Influence of Elevated Ozone and Carbon Dioxide on Insect Densities

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The combustion of fossil fuels is profoundly altering the chemical composition of the atmosphere. Beginning with the Industrial Revolution, the concentration of carbon dioxide in the atmosphere has increased from approximately 280 to 370 l l^{-1} in 2004, and it is expected to exceed 550 l l^{-1} by 2050. Tropospheric ozone has risen even more rapidly than CO_2 and average summer concentrations in the Northern Hemisphere are expected to continue to increase by 0.5–2.5% per year over the next 30 years. Although elevated CO_2 stimulates photosynthesis and productivity of terrestrial ecosystems, ozone (O_3) is deleterious. In addition to directly affecting the physiology and productivity of crops, increased concentrations of tropospheric CO_2 and O_3 are predicted to lower the nutritional quality of leaves, which has the potential to increase herbivory as insects eat more to meet their nutritional demands.

We tested the hypothesis that changes in tropospheric chemistry affect the relationship between plants and insect herbivores by changing leaf quality. The susceptibility to herbivory of soybean grown in elevated CO_2 or O_3 was examined using free air gas concentration enrichment (SoyFACE).[1] FACE technology has the advantage that plants are cultivated under realistic field conditions with no unwanted alteration of microclimate or artificial constraints on the insect community.

Elevated CO_2 (~550 l l^{-1}) substantially increased susceptibility of soybean to herbivory early in the season, whereas O_3 seemed to have no effect. For plants grown at 550 l l^{-1} CO_2, the percentage of leaf tissue removed by herbivores was more than twice the level for plants in ambient air (Fig. 1); there was no effect of elevated O_3 on herbivory during this first year, but the O_3 concentration was elevated to only 1.2× ambient. The increase in herbivory under elevated CO_2 was consistent with the corresponding increase in the size of insect populations, and the majority of leaf tissue was removed by the invasive Japanese beetle, *Popillia japonica*. Subsequent measurements indicated that the density of the invasive soybean aphid, *Aphis glycines*, also was greater on plants grown under elevated CO_2. Increased herbivory by the Japanese beetle was associated with a substantial increase in the sugar content of plants grown under elevated CO_2 (Fig. 1), because simple sugars are strong feeding stimulants for Japanese beetle.

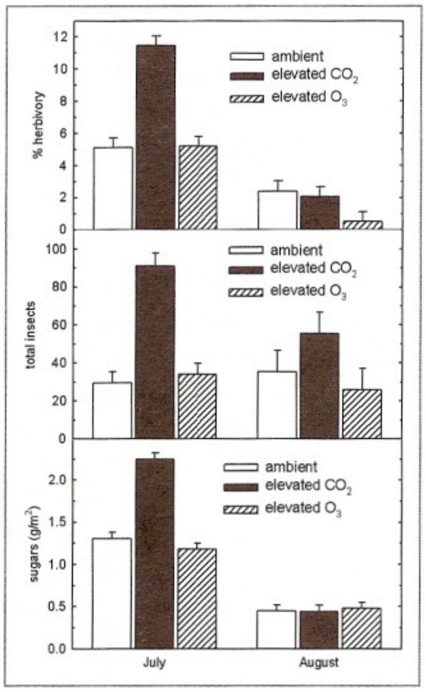

Figure 1. Responses of soybean and insect herbivores to elevated CO_2 and O_3. (A) Leaf tissue (%) consumed by insect herbivores. (B) Insect populations. (C) Leaf sugar concentrations. Sugar content was calculated as the sum of glucose, fructose, and sucrose. Data show mean ± SE. In July, values for the elevated CO_2 were significantly greater than ambient or elevated O_3 ($P \leq 0.05$).

When given a choice under controlled conditions, Japanese beetles consistently moved to and selectively fed on leaves harvested from plants grown under elevated CO_2. In addition to preferring high CO_2 leaves, female adult beetles laid more eggs and male and female beetles lived longer when fed elevated CO_2 foliage in a laboratory bioassay (Fig. 2). Moreover, because total egg production was positively correlated with the total number of days that both males and females were alive in a cage ($r = 0.490$, $P = 0.008$, $n = 28$), increased fecundity was largely attributable to this longer life span. Feeding on leaves with artificially elevated sugar content did not increase the longevity of male or female beetles (Fig. 2), but it may have increased fecundity. It seems that changes in leaf chemistry other than simply increased sugar content affects beetle fecundity.

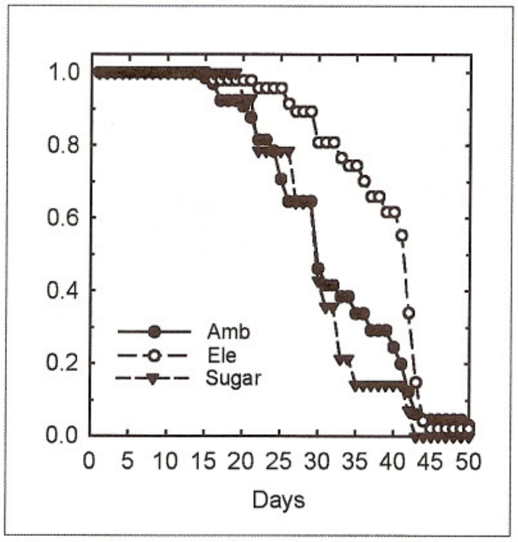

Figure 2. Survivorship of male Japanese beetles fed on foliage grown under ambient (Amb) and elevated CO_2 (Ele), and foliage grown under ambient CO_2 but fed sucrose (sugar) through the transpiration stream. The pattern of survivorship for female beetles was similar.

