INTERACTIVE EFFECTS OF CO$_2$ AND OZONE ON BIRCH TREES
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Trees grown in CO₂-enriched air nearly always exhibit increased rates of photosynthesis and biomass production, while trees grown in ozone (O₃)-enriched air tend to experience the opposite effects. So what happens when both of these trace constituents of the atmosphere increase together? This question is addressed in the present summary with respect to birch trees.

At the Free-Air CO₂ Enrichment (FACE) facility near Rhinelander, Wisconsin, USA, King et al. (2001) grew a mixture of paper birch and quaking aspen trees in 30-m-diameter plots that were maintained at atmospheric CO₂ concentrations of 360 and 560 ppm with and without exposure to elevated ozone (1.5 times the ambient ozone concentration) for a period of two years. And in their study of the belowground environment of the trees, they found that the extra ozone (O₃) had no effect on the growth of fine roots over that time period, but that elevated O₃ and CO₂ together increased the fine-root biomass of the mixed stand by 83%.

Simultaneously, and at the same FACE facility, Oksanen et al. (2001) observed O₃-induced injuries in the thylakoid membranes of the chloroplasts of the birch trees' leaves; but the injuries were partially ameliorated in the elevated CO₂ treatment. And in a study conducted two years later, Oksanen et al. (2003) say they "were able to visualize and locate ozone-induced H₂O₂ accumulation within leaf mesophyll cells, and relate oxidative stress with structural injuries." However, they report that "H₂O₂ accumulation was found only in ozone-exposed leaves and not in the presence of elevated CO₂," adding that "CO₂ enrichment appears to alleviate chloroplastic oxidative stress."

Across the Atlantic in Finland, Kull et al. (2003) constructed open-top chambers around two clones (V5952 and K1659) of silver birch saplings that were rooted in the ground and had been growing there for the past seven years. These chambers were fumigated with air containing 360 and 720 ppm CO₂ in combination with 30 and 50 ppb O₃ for two growing seasons, after which it was noted that the extra O₃ had significantly decreased branching in the trees' crowns. This malady, however, was almost completely ameliorated by a doubling of the air's CO₂ content. In addition, after one more year of study, Eichelmann et al. (2004) reported that, by itself, the increase in the air's CO₂ content increased the average net photosynthetic rates of both clones by approximately 16%, while the increased O₃ by itself caused a 10% decline in the average photosynthetic rate of clone V5952, but not of clone K1659. When both trace gases were simultaneously increased, however, the photosynthetic rate of clone V5952 once again experienced a 16% increase in net photosynthesis, as if the extra O₃ had had no effect when applied in the presence of the extra CO₂.

2 http://www.co2science.org/articles/V4/N49/B2.php
3 http://www.co2science.org/articles/V7/N26/B3.php
4 http://www.co2science.org/articles/V6/N17/B1.php
5 http://www.co2science.org/articles/V7/N24/B1.php
Working concurrently with the same trees, Riikonen et al. (2004)\(^6\) harvested them and reported finding that "the negative effects of elevated O\(_3\) were found mainly in ambient CO\(_2\), not in elevated CO\(_2\)." In fact, whereas doubling the air's O\(_3\) concentration decreased total biomass production by 13% across both clones, simultaneously doubling the air's CO\(_2\) concentration increased total biomass production by 30%, thereby more than compensating for the deleterious consequences of doubling the atmospheric ozone concentration.

In commenting on this ameliorating effect of elevated CO\(_2\), the team of Finnish scientists said it "may be associated with either increased detoxification capacity as a consequence of higher carbohydrate concentrations in leaves grown in elevated CO\(_2\), or decreased stomatal conductance and thus decreasing O\(_3\) uptake in elevated CO\(_2\) conditions (e.g., Rao et al., 1995)."

They also noted that "the ameliorating effect of elevated CO\(_2\) is in accordance with the results of single-season open-top chamber and growth chamber studies on small saplings of various deciduous tree species (Mortensen 1995; Dickson et al., 1998; Loats and Rebbeck, 1999) and long-term open-field and OTC studies with aspen and yellow-poplar (Percy et al., 2002; Rebbeck and Scherzer, 2002)."

