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Effects of elevated CO_2 and O_3 on soil respiration under ponderosa pine

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Abstract

Soil respiration represents the integrated response of plant roots and soil organisms to environmental conditions and the availability of C in the soil. A multi-year study was conducted in outdoor sun-lit controlled-environment chambers containing a reconstructed ponderosa pine/soil–litter system. The study used a 2×2 factorial design with two levels of CO_2 and two levels of O_3 and three replicates of each treatment. The objectives of our study were to assess the effects of long-term exposure to elevated CO_2 and O_3, singly and in combination, on soil respiration, fine root growth and soil organisms. Fine root growth and soil organisms were included in the study as indicators of the autotrophic and heterotrophic components of soil respiration. The study evaluated three hypotheses: (1) elevated CO_2 will increase C assimilation and allocation belowground increasing soil respiration; (2) elevated O_3 will decrease C assimilation and allocation belowground decreasing soil respiration and (3) as elevated CO_2 and O_3 have opposing effects on C assimilation and allocation, elevated CO_2 will eliminate or reduce the negative effects of elevated O_3 on soil respiration. A mixed-model covariance analysis was used to remove the influences of soil temperature, soil moisture and days from planting when testing for the effects of CO_2 and O_3 on soil respiration. The covariance analysis showed that elevated CO_2 significantly reduced the soil respiration while elevated O_3 had no significant effect. Despite the lack of a direct CO_2 stimulation of soil respiration, there were significant interactions between CO_2 and soil temperature, soil moisture and days from planting indicating that elevated CO_2 altered soil respiration indirectly. In elevated CO_2, soil respiration was more sensitive to soil temperature changes and less sensitive to soil moisture changes than in ambient CO_2. Soil respiration increased more with days from planting in elevated than in ambient CO_2. Elevated CO_2 had no effect on fine root biomass but increased abundance of culturable bacteria and fungi suggesting that these increases were associated with increased C allocation belowground. Elevated CO_2 had no significant effect on microarthropod and nematode abundance. Elevated O_3 had no significant effects on any parameter except it reduced the sensitivity of soil respiration to changes in temperature.
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1. Introduction

Soil respiration is measured as the flux of CO_2 from the soil, and it integrates both autotrophic and heterotrophic sources (Hanson et al., 2000; Zak et al., 2000). The CO_2 in autotrophic respiration comes from the respiration of roots and associated mycorrhizae; its rate is closely linked to current photosynthesis, but root carbohydrate reserves also contribute (Ekblad and Högberg, 2001; Lin et al., 2001; Högberg et al., 2001). The CO_2 in heterotrophic respiration comes from the metabolism of rhizodeposited compounds from living roots and the metabolism of plant litter and soil organic matter by soil fauna and micro-organisms (Jones et al., 2004; Horwath et al., 1994; Zak et al., 2000).

Reviewing studies from different ecosystems, Raich and Potter (1995) concluded that soil temperature was the most important environmental variable for predicting soil respiration, followed by soil moisture. For example, soil temperature alone explained 72% of the temporal variation in soil respiration in a spruce forest (Subke et al., 2003),

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and 80% of the diel and seasonal variation in a mixed temperate hardwood forest (Davidson et al., 1998). An exponential increase in soil respiration with temperature is universally reported (e.g., Raich and Potter, 1995; Davidson et al., 1998; Lavigne et al., 2004). Soil respiration decreases as the soil moisture decreases (Burton et al., 1998; Davidson et al., 1998; Yuste et al., 2003).

Elevated CO_2 increases plant C assimilation (e.g., Norby et al., 2002), leading to increased fine root growth and mycorrhizal infection (Tingey et al., 2000) and is expected to increase soil respiration as it stimulates rhizodeposition and belowground C supply (Zak et al., 2000; Phillips et al., 2002; Pendall et al., 2004). Soil respiration increases with increases in fine root mass and substrate supply (Litton et al., 2003; Wang et al., 2003). In a closed-canopy deciduous forest, elevated CO_2 shifted C allocation to fine roots and leaves leading to increased soil respiration because of their rapid turnover (Norby et al., 2002). In Scots pine, elevated CO_2 increased both soil respiration and root respiration over a growing season (Janssens et al., 1998). Over a 2-year period, elevated CO_2 consistently increased soil respiration and root respiration in Douglas-fir mesocosms (Lin et al., 2001). In four free-air carbon dioxide enrichment studies, elevated CO_2 consistently increased soil respiration and the stimulation persisted for up to 6 years (King et al., 2004). The CO_2 stimulation was greater in young developing forest stands than in more established stands.

