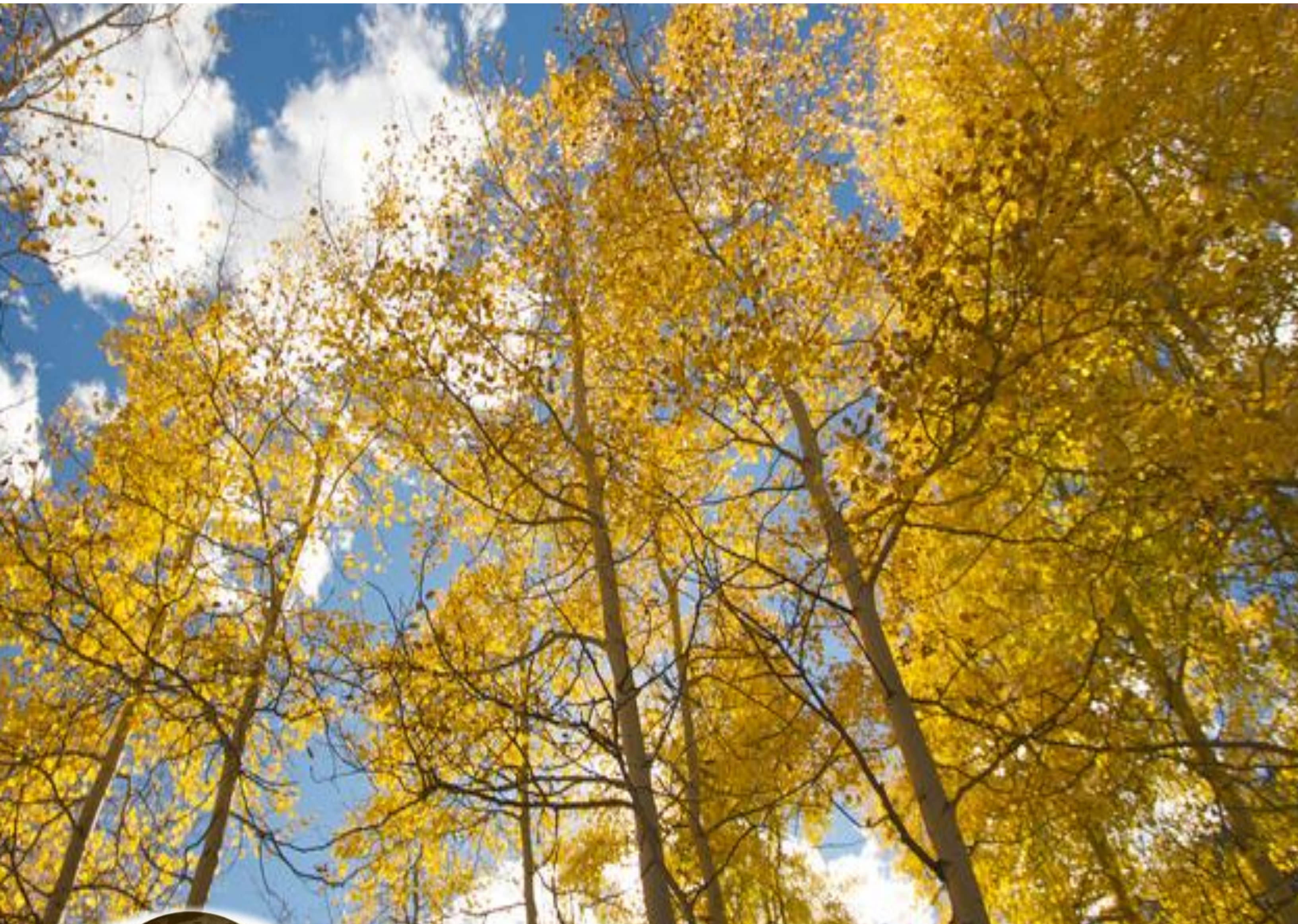
GROWTH RESPONSE OF ASPEN TREES TO ELEVATED CARBON DIOXIDE AND OZONE



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GROWTH RESPONSE OF ASPEN TREES TO ELEVATED CARBON DIOXIDE AND OZONE

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Karnosky *et al*. (1999)[1] described how they had grown O_3-sensitive and O_3-tolerant aspen clones in 30-m diameter plots at the Aspen FACE site near Rhinelander, Wisconsin, USA, where the young trees were maintained at atmospheric CO_2 concentrations of either 360 or 560 ppm either with or without exposure to elevated O_3 (1.5 times the ambient ozone concentration). And there, after one year of growth at ambient CO_2, they determined that the elevated O_3 had caused visible injury to leaves of both types of aspen, with the average percent damage in O_3-sensitive clones being more than three times as great as that observed in O_3-tolerant clones (55% vs. 17%, respectively). In combination with elevated CO_2, however, the O_3-induced damage to the leaves of these same clones was only 38% and 3%, respectively. And so they learned that elevated CO_2 prevented much of the foliar damage that would otherwise have been induced by the high O_3 concentrations.

