EFFECTS OF INCREASED CO_2 ON WOODY PLANT PESTS

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Insect pests have greatly vexed earth's trees and shrubs in the past; and they may continue to do so in the future. But the question arises: Will the anticipated increase in the atmosphere's CO_2 content exacerbate, ameliorate or have no effect on this phenomenon? In the paragraphs below, the results of several studies that address this important question are described and discussed, as they pertain to woody plants *other than* oak and maple trees, which are addressed separately in similar reports.

Docherty *et al*. (1997)[1] grew beech and sycamore saplings in glasshouses maintained at atmospheric CO_2 concentrations of 350 and 600 ppm, while groups of three sap-feeding aphid species and two sap-feeding leafhopper species were allowed to feed on them. Overall, they reported that elevated CO_2 had few significant effects on the performance of the insects, although there was a non-significant tendency for elevated CO_2 to reduce the individual weights and populations sizes of the aphids.

One year later, in a study that did *not* involve herbivores, Gleadow *et al*. (1998[2]) grew eucalyptus seedlings in glasshouses maintained at 400 and 800 ppm CO_2 for a period of six months, observing biomass increases of 98% and 134% in high and low nitrogen treatments, respectively. They also studied a sugar-based compound called *prunasin*, which produces cyanide in response to tissue damage caused by foraging herbivores. And although elevated CO_2 caused no significant change in leaf prunasin content, it was determined that the proportion of nitrogen allocated to prunasin increased by approximately 20% in the CO_2-enriched saplings, suggestive of a *potential* for increased prunasin production had the eucalyptus saplings been under attack by herbivores.

Simultaneously, in a study of *simulated* herbivory, Kruger *et al*. (1998)[3] grew seedlings of one-year-old maple (*Acer saccharum*) and two-year-old aspen (*Populus tremuloides*) trees in glasshouses with atmospheric CO_2 concentrations of 356 and 645 ppm for 70 days. At the 49-day point of the experiment, half of the leaf area on half of the trees in each treatment was removed; and this defoliation caused the final dry weights of both species growing in ambient air to decline. In the CO_2-enriched glasshouse, on the other hand, the defoliated maple trees ended up weighing just as much as the non-defoliated maple trees; while the defoliated aspen trees ended up weighing a little less, but not significantly less, than their non-defoliated counterparts. Hence, atmospheric CO_2 enrichment helped both species to better recover from the debilitating effect of leaf removal, which suggests that these trees may be better able to deal with the physical damage that might be inflicted upon them by herbivores in a future world of higher atmospheric CO_2 concentration.

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[1] http://www.co2science.org/articles/V5/N13/B2.php.

[2] http://www.co2science.org/articles/V1/N3/B5.php.

[3] http://www.co2science.org/articles/V2/N12/B4.php.

In another study of mechanical defoliation, Lovelock *et al*. (1999)[4] grew seedlings of the tropical tree *Copaifera aromatica* for 50 days in pots placed within open-top chambers maintained at atmospheric CO_2 concentrations of 390 and 860 ppm; and at the 14-day point of the experiment, half of the seedlings in each treatment had about 40% of their total leaf area removed. In this case, however, none of the defoliated trees of either CO_2 treatment fully recovered from this manipulation; but at the end of the experiment, the total plant biomass of the defoliated trees in the CO_2-enriched treatment was 15% greater than that of the defoliated trees in the ambient-CO_2 treatment, again attesting to the benefits of atmospheric CO_2 enrichment in helping trees to deal with herbivory.

In a longer-term study, Hattenschwiler and Schafellner (1999)[5] grew seven-year-old spruce (*Picea abies*) trees at atmospheric CO_2 concentrations of 280, 420 and 560 ppm and various nitrogen deposition treatments for three years, allowing nun moth larvae to feed on current-year needles for a period of 12 days. Larvae placed upon the CO_2-enriched foliage consumed less needle biomass than larvae placed upon the ambiently-grown foliage, regardless of nitrogen treatment. In fact, this effect was so pronounced that the larvae feeding on needles produced by the CO_2-enriched trees attained an average final biomass that was only two-thirds of that attained by the larvae that fed on needles produced at 280 ppm CO_2. And since the nun moth is a deadly defoliator that resides in most parts of Europe and East Asia between 40 and 60°N latitude and is commonly regarded as the coniferous counterpart of its close relative the gypsy moth, which feeds primarily on deciduous trees, the results of this study suggest that the ongoing rise in the air's CO_2 content will likely lead to significant reductions in damage to spruce and other coniferous trees by this voracious insect pest in the years and decades ahead.

