

## FEEDBACKS BETWEEN CLIMATE AND THE ATMOSPHERE IN DETERMINING FOREST GROWTH: CLIMATIC VARIATION MEDIATES CO<sub>2</sub> AND O<sub>3</sub> EFFECTS.

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### ABSTRACT

CO<sub>2</sub> and O<sub>3</sub> are accumulating in the atmosphere and are potent modifiers of forest growth, causing changes that could alter composition and functioning of forest ecosystems. We have examined the effects of elevated CO<sub>2</sub> (+CO<sub>2</sub>; 560ppm), elevated O<sub>3</sub> (+O<sub>3</sub>; 1.5X ambient), and their combination (+CO<sub>2</sub>+O<sub>3</sub>), on the growth and productivity of model aspen (*Populus tremuloides* Michx.) and aspen-birch (*Betula papyrifera* Marsh.) forest ecosystems growing in an open free-air exposure (FACE) system in northern Wisconsin USA. After eight years of fumigation, +CO<sub>2</sub> increased aspen tree and stand volume growth by 39 ± 9% and 38 ± 10%, respectively, whereas +O<sub>3</sub> decreased them by 27 ± 6% and 34 ± 4%, respectively. +CO<sub>2</sub>+O<sub>3</sub> resulted in a net canceling of the effects of the single gases on aspen growth. Forest growth responses to +CO<sub>2</sub> and +O<sub>3</sub> interacted strongly with present-day interannual variability in climatic conditions. The amount and timing of photosynthetically active radiation and temperature coinciding with growth phenology explained 33-61% of the annual variation in growth responses of aspen trees, and explained 20-63% of annual variation in growth responses of aspen tree stands.

During the extremely dry 2003 growing season the number of birch trees infested with bronze birch borer was 5.6-fold greater in +O<sub>3</sub> compared to controls, and 3.0-fold greater in O<sub>3</sub> compared to +CO<sub>2</sub> and +CO<sub>2</sub>+O<sub>3</sub> treatments. Decreased resistance to the wood borer and/or increased olfactory and visual cues for infesting drought-stricken trees whose stomates were leaky in the +O<sub>3</sub> treatments may be responsible for the heightened infestation rates of these important forest pests.

All of these results demonstrate multi-layered interacting influences of climate on tree responses to elevated CO<sub>2</sub> and O<sub>3</sub> and on other organisms that impact forest productivity.

### INTRODUCTION

There are two points of intersection between climate and the C cycle. First, climate models incorporate atmospheric CO<sub>2</sub> concentration as a parameter to mathematically force warming of the atmosphere within the models. Second, changes in climate can affect the function of C sources and sinks, both abiotic (e.g. carbonate rock weathering and reprecipitation) and biotic (e.g. photosynthesis and respiration by

terrestrial and marine organisms). However little is known about the second linkage: few have coupled the reverse process of climate change with potential effects on terrestrial ecosystem functioning in CO<sub>2</sub>-enriched and O<sub>3</sub>-enriched atmospheres. Effects of future climate change on forest ecosystems are largely unknown because many potential interacting processes are not clearly understood, especially growth responses and trophic interactions in elevated CO<sub>2</sub> interacting with climatic variables and other predominating pollutants such as tropospheric O<sub>3</sub>.

## RESULTS AND DISCUSSION

After eight years of treatments, +CO<sub>2</sub> increased aspen tree and stand volume growth by  $39 \pm 9\%$  and  $38 \pm 10\%$ , respectively, whereas +O<sub>3</sub> decreased them by  $27 \pm 6\%$  and  $34 \pm 4\%$ , respectively. Effects of both CO<sub>2</sub> and O<sub>3</sub> were negated for aspen when present in combination. It is not known if CO<sub>2</sub> and O<sub>3</sub> effects are additive in all circumstances. Likewise, cumulative stand basal area (BA) and volume for aspen were significantly greater in +CO<sub>2</sub> and lower in +O<sub>3</sub> compared to control ( $P < 0.05$ ). There was no difference in aspen stand BA or stand volume between the combination treatment (+CO<sub>2</sub>+O<sub>3</sub>) and the current ambient control. We found large year-to-year variation in the responses of annual relative growth increment (RGI) to the treatment gasses in aspen stands. The variation was not explained by the potentially limiting soil resources of N and H<sub>2</sub>O. Instead, we found a high correlation of RGI with the mean daily photosynthetic photon flux (PPF) during July and mean daily temperature during October of the previous year (Fig. 1). Both of these variables are known to interact with CO<sub>2</sub> and O<sub>3</sub> concentrations to affect photosynthetic carbon fixation.

Bronze birch borer infestations of paper birch significantly increased in +O<sub>3</sub> during the 2003 growing season. The number of infested birch trees in elevated O<sub>3</sub> was 5.6 times that of controls, and 3.0 times that of +CO<sub>2</sub> and +CO<sub>2</sub>+O<sub>3</sub> treatments. Before 2003, paper birch exhibited minimal foliar symptoms and no growth reductions in response to +O<sub>3</sub>. However, 2003 was marked by an unusually cool, cloudy spring and very dry summer. We hypothesize that either or both of these conditions predisposed paper birch to increased O<sub>3</sub> sensitivity that, in turn, decreased its resistance to the wood borer and/or increased olfactory and visual cues for infesting trees in the +O<sub>3</sub> treatments.

These relationships demonstrate interactions between interannual climatic variability and forest ecosystem responses to elevated CO<sub>2</sub> and O<sub>3</sub> that indicate a second, less-well-defined linkage between climate and the carbon cycle. The first linkage is the well-known contribution of atmospheric CO<sub>2</sub> to the “greenhouse” effect that makes Earth habitable and is implicated in global warming. The second, demonstrated here, is interannual changes in climatic variables interacting with atmospheric CO<sub>2</sub> and O<sub>3</sub> concentrations to affect ecosystem functions which include growth and plant-insect interactions. Some predictions of global atmospheric CO<sub>2</sub> build-up have begun to include the potential ameliorating effects of terrestrial ecosystem C storage, and some global climate models are beginning to appreciate the role of terrestrial vegetation in canopy-atmosphere heat exchanges. Predictions of forest ecosystem responses to increased atmospheric CO<sub>2</sub> and O<sub>3</sub> should also include the influence of interannual climatic variability on ecosystem responses to CO<sub>2</sub> and O<sub>3</sub>.

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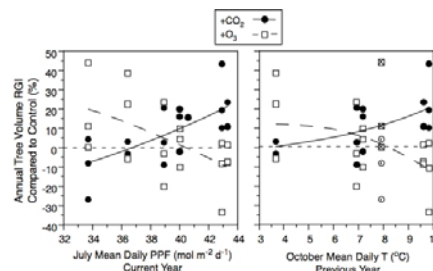


Figure 1. Significant ( $P < 0.05$ ) relationships of climatological variables versus annual relative volume growth increment (RGI) of aspen forests grown in atmospheres of +CO<sub>2</sub> or +O<sub>3</sub> compared to those in current atmosphere ( $n=3$ ).