King *et al*. (2001)[2] studied the same young trees for a period of two years, concentrating on belowground growth, where elevated O_3 alone had no effect on fine-root biomass. When the two aspen clones were simultaneously exposed to elevated CO_2 and O_3, however, there was an approximate 66% *increase* in the fine-root biomass of both of them, while back aboveground, Wustman *et al*. (2001)[3] found that the aspen clones exposed to both elevated ozone and CO_2 had 40% fewer visible foliar injuries than clones exposed to elevated ozone and ambient CO_2.

> *CO_2-induced increases in maximal rates of net photosynthesis were typically maintained, and sometimes even increased, during simultaneous exposure to elevated O_3.*

Also working at the same experimental facility, Noormets *et al*. (2001)[4] studied the interactive effects of O_3 and CO_2 on photosynthesis, finding that elevated CO_2 increased rates of photosynthesis in both clones at all leaf positions. Maximum rates of photosynthesis were increased in the O_3-tolerant clone by averages of 33 and 49% due to elevated CO_2 alone and in combination with elevated O_3, respectively, while in the O_3-sensitive clone they were increased by 38% in both cases. Hence, CO_2-induced increases in maximal rates of net photosynthesis were typically maintained, and sometimes even *increased*, during simultaneous exposure to elevated O_3.

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[1] http://www.co2science.org/articles/V3/N6/B1.php.
[2] http://www.co2science.org/articles/V4/N26/B1.php.
[3] http://www.co2science.org/articles/V5/N2/B1.php.
[4] http://www.co2science.org/articles/V4/N26/B3.php.

In another phase of the same experiment, Oksanen *et al*. (2001)[5] found that after three years of treatment, ozone exposure caused significant structural injuries to thylakoid membranes and the stromal compartments within the chloroplasts of the trees' leaves; but they reported that these injuries were largely ameliorated by atmospheric CO_2 enrichment. Likewise, leaf thickness, mesophyll tissue thickness, the amount of chloroplasts per unit cell area, and the amount of starch in the leaf chloroplasts were all decreased in the high ozone treatment; but simultaneous exposure of the ozone-stressed trees to elevated CO_2 *more* than compensated for the ozone-induced reductions.

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Then, after *four* years of growing five aspen clones with varying degrees of tolerance to ozone under the same experimental conditions, McDonald *et al*. (2002)[6] developed what they termed a "competitive stress index," based on the heights of the four nearest neighbors of each tree, in order to study the influence of competition on the CO_2 growth response of the various clones as modified by ozone. In general, elevated O_3 reduced aspen growth independent of competitive status, while the authors noted an "apparent convergence of competitive performance responses in $+CO_2$ $+O_3$ conditions," which they said suggests that "stand diversity may be maintained at a higher level" in such circumstances.

Percy *et al*. (2002)[7] also utilized the same experimental setting to assess a number of the aspen trees' growth characteristics, as well as the responses of one plant pathogen and two insects with different feeding strategies that typically attack the trees. Of the plant pathogen studied, they noted that "the poplar leaf rust, *Melampsora medusae*, is common on aspen and belongs to the most widely occurring group of foliage diseases." As for the two insects, they reported that "the forest tent caterpillar, *Malacosoma disstria*, is a common leaf-chewing lepidopteran in North American hardwood forests" and that "the sap-feeding aphid, *Chaitophorus stevensis*, infests aspen throughout its range." Hence, the rust and the two insect pests the scientists studied are widespread and have significant deleterious impacts on trembling aspen and other tree species. As but one example of this fact, Percy *et al*. noted that, "historically, the forest tent caterpillar has defoliated more deciduous forest than any other insect in North America" and that "outbreaks can reduce timber yield up to 90% in one year, and increase tree vulnerability to disease and environmental stress."