In another paper to come out of the Finnish silver birch study, Peltonen et al. (2005)\(^7\) evaluated the impacts of doubled atmospheric CO\(_2\) and O\(_3\) concentrations on the accumulation of 27 phenolic compounds in the leaves of the trees, finding that elevated CO\(_2\) increased the concentration of phenolic acids (+25%), myricetin glycosides (+18%), catechin derivatives (+13%) and soluble condensed tannins (+19%). Elevated O\(_3\), on the other hand, increased the concentration of one glucoside by 22%, chlorogenic acid by 19%, and flavone aglycons by 4%. However, Peltonen et al. say that this latter O\(_3\)-induced production of antioxidant phenolic compounds "did not seem to protect the birch leaves from detrimental O\(_3\) effects on leaf weight and area, but may have even exacerbated them." Last of all, in the combined elevated CO\(_2\) and O\(_3\) treatment, they found that "elevated CO\(_2\) did seem to protect the leaves from elevated O\(_3\) because all the O\(_3\)-derived effects on the leaf phenolics and traits were prevented by elevated CO\(_2\)."

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6 http://www.co2science.org/articles/V8/N4/B3.php
7 http://www.co2science.org/articles/V8/N41/B2.php
Meanwhile, back at the FACE facility near Rhinelander, Wisconsin, USA, Agrell et al. (2005) had examined the effects of ambient and elevated concentrations of atmospheric CO$_2$ and O$_3$ on the foliar chemistry of birch and aspen trees, plus the consequences of these effects for host plant preferences of forest tent caterpillar larvae. In doing so, they had found that "the only chemical component showing a somewhat consistent co-variation with larval preferences was condensed tannins," and they discovered that "the tree becoming relatively less preferred as a result of CO$_2$ or O$_3$ treatment was in general also the one for which average levels of condensed tannins were most positively (or least negatively) affected by that treatment."

In this regard, it is of interest to note that the mean condensed tannin concentration of birch leaves was 18% higher in the elevated CO$_2$ and O$_3$ treatment. Consequently, as atmospheric concentrations of CO$_2$ and O$_3$ continue to rise, the increases in condensed tannin concentrations likely to occur in the foliage of birch trees should lead to their leaves becoming less preferred for consumption by the dreaded forest tent caterpillar, which according to Agrell et al. is "an eruptive generalist defoliator in North American hardwood forests, causing extensive damage during outbreak years (Fitzgerald, 1995)."

Also, because the amount of methane expelled in the breath of ruminants is an inverse function of the condensed tannin concentration of the foliage they consume, the increased foliage tannin concentrations likely to exist in a high-CO$_2$ world of the future should result in less methane being released to the atmosphere via ruminants ingesting such foliage, which phenomenon would tend to decrease the impetus for methane-induced global warming.

Concurrent with the work of Agrell et al., King et al. (2005) evaluated the effect of CO$_2$ enrichment alone, O$_3$ enrichment alone, and the net effect of both CO$_2$ and O$_3$ enrichment together on the growth of the Rhinelander birch trees, finding that relative to the ambient-air control treatment, elevated CO$_2$ increased total biomass by 45% in the aspen-birch community, while elevated O$_3$ caused a 13% reduction in total biomass relative to the control. Of most interest of all, the combination of elevated CO$_2$ and O$_3$ resulted in a total biomass increase of 8.4% relative to the control aspen-birch community. King et al. thus concluded that "exposure to even moderate levels of O$_3$ significantly reduces the capacity of net primary productivity to respond to elevated CO$_2$ in some forests." Consequently, they suggested that it makes sense to move forward with technologies that reduce anthropogenic precursors to photochemical O$_3$ formation, because the implementation of such a policy would decrease an important constraint on the degree to which forest ecosystems can positively respond to the ongoing rise in the air's CO$_2$ concentration.