Preliminary data indicate that soybean cultivars may be differentially susceptible to herbivory under elevated CO_2 and O_3 (Fig. 3). Half of each plot in the SoyFACE experiment is planted in Pioneer 93B15, a cultivar commonly planted in east central Illinois, whereas the other half of each plot is planted in 1.9-m^2 subplots containing 22 different soybean genotypes provided by the USDA Soybean/Maize Germplasm, Pathology, and Genetics Research Unit at the University of Illinois. Cultivars were selected for variation in date of origin and responsiveness to elevated CO_2 and O_3. In 2003, we made preliminary measurements on 10 of 22 soybean genotypes of the numbers of three common insects, Japanese beetle, corn rootworm (*Diabrotica* spp.), and potato leafhopper (*Empoasca fabae*), to determine whether cultivars are differentially susceptible to herbivory when exposed to two major components of global change. Although our replicate size was low, a three-way analysis of variance (ANOVA) revealed highly significant differences among cultivars in total number of insects ($P < 0.01$), and combining all cultivars, more insects were found in the high CO_2 plots than the others ($P = 0.02$). There was no statistically significant cultivar by O_3 by CO_2 interaction. However, a comparison of the two cultivars with greatest (Corsoy, white bars) and smallest (L600-631, black bars) insect populations revealed a marginally significant CO_2 by cultivar interaction ($P = 0.08$). These measurements were made only once during a year in which insect populations were low; a more aggressive and complete sampling effort should reveal strong differences in the effects of elevated CO_2 and O_3 on insect damage among different soybean genotypes.

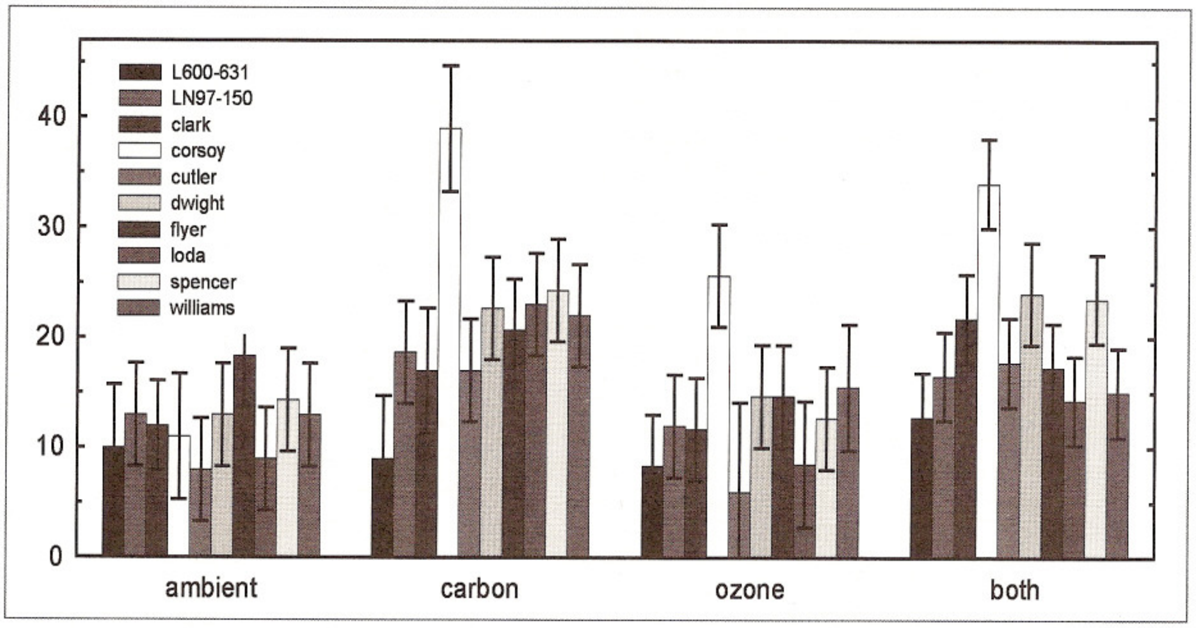

Figure 3. Total number of insects harvested from 1.9-m^2 plots of 10 different soybean cultivars. Insects were almost entirely comprised of three species: corn rootworm (*Diabrotica* complex), Japanese beetle, and potato leafhopper. Each bar represents a least squares mean of three ambient plots, 3 +CO_2 (carbon) plots, 2 +O_3 (ozone) plots, and 4 +CO_2 +O_3 plots (both) ± 1 SE. Insects were sampled over a 4-h period in August 2003.

Soybean constitutes approximately 25% of all planted agricultural acreage in the United States. In 2001, almost 75 million acres was planted, with Iowa and Illinois producing approximately one-third of the total U.S. crop. Soybean is the leading crop in terms of exports, totaling more than $6 billion in 1999[2] and accounting for one-half of the world's soy production. More than 700 species of herbivorous insects are known to consume soybean in the United States. Although in the Midwest soybean historically has rarely experienced serious insect problems, this may be changing with the introduction of invasive insects, including Japanese beetle and soybean aphid. Because acreage is so extensive in the Midwest, when problems occur, losses can be devastating.

Our data suggest that global change in the form of elevated levels of CO_2 and O_3 may exacerbate pest problems and that changes in tropospheric chemistry alter key aspects of leaf chemistry that affect the feeding and demographic performance of insects, thereby modulating crop damage by insect herbivores. Associated with this increased potential damage will be increased need for sustainable management techniques. A deeper understanding of the mechanisms and genetic variation contributing the susceptibility to herbivory

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[1] http://www.soyface.uiuc.edu/.

[2] http://www.unitedsoybean.org/soystats2000/ page_02.htm.

[3] This research was support by funds from the USDA National Research Initiative; the Illinois council for Food and Agricultural Research (C-FAR) and the Archer Daniels Midland Company support the SoyFACE facility.