[5] http://www.co2science.org/articles/V4/N49/B2.php.
[6] http://www.co2science.org/articles/V6/N8/B1.php.
[7] http://www.co2science.org/articles/V6/N9/B1.php.

By itself, Percy *et al*. found that elevated O_3 decreased tree height and trunk diameter, increased rust occurrence by nearly fourfold, improved tent caterpillar performance by increasing female pupal mass by 31%, and had a strong negative effect on the natural enemies of aphids. The addition of the extra CO_2, however, *completely ameliorated* the negative effects of elevated O_3 on tree height and trunk diameter, *reduced* the O_3-induced enhancement of rust development from nearly fourfold to just over twofold, *completely ameliorated* the enhancement of female tent caterpillar pupal mass caused by elevated O_3, and also *completely ameliorated* the reduction in the abundance of natural enemies of aphids caused by elevated O_3.

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One year later in another study from the Aspen FACE site, Holton *et al*. (2003)[8] raised parasitized and non-parasitized forest tent caterpillars on two quaking aspen genotypes (O_3-sensitive and O_3-tolerant) alone and in combination for one full growing season; and they too found that elevated O_3 improved tent caterpillar performance under ambient CO_2 conditions, *but not in CO_2-enriched air*. Thus, it is clear that elevated ozone concentrations have a number of significant negative impacts on the well-being of North America's most widely distributed tree species, while elevated carbon dioxide concentrations have a number of significant positive impacts that often *completely eliminate* the negative impacts of elevated O_3. Hence, if the tropospheric O_3 concentration continues to rise as expected (Percy *et al*. note that "damaging O_3 concentrations currently occur over 29% of the world's temperate and subpolar forests but are predicted to affect fully 60% by 2100"), we had better hope that the air's CO_2 content continues to rise as well, for if it doesn't rise, aspen trees will likely find themselves in a world of hurt.

Working at the same site and publishing concurrently were Oksanen *et al*. (2003)[9], who reported they were able to "visualize and locate ozone-induced H_2O_2 [hydrogen peroxide] accumulation within leaf mesophyll cells, and relate oxidative stress with structural injuries in aspen." In addition, they discovered that "H_2O_2 accumulation was found only in ozone-exposed

[8] http://www.co2science.org/articles/V6/N51/B2.php.
[9] http://www.co2science.org/articles/V7/N26/B3.php.

leaves and not in the presence of elevated CO_2," leading them to conclude that "CO_2 enrichment appears to alleviate chloroplastic oxidative stress."

Two years later, and still hard at work at the Aspen FACE site near Rhinelander, Wisconsin, King *et al*. (2005)[10] 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 after seven full years of treatment. This work revealed that relative to the ambient-air treatment, elevated CO_2 increased total biomass by 25% while elevated O_3 decreased it by 23%. Of most interest of all, however, the combination of elevated CO_2 and O_3 resulted in a total biomass response of -7.8% relative to the control. 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." And they consequently 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.

We had better hope that the air's CO_2 content continues to rise as well, for if it doesn't rise, aspen trees will likely find themselves in a world of hurt.

After one more year of data collection, Kubiske *et al*. (2006)[11] found that individual tree and stand growth at the Wisconsin FACE site were significantly increased by the elevated CO_2 treatment but decreased by the elevated O_3 treatment, while the two effects essentially negated each other for no net change in the combined CO_2 plus O_3 treatment. However, they also found that "growth in elevated CO_2 continued to increase each year but at a decreasing rate," such that "the annual growth increases under elevated CO_2 became smaller with each successive year." And thus it was that they examined several possible explanations for this phenomenon, including N limitations and water limitations.

In conducting this investigation, the eight researchers found that "inter-annual variation in soil moisture did not modify the CO_2 or O_3 responses," and that "N limitations on growth did not differ among treatments." In addition, they determined that "root-specific uptake of nitrate or ammonium was not affected by elevated CO_2 or O_3." What they *did* find, however, was that the growth response to elevated CO_2 "paralleled decreasing July PPF [photosynthetic photon flux] from 2001 through 2004, and decreasing previous October temperatures from 2001 to 2003." Therefore, Kubiske *et al*. concluded that "a several-year trend of increasingly cloudy summers and cool autumns were responsible for the decrease in CO_2 growth response," explaining that "July PPF directly influences the amount of photosynthate available for stem volume growth," and that "October temperature in the north-temperate latitudes is of major importance in the photosynthetic activity of trees before leaf senescence," the stored products of which are used "to support the determinate growth phase the following year."