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8 http://www.co2science.org/articles/V8/N31/B1.php
9 http://www.co2science.org/articles/V9/N13/B2.php
Another paper to come out of the Finnish silver birch study was that of Kostiainen et al. (2006)\(^{10}\), who studied the effects of elevated \(\text{CO}_2\) and \(\text{O}_3\) on various wood properties. Their work revealed that the elevated \(\text{CO}_2\) treatment had no effect on wood structure, but that it increased annual ring width by 21%, woody biomass by 23% and trunk starch concentration by 7%. Elevated \(\text{O}_3\), on the other hand, decreased stem vessel percentage in one of the clones by 10%; but it had no effect on vessel percentage in the presence of elevated \(\text{CO}_2\).

In discussing their results, Kostiainen et al. noted that "in the xylem of angiosperms, water movement occurs principally in vessels (Kozlowski and Pallardy, 1997)," and that "the observed decrease in vessel percentage by elevated \(\text{O}_3\) may affect water transport," obviously lowering it. However, as they continued, "elevated \(\text{CO}_2\) ameliorated the \(\text{O}_3\)-induced decrease in vessel percentage." In addition, they noted that "the concentration of nonstructural carbohydrates (starch and soluble sugars) in tree tissues is considered a measure of carbon shortage or surplus for growth (Korner, 2003)." Hence, they concluded that "starch accumulation observed under elevated \(\text{CO}_2\) in this study indicates a surplus of carbohydrates produced by enhanced photosynthesis of the same trees (Riikonen et al., 2004)." In addition, they reported that "during winter, starch reserves in the stem are gradually transformed to soluble carbohydrates involved in freezing tolerance (Bertrand et al., 1999; Piispanen and Saranpaa, 2001)," so that "the increase in starch concentration may improve acclimation in winter." Considering these several responses, therefore, it can be appreciated that the ongoing rise in the air's \(\text{CO}_2\) content should be a boon to silver birch (and likely many other trees) in both summer and winter in both pristine and ozone-polluted air.

Returning to the suite of Rhinelander FACE studies of paper birch, Darbah et al. (2007)\(^{11}\) found that the total number of trees that flowered increased by 139% under elevated \(\text{CO}_2\) but only 40% under elevated \(\text{O}_3\). Likewise, with respect to the quantity of flowers produced, they found that elevated \(\text{CO}_2\) led to a 262% increase, while elevated \(\text{O}_3\) led to only a 75% increase. They also determined that elevated \(\text{CO}_2\) had significant positive effects on birch catkin size, weight, and germination success rate, with elevated \(\text{CO}_2\) increasing the germination rate of birch by 110%, decreasing seedling mortality by 73%, increasing seed weight by 17% and increasing new seedling root length by 59%. On the other hand, they found that just the opposite was true of elevated \(\text{O}_3\).

\(^{10}\) http://www.co2science.org/articles/V9/N44/B1.php
\(^{11}\) http://www.co2science.org/articles/V10/N33/B2.php
success rate, with elevated CO\textsubscript{2} increasing the germination rate of birch by 110%, decreasing seedling mortality by 73%, increasing seed weight by 17% and increasing new seedling root length by 59%. On the other hand, they found that just the opposite was true of elevated O\textsubscript{3}, as it decreased the germination rate of birch by 62%, decreased seed weight by 25%, and increased new seedling root length by only 15%.

In discussing their findings, Darbah \textit{et al.} additionally reported that "the seeds produced under elevated O\textsubscript{3} had much less stored carbohydrate, lipids, and proteins for the newly developing seedlings to depend on and, hence, the slow growth rate." As a result, they concluded that "seedling recruitment will be enhanced under elevated CO\textsubscript{2} but reduced under elevated O\textsubscript{3}," which is another important reason to hope that the atmosphere's CO\textsubscript{2} concentration continues to climb as long as the air's O\textsubscript{3} content is in a significantly ascending mode.

One year later, back at the Aspen FACE site near Rhinelander, Wisconsin, \textit{Riikonen \textit{et al.} (2008)}\textsuperscript{12} studied physiological consequences of increases in the atmospheric concentrations of CO\textsubscript{2} (+36%) and O\textsubscript{3} (+39%) - both alone and in combination - in paper birch trees during the 8th-9th years of growing-season CO\textsubscript{2} enrichment.