> ***Higher condensed tannin concentrations that were present in the birch fine roots may offer these tissues greater protection against soil-borne pathogens and herbivores.***

Four years later, Parsons *et al*. (2003)[6] grew 2-year-old saplings of paper birch (*Betula papyrifera* Marsh.) and 3-year-old saplings of sugar maple (*Acer saccharum* Marsh.) in well-watered and fertilized 16-L pots from early May until late August in glasshouse rooms maintained at either 400 or 700 ppm CO_2. This work revealed that the whole-plant biomass of paper birch was increased by 55% in the CO_2-enriched rooms, while that of sugar maple was increased by 30%. Condensed tannins, on the other hand, were unaltered in sugar maple; but they were increased by 27% in paper birch in the CO_2-enriched treatment.

The growth benefits conferred by the elevated CO_2 in this experiment are obvious. But to this observation the three researchers added that "the higher condensed tannin concentrations that were present in the birch fine roots may offer these tissues greater protection against soil-borne pathogens and herbivores." And it is interesting to note, in this regard, that CO_2-induced

[4] http://www.co2science.org/articles/V3/N7/B4.php.
[5] http://www.co2science.org/articles/V3/N2/B2.php.
[6] http://www.co2science.org/articles/V6/N36/B1.php.

increases in fine root concentrations of total phenolics and condensed tannins have also been observed in warm temperate conifers by King *et al*. (1997), Entry *et al*. (1998), Gebauer *et al*. (1998) and Runion *et al*. (1999), as well as in cotton by Booker (2000).

Working concurrently, Holton *et al*. (2003)[7] reared parasitized and non-parasitized forest tent caterpillars (*Malacosoma disstria*) on two quaking aspen (*Populus tremuloides*) genotypes (216, which is O_3-tolerant, and 259, which is O_3-sensitive) alone and in combination at the Aspen FACE site in northern Wisconsin, USA, in plots exposed to ambient air, ambient air + 200 ppm extra CO_2, ambient air + 50% extra ozone, and ambient air + 200 ppm extra CO_2 and 50% extra O_3 during the daylight hours of one full growing season. This effort revealed, in the words of the researchers, that "elevated CO_2 had little effect on both primary and secondary metabolites of aspen." Hence, it was not surprising to learn, as they reported, that "elevated CO_2 had few biologically significant effects on forest tent caterpillar performance." Elevated O_3, on the other hand, altered foliar composition much more than did elevated CO_2; and, as they discovered, it *improved* tent caterpillar performance under ambient CO_2 conditions, *but not in CO_2-enriched air*. In fact, the extra CO_2 of this study *totally thwarted* the positive impact of the extra O_3 on caterpillar performance, thus eliminating a major negative consequence for the trees.

Also with a paper appearing in the same year were Kuokkanen *et al*. (2003)[8], who grew two-year-old birch (*Betula pendula* Roth) seedlings in ambient air of 350 ppm CO_2 or air enriched to a CO_2 concentration of 700 ppm under conditions of either ambient temperature or ambient temperature plus 3°C for one full growing season in the field in closed-top chambers at the Mekrijarvi Research Station of the University of Joensuu in eastern Finland. Then, during the middle of the summer, when carbon-based secondary compounds of birch leaves are fairly stable, they picked several leaves from each tree and determined their condensed tannin concentrations, along with the concentrations of a number of other physiologically-important substances.