[10] http://www.co2science.org/articles/V9/N13/B2.php.
[11] http://www.co2science.org/articles/V9/N35/B1.php.

Reporting the results of their study of the Wisconsin aspen trees during the 8th and 9th years of growing-season CO_2 enrichment, Riikonen *et al*. (2008)[12] stated that elevated O_3 decreased net photosynthesis in aspen clone 42E by 30% and clone 271 by 13%, averaged over the growing season, and in aspen clone 216 by 42% in the late-season, while elevated CO_2 increased net photosynthesis in aspen clones 42E and 271 by 73 and 52%, respectively, averaged over the growing season, and that in aspen clone 216, measured in the late-season only, elevated CO_2 enhanced net photosynthesis by 42%. They also observed that "elevated CO_2 delayed, and elevated O_3 tended to accelerate, leaf abscission in autumn." And when both treatments were applied together, they found that "elevated CO_2 generally ameliorated the effects of elevated O_3," noting that "leaf stomatal conductance was usually lowest in the combination treatment, which probably caused a reduction in O_3 uptake."

Writing contemporaneously, Kostiainen *et al*. (2008)[13] reported the results of their study of interactive effects of elevated concentrations of CO_2 and O_3 on radial growth, wood chemistry and structure of five 5-year-old trembling aspen clones at the Wisconsin FACE facility, where they had been exposed to four treatments - control, elevated CO_2 (560 ppm), elevated O_3 (1.5 x ambient) and their combination - for five full growing seasons. This work revealed that "elevated CO_2 in the presence of ambient O_3 tended to increase, and elevated O_3 in the presence of ambient CO_2 tended to decrease, stem radial growth," whereas "stem radial growth of trees in the combined elevated CO_2 + O_3 treatment did not differ from controls." In addition, they indicated that none of the structural variables of the aspen wood were affected by the elevated CO_2 treatment, but that elevated O_3 tended to decrease vessel lumen diameter.

Reporting on another aspect of the long-term aspen study at the Wisconsin FACE facility, Udling *et al*. (2008)[14] investigated how a 40% increase above ambient values in CO_2 and O_3, alone and in combination, affected tree water use where "measurements of sap flux and canopy leaf area index (*L*) were made 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 increased tree size and *L* by 40%, while the 40% increase in O_3 concentration decreased tree size and *L* by 22%. Hence, 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 addition, they observed that elevated O_3 predisposed aspen stands to drought-induced sap flux reductions, whereas increased tree water use in response to elevated CO_2 did not result in lower soil water content in the upper soil or decreasing sap flux relative to control values during dry periods.

It can thus be appreciated that the negative effects of O_3 enrichment on tree growth and leaf development were *more* than compensated by the positive effects of an equal percentage increase in atmospheric CO_2 concentration. And although the net effect on sap flux was positive (so that the trees transferred more water to the atmosphere), when the aspen stands needed moisture most (during times of drought), the water they needed was available to them, possibly because they "were growing in soil with CO_2-induced increases in litter build-up and

[12] http://www.co2science.org/articles/V11/N20/B3.php.
[13] http://www.co2science.org/articles/V11/N48/B1.php.
[14] http://www.co2science.org/articles/V11/N49/B1.php.

water-holding capacity of the upper soil," whereas these latter two benefits and the extra water they could supply to the trees were lacking when the trees were exposed to elevated ozone.

Also publishing new and related results in the same year were Pregitzer *et al*. (2008)[15], who reported that "all root biomass sampling previous to 2002 showed that O_3 exposure, alone or in combination with elevated CO_2, consistently resulted in lower coarse root biomass." In analyzing more recent data, however, they found that the elevated O_3 treatment significantly *increased* fine-root biomass in the aspen trees, and, in combination with elevated CO_2, increased *coarse* root biomass in them as well. Hence, they concluded that "the amount of carbon being allocated to aspen fine-root biomass under elevated O_3 is increasing over time relative to the control, especially in the elevated CO_2 and elevated O_3 treatment, in contrast with most shorter-term results, including those of King *et al*. (2001). And as a result, they further concluded that "the positive effects of elevated CO_2 on belowground net primary productivity may not be offset by negative effects of O_3."