And in doing so, they determined that elevated O\textsubscript{3} decreased net photosynthesis in birch short-shoot leaves by 27%, averaged over the growing season, and in birch long-shoot leaves by 23% in the late-season, while elevated CO\textsubscript{2} increased net photosynthesis in birch short-shoot leaves by 49% averaged over the growing season, and that in birch long-shoot leaves, measured in the late-season only, elevated CO\textsubscript{2} enhanced net photosynthesis by 42%. In addition, they observed that "elevated CO\textsubscript{2} delayed, and elevated O\textsubscript{3} tended to accelerate, leaf abscission in autumn." And when both treatments were applied together, they found that "elevated CO\textsubscript{2} generally ameliorated the effects of elevated O\textsubscript{3}," noting that "leaf stomatal conductance was usually lowest in the combination treatment, which probably caused a reduction in O\textsubscript{3} uptake."

Also publishing in the same year were \textit{Darbah \textit{et al.} (2008)}\textsuperscript{13}, who at various times over the 2004-2007 growing seasons collected many types of data pertaining to flowering, seed production, seed germination and new seedling growth and development of young paper birch trees. And giving results for \textit{O\textsubscript{3} elevation first and CO\textsubscript{2} enrichment second} (as best can be determined from Darbah \textit{et al.}'s graphs and text), the following percentage changes were derived for: (1) number of \textit{trees} producing male flowers: (+86%, +140%) in 2006, (+70%, +70%) in 2007, (2) total number of male \textit{flowers} produced (+58%, +260%) in 2006, (+68%, +82%) in 2007, (3) mean catkin or flower cluster mass (-8%, +12%) in 2004, (4) mean seed mass (-22%, +10%) in 2004, (-24%, +17%) in 2005, (-22%, -2%) in 2006, (5) mean seed germination success (-70%, +70%) in 2004, (-60%, +110%) in 2005, (-50%, +20%) in 2006, (6) mean seedling mortality, where the greatest reductions represent the greatest benefits, (-9%, -73%) in 2004, (7) mean seedling root length (+15%, +59%) in 2004, (8) mean seedling shoot length (-7%, +21%) in 2004, (9) mean seedling cotyledon length (-5%, +13%) in 2004, and (10) mean seedling dry mass after ~5 months growth in \textit{ambient} air (-38%, +69%) in 2004. And in summarizing their findings, the six researchers wrote that "in this study, we found that elevated CO\textsubscript{2} enhances and elevated O\textsubscript{3} decreases birch reproduction and

\textsuperscript{12}http://www.co2science.org/articles/V11/N20/B3.php
\textsuperscript{13}http://www.co2science.org/articles/V11/N43/B1.php
early seedling growth," while in the concluding sentence of their abstract, they wrote that "the evidence from this study indicates that elevated CO$_2$ may have a largely positive impact on forest tree reproduction and regeneration while elevated O$_3$ will likely have a negative impact." Yet radical environmentalists and climate alarmists continue to brand CO$_2$ a harmful air pollutant, with many governmental agencies in nations the world over actually buying into this outrageous misrepresentation of reality.

In another study from the same year, Kostiainen et al. (2008)$^{14}$ investigated the interactive effects of elevated concentrations of CO$_2$ and O$_3$ on the wood chemistry of paper birch saplings at the Aspen FACE facility in Rhinelander, Wisconsin, where the saplings had been exposed to four treatments - control, elevated CO$_2$ (560 ppm), elevated O$_3$ (1.5 x ambient) and their combination - for five growing seasons. And in doing so, they found that the paper birch saplings exhibited a tendency for increased stem diameter in elevated CO$_2$, which also caused "an increase in extractives" - such as fats, waxes, triterpenoids and steroids - which have important roles to play in defense against pathogens and other biotic attacks. And as a result, the nine researchers concluded that the increased growth they observed in response to elevated CO$_2$ "can be foreseen to shorten rotation lengths, with only moderate changes in wood properties," which is good. On the other hand, they said that "in response to elevated O$_3$, stem wood production decreased and was accompanied by changes in vessel properties, which may indicate decreasing efficiency of water and nutrient transport," which is not good. Hence, it is indeed fortunate that the major negative effects of the elevated O$_3$ concentration were reversed by the positive effects of the elevated CO$_2$ concentration.