This work revealed that the concentration of total phenolics, condensed tannins and their derivatives significantly increased in the birch leaves produced in the CO_2-enriched air, as had also been observed by Lavola and Julkunen-Titto (1994), Williams *et al*. (1994), Kinney *et al*. (1997), Bezemer and Jones (1998) and Kuokkanen *et al*. (2001). In fact, the extra 350 ppm of CO_2 nearly tripled condensed tannin concentrations in the ambient-temperature air, while it increased their concentrations in the elevated-temperature air by *a factor in excess of 3.5*. These findings are extremely important, for the presence of condensed tannins in leaves tends to greatly reduce methane emissions from ruminants that feed upon them, which in turn reduces the magnitude of the global warming impetus provided by this powerful greenhouse gas.

Moving ahead another year, Mattson *et al*. (2004)[9] noted that "although there have been many studies on the effects of elevated CO_2 on the interaction between plants and their insect herbivores (see Bezemer and Jones, 1998; Hunter, 2001), comparable studies on mammalian herbivores are lacking altogether, even though mammals play important roles in dynamics of

[7] http://www.co2science.org/articles/V6/N51/B2.php.
[8] http://www.co2science.org/articles/V6/N52/B1.php.
[9] http://www.co2science.org/articles/V7/N40/B3.php.

many ecosystems (McNaughton and Sabuni, 1988; Pastor and Naiman, 1992)." Thus, in one experiment, Mattson *et al*. grew one-year-old seedlings of silver birch (*Betula pendula*) in closed-top chambers for one summer and autumn in pots containing an unfertilized commercial peat maintained at three different soil nitrogen (N) levels (low = 0 kg N ha^{-1}, medium = 150 kg N ha^{-1}, high = 500 kg N ha^{-1}) and two temperature (T) levels (ambient and ambient + 3°C) in air of either 362 or 700 ppm CO_2 concentration, after which feeding trials with caged Eurasian hares (*Lepus timidus*) were carried out and a number of chemical analyses were made of the tops of the seedlings and the basal parts of their stems.

In a second experiment, they grew paper birch (*Betula papyrifera*) from seed for two 140-day growing seasons in well-watered and fertilized pots placed within FACE rings maintained at atmospheric CO_2 concentrations of either 362 or 562 ppm, after which (in an unplanned aspect of the study) North American eastern cottontail rabbits (*Sylvilagus floridanus*) fed *ad libitum*, consuming bark tissue down to and scoring the wood, on the basal third of the seedlings, which tissues were also tested for the presence of various herbivore-deterring chemical constituents.

"As expected," in the words of the six scientists, "elevated CO_2 substantially increased the above-ground woody biomass growth of both paper birch (63%) and silver birch (21%)." In addition, noting that "numerous studies have shown that elevated atmospheric CO_2 often, but not always, elicits increases in carbon partitioning to carbon-based secondary plant compounds," which often act as deterrents to herbivory, they said that their findings "confirm this general pattern in silver and paper birch." Last of all, they reported that high CO_2 reduced hare feeding on silver birch shoots by as much as 48%, and that it reduced rabbit feeding on paper birch stems by about 51%, while neither temperature nor severe early-season defoliation (another treatment) affected tree resistance against these mammalian herbivores.

High CO_2 reduced hare feeding on silver birch shoots by as much as 48%, and reduced rabbit feeding on paper birch stems by about 51%, while neither temperature nor severe early-season defoliation (another treatment) affected tree resistance against these mammalian herbivores.

Calling the anti-herbivory effect of elevated CO_2 "remarkably strong," and noting that rabbits "overwhelmingly preferred ambient CO_2 plants," Mattson *et al*. went on to say that their data "clearly suggest that the defensive biochemistry of paper birch twigs as well as the main stem were [positively] altered as the result of elevated CO_2." Hence, one can expect that as the air's CO_2 content continues to rise, at least these two species of birch trees will have a significantly easier time of getting established and growing to maturity, in that they will likely not be hassled nearly as much by rabbits and hares munching away at their trunks and branches while in their early growth years.

Jumping ahead three years, and noting that the "detrimental effects of ozone on plants are well known," and that "carbon dioxide generally affects trees in opposite ways to ozone," Valcama *et al*. (2007)[10] conducted a literature review that they described as "the first quantitative analysis of the interactive effects of elevated O_3 and elevated CO_2 on tree chemistry and herbivore performance," based on the results of "63 studies conducted on 22 tree species and 10 insect herbivore species and published between 1990 and 2005." And what did they thereby learn?

