rising tropospheric O$_3$ has been recognized as a possibly potent modifier of forest ecosystem responses to elevated atmospheric CO$_2$ (Bortier et al. 2000). The few OTC studies that have examined the interaction of elevated CO$_2$ and O$_3$ on woody perennial biomass (Dickson et al. 1998; Volin et al. 1998; Loats and Rebbeck 1999) show that elevated CO$_2$ tends to ameliorate the negative effects of O$_3$ on photosynthesis and growth (or conversely that O$_3$ decreased the stimulation due to elevated CO$_2$), but this is not always the case (Kull et al. 1996).

The importance of forests to the global carbon (C) cycle, particularly the potential to sequester C from that accumulating in the atmosphere, has been the focus of much ecophysiological science (Kramer 1981; Strain and Bazzaz 1983; Eamus and Jarvis 1989; Schimel 1995; Koch and Mooney 1996; Schlesinger 1997; Jarvis 1998). Of particular importance is how the capacity for long-term C storage of forest soils will be affected by the growth dynamics and chemical composition of ephemeral tissues (fine roots and foliage) (Allen et al. 2000; Martens 2000; Rosenzweig and Hillel 2000). Soil is the largest, most persistent reservoir of C in forests (Dixon et al. 1994; Schlesinger 1997), and turnover of ephemeral tissues provides the greatest annual input of C to that reservoir (Waring and Schlesinger 1985; Vogt et al. 1986). Quantification of belowground pools and fluxes of C has proven to be an exceedingly difficult task, however, because of high spatial heterogeneity and difficulty of observation within the soil. Although our knowledge of fine-root dynamics and responses to environmental change is improving (e.g., Hendrick and Pregitzer 1992; Pregitzer et al. 1995, 2000; Bernston and Bazzaz 1996; Reuss et al. 1996; Kubiske et al. 1998), the fate of C once allocated belowground is still poorly understood (Zak et al. 2000). By constraining estimates of C entering and exiting the system, and elucidating the transformations of C as it is converted from plant litter to stable soil organic matter, we should be able to arrive at a mechanistic understanding of the belowground C cycle.

To investigate the interactive effects of elevated CO$_2$ and O$_3$ on the belowground C cycle of an aggrading north-temperate forest, we monitored C pools and fluxes in soil during the first 2 years of fumigation at the FACTS-II, Aspen FACE project. This project uses FACE technology (Dickson et al. 2000) similar to that of the FACTS-I project in Durham, N.C., to enrich the air with CO$_2$ and O$_3$ in forest ecosystems while minimizing artifacts due to the fumigation hardware (Hendrey et al. 1999). In addition to the O$_3$ treatment, another factor that distinguishes this site from FACTS-I is the use of communities dominated by single (aspen) and multiple (aspen-birch) deciduous tree species. Trembling aspen (Populus tremuloides Michx.) is an early successional tree with high rates of photosynthesis and growth, and responds vigorously to disturbance. It has the widest distribution of any tree species in North America and is commercially important across its range (Perala 1990). Paper birch (Betula papyrifera Marsh.) is also an early successional species that co-occurs with trembling aspen across much of its range, and can be a strong competitor for resources when both species occupy the same sites (Barnes and Wagner 1981). We hypothesized that forest communities developing under elevated atmospheric CO$_2$ would exhibit greater soil C inputs due to greater production of fine roots, and that these responses would be decreased by elevated O$_3$. We expected the greater fine-root biomass under elevated CO$_2$ to stimulate soil C efflux as soil respiration and the production of dissolved organic C (DOC), but that these responses would be dampened with the addition of O$_3$. Finally, we reasoned that competition would be minimal at this early stage of stand development and did not expect to see large differences in response between the two community types.