Contemporaneously, Uddling et al. (2008)$^{15}$ studied how a 40% increase in CO$_2$ and O$_3$, alone and in combination, affected tree water use of mixed aspen-birch forests in the Rhinelander, Wisconsin FACE study, where sap flux and canopy leaf area index ($L$) were measured during two growing seasons, when steady-state $L$ had been reached after more than 6 years of exposure to elevated CO$_2$ and O$_3$. This work revealed that the 40% increase in atmospheric CO$_2$ concentration increased tree size and $L$ by 40%, while the 40% increase in O$_3$ concentration decreased tree size and $L$ by 22%, in the aspen-birch stands. And thus it was not surprising to learn that the combined effect of the two trace gas increases was an 18% increase in maximum stand-level sap flux in the mixed tree stands.

Also publishing in this very productive research year at the Wisconsin FACE facility were Pregitzer et al. (2008)$^{16}$, who reported that "all root biomass sampling previous to 2002 showed that O$_3$ exposure, alone or in

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$^{14}$ http://www.co2science.org/articles/V11/N48/B1.php  
$^{15}$ http://www.co2science.org/articles/V11/N49/B1.php  
$^{16}$ http://www.co2science.org/articles/V11/N51/EDIT.php
combination with elevated CO\textsubscript{2}, consistently resulted in lower coarse root biomass for all plant communities." In their analysis of subsequent data, however, they found that +O\textsubscript{3} in combination with +CO\textsubscript{2} increased coarse root biomass in birch/aspen communities, leading them to conclude that the amount of carbon being allocated to fine-root biomass under elevated O\textsubscript{3} was increasing over time relative to the control, especially in the +CO\textsubscript{2} +O\textsubscript{3} treatment, in contrast with most shorter-term results. And in light of these findings, they concluded that "the positive effects of elevated CO\textsubscript{2} on belowground net primary productivity may not be offset by negative effects of O\textsubscript{3}.

Back in Finland, Vapaavuori et al. (2009)\textsuperscript{17} grew 20 initially-seven-years-old individual trees of each of two different silver birch (Betula pendula Roth) clones -- 4 and 80 (V5952 and K1659, respectively, in the Finnish forest genetic register) -- for a period of three years (1999-2001) out-of-doors at the Suonenjoki Research Unit site of the Finnish Forest Research Institute within individual open-top chambers maintained at all combinations of (1) ambient CO\textsubscript{2} and ambient O\textsubscript{3}, (2) ambient CO\textsubscript{2} and double O\textsubscript{3}, (3) double CO\textsubscript{2} and ambient O\textsubscript{3}, and (4) double CO\textsubscript{2} and double O\textsubscript{3}, where CO\textsubscript{2} treatments were imposed 24 hours per day, and where O\textsubscript{3} treatments were imposed for 12, 12 and 14 hours per day in 1999, 2000 and 2001, respectively, throughout the course of which experiment they measured a variety of plant physiological responses to the four different treatments, including net photosynthesis, leaf stomatal conductance, leaf soluble proteins, leaf phenolic compounds, leaf nutrient concentrations, trunk and branch growth, physiology of the foliage and root systems, crown structure, wood properties, and interactions with folivorous insects. And when all was said and done, the twelve scientists reported that the negative effects of elevated O\textsubscript{3} on the various growth parameters and properties of the trees "were mainly found in ambient CO\textsubscript{2}," noting that elevated CO\textsubscript{2} typically "reversed or diminished the effects of elevated O\textsubscript{3}.

Lastly, returning to the Rhinelander (Wisconsin, USA) FACE facility, Zak et al. (2011)\textsuperscript{18} preface their work by noting an insufficient amount of soil nitrogen (N) and an overabundance of atmospheric ozone (O\textsubscript{3}) have often been claimed to either partially or totally repress the many positive effects of elevated atmospheric CO\textsubscript{2} concentrations on plant growth and development, especially in the case of long-lived woody plants such as trees; but they state that the combined effects of elevated CO\textsubscript{2} and O\textsubscript{3} (eCO\textsubscript{2} and eO\textsubscript{3}) "remain undocumented in the context of long-term, replicated field experiments." And to fill this void, they describe how they conducted such an experiment and what they learned from it.