With respect to ways by which elevated O_3 may *benefit* insect herbivores that tend to damage trees, Valkama *et al*. determined that "elevated O_3 significantly shortened development time of insect herbivores [when they are exposed and vulnerable to attack by various enemies] and increased their pupal mass in the overall dataset." In addition, they found that the "relative growth rate of chewers was significantly increased by 3.5% under elevated O_3." However, they discovered that "these effects were counteracted by elevated CO_2," such that "elevated O_3 in combination with CO_2 had no effect on herbivore performance," with the exception that when elevated CO_2 was added to the O_3-enriched air, it not only *counteracted* the O_3-induced increase in pupal biomass, it actually *reduced* it below what it was in ambient air by 7%. Thus, this analysis of the vast majority of pertinent experimental data obtained prior to 2006 suggests that in the never-ending battle between insect herbivores and the trees on whose foliage they feast, the ongoing rise in the air's CO_2 content likely plays an extremely important role in *negating*, and in some cases even *more* than negating, the damage otherwise capable of being done to earth's forests by voracious insect pests. And subsequent research has continued to demonstrate these facts.

A case in point is the study of Huttunen *et al*. (2007)[11], who grew silver birch (*Betula pendula* Roth) seedlings in pots filled with peat at three different levels of nitrogen (N) fertility - no N, moderate N (130 kg N ha^{-1}), high N (270 kg N ha^{-1}) - within climate-controlled closed-top chambers from mid-June to October of 2002 at the Mekrijarvi Research Station of the University of Joensuu, Finland, where the chambers were maintained at atmospheric CO_2 concentrations of either 360 or 720 ppm and at either ambient air temperatures or elevated air temperatures that were 2°C above ambient from June to August and 4°C above ambient for the remainder of the growing season, while mimicing larval and adult leaf-feeding patterns exhibited during real-world defoliation by manually damaging the leaves of the seedlings by tearing off the apical halves of either 25% or 50% of all leaves greater than 1 cm in length on 1 July (mid-season) and again on 29 July (late-season), after which total plant shoot and root biomass was determined once the plants had gone dormant in October.

As best as can be determined from the six scientists' bar graphs of their results, and averaged over all three defoliation treatments, the elevated CO_2 treatment increased the biomass of the seedlings in the moderate and high N fertility treatments much more than it increased the biomass of the seedlings in the no N fertility treatment (29 and 30%, respectively, vs. 13%). The same was also true of the combined elevated CO_2 and elevated temperature treatment, where the corresponding treatment-induced biomass increases were 34 and 36% vs. 20%, which demonstrates that the heightened temperatures tended to *augment* the beneficial effects of the elevated CO_2 treatment, with the greatest amplification being manifest in the no N fertility

[10] http://www.co2science.org/articles/V10/N16/B1.php.
[11] http://www.co2science.org/articles/V10/N38/B3.php.

treatment (54% vs. 17 and 20% in the moderate and high N treatments, respectively). Also, averaged over all three N fertility treatments, the effect of the elevated CO_2 was to increase the plant biomass of the undefoliated seedlings by approximately 25%, that of the 25%-defoliated seedlings by 24%, and that of the 50%-defoliated seedlings by 22%, while the effect of the combined elevated CO_2 and elevated temperature treatment was to increase the plant biomass of the same three categories of seedlings by approximately 31%, 30% and 29%, respectively. And, therefore, in the words of Huttunen *et al*., "climatic change" - which they specifically define to mean *elevated atmospheric temperature and* CO_2 - "will have a positive impact on the compensatory ability of defoliated silver birch seedlings." In fact, it may actually help them *overcompensate* for the effects of herbivory.

In another study that was conducted with the same trees under the same conditions, Huttunen *et al*. (2008)[12] studied leaf palatability to adult blue alder leaf beetles (*Agelastica alni*), while they periodically measured a host of seedling parameters related to plant chemical and morphological defense properties. And as might have been imagined, the researchers' findings were varied and complex; but their most basic finding of all was that the blue alder leaf beetle's "total leaf consumption was higher under the ambient climatic conditions than under elevated temperature, elevated CO_2, or the combination of elevated temperature and CO_2."