Ozone causes foliar injury, impairs stomatal function, reduces photosynthetic capacity, causes premature needle loss, decreases carbohydrate allocation to and storage in roots, and root biomass (Andersen, 2003). Consequently, O_3 is expected to decrease soil respiration, as it is closely related to C allocation to the roots and fine root biomass. For example, O_3 reduced soil respiration in both loblolly pine (Edwards, 1991b) and aspen stands (Coleman et al., 1996). However, increased soil respiration has also been reported (Andersen, 2000) which was linked to altered root metabolism and increased soil microbial respiration associated with increased root mortality and turnover.

The objectives of our study were to assess the effects of long-term exposure to elevated CO_2 and O_3, singly and in combination, on soil respiration, fine root growth and soil organisms. Fine root growth and soil organisms were included in the study as indicators of the autotrophic and heterotrophic components of soil respiration. Elevated CO_2 and O_3 have opposing effects on C allocation to roots, root growth and soil respiration. We tested three hypotheses: (1) Because elevated CO_2 increases C assimilation and allocation belowground, it will increase soil respiration; (2) Because elevated O_3 decreases C assimilation and allocation belowground, it will decrease soil respiration; and (3) Because of the opposing effects of elevated CO_2 and O_3 on C assimilation and allocation, elevated CO_2 will eliminate or reduce the negative effects of elevated O_3 on soil respiration.

2. Methods and materials

2.1. Experimental design

The experiment used a completely randomized design with two CO_2 treatments (ambient and elevated) and two O_3 treatments (low and elevated) with three replicates (three chambers per treatment combination) using a total of 12 chambers. The four treatment combinations were: ambient CO_2 and low O_3 (ACLO), ambient CO_2 and elevated O_3 (ACEO), elevated CO_2 and low O_3 (ECLO), and elevated CO_2 and elevated O_3 (ECEO).

2.2. Chamber design and operation

The trees were grown in 12 individual outdoor, sun-lit controlled-environment chambers, each of which controlled and manipulated CO_2 and O_3 concentrations as well as climatic and edaphic (soil temperature and volumetric soil moisture) conditions while maintaining natural diurnal and seasonal variability (Tingey et al., 1996). The aboveground portion of each chamber was 2 m wide, 1 m deep and 1.5 m tall at the back sloping to 1.3 m in the front. The aboveground chamber was covered with clear Teflon film except the rear wall which was Plexiglas. The above ground portion of the chamber was placed on a 0.2 m high wooden base and attached to the water-tight belowground chamber (2 m × 1 m × 1 m deep). The belowground chamber was made of 6 mm welded-aluminum plate and leak-tested prior to use (Tingey et al., 1996). The belowground chamber was placed in a pit in the ground so that the top of the chamber was just above ground level. The exterior walls of the belowground chamber were insulated with extruded polystyrene to minimize heat exchange between the belowground chamber and the surrounding soil (Tingey et al., 1996). Each belowground chamber contained two drains in the bottom to insure that water did not pool in the chamber.

Air temperature, dew point, CO_2 and O_3 concentrations were measured continuously at an instrument tower adjacent to the chambers and in each of the individual chambers at the top of the plant canopy (Tingey et al., 1996). Air temperature was measured using shielded-aspirated thermistors (Campbell Scientific, Logan Utah). The CO_2 concentration and dew point were measured in each chamber with a LI-COR LI-6262 CO_2/Dew Point monitor (Lincoln, NE). The target levels for the air temperature, CO_2, and dew point in each chamber were established in relation to ambient conditions. Every minute, the CO_2 concentration, air temperature and dew point (average of previous 60, 1 s values) data were sent to each chamber's programmable logic controller that used these ambient conditions and internal computer logic to determine the target level for CO_2, air temperature and dew point and controlled each chamber to their individual target levels (Tingey et al., 1996). Air temperature and vapor pressure deficit were continuously monitored in the