The four researchers tell how in 1997 they planted one-half of each of 12 FACE plots with various trembling aspen (Populus tremuloides) genotypes (8, 42, 216, 259, 271) of differing CO\textsubscript{2} and O\textsubscript{3} sensitivities, while one-quarter of each ring was planted with a single aspen genotype (226) and paper birch (Betula papyrifera), and another quarter of each ring was planted with the same single aspen genotype and sugar maple (Acer saccharum). These treatments, each of which was replicated four times, were maintained for the following twelve years at either ambient CO\textsubscript{2} and O\textsubscript{3} (aCO\textsubscript{2} and aO\textsubscript{3}), aCO\textsubscript{2} and eO\textsubscript{3}, eCO\textsubscript{2} and aO\textsubscript{3}, or eCO\textsubscript{2} and eO\textsubscript{3} -- where eCO\textsubscript{2} was 560 ppm,

\textsuperscript{17} http://www.co2science.org/articles/V13/N15/B3.php
\textsuperscript{18} http://www.co2science.org/articles/V15/N12/EDIT.php
and where eO$_3$ was in the range of 50-60 nmol/mol -- while numerous types of pertinent data were concurrently collected.

In reference to the notorious progressive nitrogen limitation hypothesis, Zak et al. say they "found no evidence of this effect after 12 years of eCO$_2$ exposure." In fact, they report that relative to net primary production (NPP) under aCO$_2$, there was a 26% increase in NPP over the last three years of the study, which for a more standard 300-ppm increase in atmospheric CO$_2$ concentration equates to an approximate 42% increase in NPP, which they say "was sustained by greater root exploration of soil for growth-limiting N, as well as more rapid rates of litter decomposition and microbial N release during decay."

With respect to the concomitant stress of O$_3$ pollution, the researchers report that "despite eO$_3$-induced reductions in plant growth that occurred early in the experiment (i.e., after three years of exposure), eO$_3$ had no effect on NPP during the 10th-12th years of exposure," which response, in their words, "appears to result from the compensatory growth of eO$_3$-tolerant genotypes and species as the growth of eO$_3$-sensitive individuals declined over time (Kubiske et al., 2007; Zak et al., 2007), thereby causing NPP to attain equivalent levels under ambient O$_3$ and elevated O$_3$."

In discussing various aspects of their long-term findings, Zak et al. state that "NPP in the three plant communities responded similarly to the combined eCO$_2$ and eO$_3$ treatment." And they say that "given the degree to which eO$_3$ has been projected to decrease global NPP (Felzer et al., 2005), the compensatory growth of eO$_3$-tolerant plants in our experiment should be considered in future simulations and, depending on the generality of this response, could dramatically diminish the negative effect of eO$_3$ on NPP and carbon storage on land as well as projected increases in anthropogenic CO$_2$ and climate warming (Stitch et al., 2007)."

Continuing in this vein, the four researchers ultimately conclude -- contrary to the analysis of Norby et al. (2010) -- that if forests of similar composition growing throughout northeastern North America respond in the same manner as those in their experiment (Cole et al., 2009), then enhanced forest NPP under eCO$_2$ may be sustained for a longer duration than had previously been thought possible. In addition, they suggest that "the negative effect of eO$_3$ may be diminished by compensatory growth of eO$_3$-tolerant plants as they begin to dominate forest communities (Kubiske et al., 2007; Zak et al., 2007), suggesting that aspects of biodiversity like genetic diversity and species composition are important components of ecosystem response to this agent of global change."

In brief summation of these many positive findings, it can safely be concluded that from the tops of their crowns to the tips of their roots, Earth's birch trees are generally negatively affected by rising ozone concentrations; but when the air's carbon dioxide concentration is also rising, these negative effects are often totally eliminated and replaced by positive responses.

**REFERENCES**