Fast-forwarding four years, Nabity *et al*. (2012)[13] wrote that "arthropod herbivory can reduce plant productivity by removing photosynthetic leaf area," noting that the studies of Zangerl *et al*. (2002), Aldea *et al*. (2005, 2006) and Patankar *et al*. (2011) indicated that, in some cases, "damage to leaf surfaces causes a reduction in the quantum efficiency of photosystem II fluorescence, which is highly correlated with the rate of carbon assimilation." Therefore, while working at the Aspen FACE site in north-central Wisconsin (USA), the four researchers studied how different types of herbivore damage (leaf-chewing, gall-forming and leaf-folding) altered component processes of photosynthesis under both ambient and elevated (ambient + 200 ppm) atmospheric CO_2 concentrations in aspen (*Populus tremuloides*, genotype 216) trees, as well as how the damage caused by leaf-chewing insects impacted photosynthesis in birch (*Betula papyrifera*) trees. And in the words of the four researchers who conducted the work, they thereby found that "growth under elevated CO_2 reduced the distance that herbivore-induced reductions in photosynthesis propagated away from the point of damage in aspen and birch," which led them to conclude that "at least for these species," as they put it, elevated CO_2 "may reduce the impact of herbivory on photosynthesis," which would be a very positive development indeed.

> *Elevated atmospheric temperature and CO_2 will have a positive impact on the compensatory ability of defoliated silver birch seedlings. In fact, it may actually help them overcompensate for the effects of herbivory.*

[12] http://www.co2science.org/articles/V11/N30/B2.php.
[13] http://www.co2science.org/articles/V16/N2/B1.php.

Last of all, Hamilton *et al*. (2012)[14] began the report of their study by noting that "the response of complex plant and animal communities to global change is highly variable (Tylianakis *et al*., 2008)," but stating that "recent studies have documented that loss of foliage to arthropod herbivores decreases under elevated CO_2 in woody communities (Hamilton *et al*., 2004; Knepp *et al*., 2005; Stiling and Cornelissen, 2007)." They also stated that the fitness and in some cases the population size of herbivorous insects may decline in communities exposed to elevated CO_2 (Hillstrom and Lindroth, 2008; Hillstrom *et al*., 2010)," although they indicated that the "effects of elevated CO_2 on naturally-occurring arthropod assemblages have not yet been widely characterized."

Hoping to shed some light on this latter subject while working at the Duke Forest FACE facility in the Piedmont region of North Carolina (USA) - where three 30-meter-diameter plots of an expansive stand of loblolly pine had their atmospheric CO_2 concentrations boosted by about 200 ppm, and where three other such plots were maintained at the normal ambient CO_2 concentration - Hamilton *et al*. counted the numbers of different types of arthropods found in each of the six plots every two weeks throughout June and July of 2005, in order to be able to assign them to different feeding guilds. In addition, they analyzed stable isotope data for spiders collected in the ambient and elevated CO_2 plots in order to determine the extent to which herbivorous prey species moved into and out of the elevated CO_2 plots.

The seven U.S. scientists reported that their isotopic data "gave no indication that the treatment plots represented a 'boundary' to the movement of insects." In addition, they determined there was *no detectable effect* of elevated CO_2 on the *total* number of individual arthropods in the two sets of treatment plots. However, they said "there was an increase in the numbers of individuals collected in primarily predaceous orders (Araneae and Hymenoptera; from 60% to more than 150%) under elevated CO_2 and a decrease in the numbers in primarily herbivorous orders (Lepidoptera and Coleoptera; from -30 to -45%)."

In the closing sentence of their paper, Hamilton *et al*. thus concluded what was pretty obvious, i.e. that "decreases in herbivorous arthropods and increases in predaceous arthropods may contribute to reduced herbivory under elevated CO_2 in forest systems," which is basically what has also been observed in the other studies that have experimentally explored the subject, all of which bodes well for earth's forests and shrubs in a CO_2-enriched world of the future.

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[14] http://www.co2science.org/articles/V16/N9/B3.php.

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