One year later, noting that *sporocarps* (the reproductive structures of fungi) can be significant carbon sinks for the *ectomycorrhizal fungi* that develop symbiotic relationships with plants by forming sheaths around their root tips, where they are the last sinks for carbon in the long and winding pathway that begins at the source of carbon assimilation in plant leaves, Andrew and Lilleskov (2009)[16] wrote that "it is critical to understand how ectomycorrhizal fungal sporocarps are affected by elevated CO_2 and O_3" *because*, as they continue, "sporocarps facilitate genetic recombination, permit long-distance dispersal and contribute to food webs," stressing that we need to know how these important processes will be affected by continued increases in the concentrations of these two trace constituents of the atmosphere.

The ongoing rise in the air's CO_2 content appears destined to enhance the genetic recombination and long-distance dispersal of the ectomycorrhizal fungi that form symbiotic relationships with the roots of aspen and other trees, thereby positively contributing to various food webs that will be found within earth's forests of the future.

In light of the importance of these considerations, the two researchers sampled aboveground sporocarps for four long years at the Aspen FACE site near Rhinelander, Wisconsin, which provided, in their words, a "unique opportunity to examine the effects of both elevated CO_2 and O_3 on a forested ecosystem," which examination was conducted during years 4 through 7 of the long-term study. And by so doing, they found that total mean sporocarp biomass "was

[15] http://www.co2science.org/articles/V11/N51/EDIT.php.
[16] http://www.co2science.org/articles/V12/N44/B1.php.

generally lowest under elevated O_3 with ambient CO_2," and that it "was greatest under elevated CO_2, regardless of O_3 concentration," while in another place in their paper, they said there was "a complete elimination of O_3 effects on sporocarp production when [extra] CO_2 was added." And they stated that they "expect that the responses seen in the present study were conservative compared to those expected under regional to global changes in CO_2 and O_3."

By itself, or in combination with rising ozone concentrations, therefore, the ongoing rise in the air's CO_2 content appears destined to enhance the genetic recombination and long-distance dispersal of the ectomycorrhizal fungi that form symbiotic relationships with the roots of aspen and other trees, thereby positively contributing to various food webs that will be found within earth's forests of the future.

Earth's trees, like much of the rest of the biosphere, are better equipped to "live long and prosper" in CO_2-enriched air, even when faced with the generally negative influence of concomitant atmospheric ozone pollution.

Three years later, Zak *et al*. (2011)[17] noted how both an insufficient amount of soil nitrogen (N) and an over-abundance of atmospheric ozone have often been claimed to either partially or totally repress the many positive effects of elevated atmospheric CO_2 concentrations on plant growth and development, especially in the case of long-lived woody plants such as trees; but they added that the *combined* effects of *elevated* CO_2 and *elevated* O_3 (eCO_2 and eO_3) "remain undocumented in the context of long-term, replicated field experiments." At this point, however, they had already begun to fill this void; and they thus went on to describe how they had conducted just such an experiment and what they had learned from it.

Working at the Rhinelander (Wisconsin, USA) FACE facility, the four researchers first told how in 1997 they had planted one-half of each of 12 FACE plots with various trembling aspen (*Populus tremuloides*) genotypes (8, 42, 216, 259, 271) of differing CO_2 and O_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_2 and O_3 (aCO_2 and aO_3), aCO_2 and eO_3, eCO_2 and aO_3, or eCO_2 and eO_3 - where eCO_2 was 560 ppm, 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*. (2011) said 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 in the eCO_2 treatment over the last three years of the study, which for a more standard 300-ppm

[17] http://www.co2science.org/articles/V15/N12/EDIT.php.

increase in atmospheric CO_2 concentration equates to an approximate 42% increase in NPP, which they said "was sustained by greater root exploration of soil for growth-limiting N, as well as more rapid rates of liter decomposition and microbial N release during decay."

With respect to the concomitant stress of O_3 pollution, the researchers reported 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*. (2011) wrote that "NPP in the three plant communities responded similarly to the combined eCO_2 and eO_3 treatment." And they said 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."

Continuing in this vein, the four researchers ultimately concluded 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 suggested 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."

And so one begins to understand that, ultimately, the *good* gas - CO_2, which some have called the *elixir of life* - wins in the end … because earth's trees, like much of the rest of the biosphere, are better equipped to "live long and prosper" in CO_2-enriched air, even when faced with the generally negative influence of concomitant atmospheric ozone pollution.

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