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Elm Leaf Beetle Performance on Ozone-Fumigated Elm

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Abstract

Leaves harvested in 1986 from clonally propagated elm hybrids ('Pioneer', 'Homestead', '970') previously fumigated in open-top chambers with ozone at 15 parts per hundred million (pphm) or with charcoal-filtered air (CFA) were evaluated for water and nitrogen content or were fed to adult elm leaf beetles (ELB), *Xanthogaleruca = (Pyrrhalta) luteola* (Muller), to determine host suitability for beetle fecundity and survivorship. For all three hybrids, ELB females fed ozone-fumigated leaves laid significantly fewer eggs than females fed CFA-fumigated leaves. Fecundity of females fed '970' leaves was higher than for females fed 'Pioneer' or 'Homestead' foliage. Fumigation treatment had no significant effect on leaf nitrogen or water content. There was a significant positive linear relationship between leaf nitrogen content and beetle fecundity for all hybrids combined. In 1988, hybrid '970' was fumigated with CFA, 15, 30, or 45 pphm ozone to determine concentration effects on ELB fecundity, leaf consumption, and survivorship. Significantly fewer eggs were laid only at the higher concentration of ozone. Mean leaf area consumed by beetles did not vary among fumigation treatments. For both years, beetle survivorship was unaffected by hybrid or ozone concentration.

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Introduction

Host-plant quality for a variety of insects has been shown to be affected by atmospheric deposition. In earlier studies, we demonstrated that fecundity of elm leaf beetle (ELB), *Xanthogaleruca = (Pyrrhalta) luteola* (Muller), on certain elms, *Ulmus* spp., was negatively affected by acidic precipitation (Hall et al. 1988). Other studies have shown that ozone fumigation influences insect feeding preference and suitability of host plants for insect nutrition (Elden et al. 1978; Endress and Post 1985; Trumble et al. 1987; Coleman and Jones 1988; Jones and Coleman 1988). Because higher levels of ozone are found in urban areas and because municipalities often replace American elms, *Ulmus americana* L., with Dutch elm disease-resistant elm hybrids that are susceptible to ELB defoliation, it is important to explore the relationships between ozone sensitivity of elm and susceptibility to ELB herbivory before recommending replacement use of these elms to municipal arborists. This study was conducted to determine whether ozone pollution influences host quality of elm for ELB and how ELB fecundity, leaf consumption rate, and survivorship are affected.

Materials and Methods

1986 Experiment

One- and two-year-old potted elm trees [cuttings of the clonally propagated hybrids 'Pioneer', 'Homestead', and '970' (Townsend and Masters 1984a,b)] growing in Metro-Mix 500 (W. R. Grace and Co., Cambridge, MA) were fumigated for 12 weeks in open-top chambers (Heagle et al. 1973) located at the USDA Forest Service's Forestry Sciences Laboratory at Delaware, Ohio. Fumigation treatments began on 20 May when trees were in full leaf. Fumigation treatments were 15 parts per hundred million (pphm) ozone and charcoal-filtered air (CFA at $<$ 2 pphm ozone). Ozone was generated by passing oxygen over an ultraviolet light source (Model 03V10-0, Ozone Research and Equipment Corp., Phoenix, AZ) and was added to the CFA stream entering between each chamber's lower flow-distribution films. Chamber ozone concentration was monitored within the flow-distribution area with a Ultraviolet Photometric Analyzer (Model 49, ThermoElectron, Hopkinton, MA) calibrated with an ozone source having a rate of production traceable to a standard obtained from the National Bureau of Standards. There were 7 to 11 trees of each hybrid per chamber, and two chambers for each treatment (total of four chambers).

At the end of 12th week of fumigation (11 August), about 50 percent of the leaves were randomly harvested from each tree. Some leaves were used for determining nitrogen and water content and others for conducting beetle bioassays. Leaves not immediately used in bioassays were sealed in plastic bags and were refrigerated at 10°C for up to 4 days. At the end of 13th week of fumigation, all remaining leaves were harvested for completing the bioassays. ELB were field-collected in August as mature third instars from local Siberian elm (*Ulmus pumila* L.) and held in a growth chamber at 25°C on a photoperiod of 15:9 (L:D) until adult emergence. Pairs (male plus female) of newly eclosed, unfed, adult ELB were assigned to 15 by 100-mm plastic petri dishes containing foliage from each tree (replicated five times) which had been subjected to each fumigation treatment. Every 3 or 4 days, leaves were replaced and beetle mortality and fecundity were recorded. Number of eggs per female was calculated for each tree. Bioassays were run in a laboratory at 25 ± 2°C under constant light for 2 weeks.

Leaf samples from each tree were weighed, dried, and reweighed to determine water content. Leaf nitrogen content was determined by micro-Kjeldahl analysis (McKenzie and Wallace 1954). Data were subjected to an analysis of variance (alpha = 0.05) and a Student-Newman-Keuls multiple comparison test at the 5-percent level (Sokal and Rohlf 1981). The relationship between leaf water and nitrogen content and beetle fecundity was examined by linear regression analysis.

1988 Experiment

Two-year-old potted trees of hybrid '970' were subjected to four fumigation treatments of 15-, 30-, and 45-pphm ozone and CFA (1986 conditions). We choose '970' because of the 1986 experiment results and because '970' was more readily available than other elm hybrids. There were 10 elm trees per chamber, and two chambers per fumigation treatment (total of eight chambers). Fumigation treatments began 23 May and continued for 13 weeks.

ELB was field-collected in August from local English elm (*U. procera* Salisbury) as mature third instars and held as in 1986. Bioassays using harvested leaves were conducted as in 1986 except that the temperature was increased by 5°C to 30 ± 2°C. Bioassay temperature was increased to increase fecundity (King and Price 1986) and perhaps accentuate treatment differences. No nitrogen and water content analyses were conducted in 1988. Leaf area was determined with a Delta-T Area Meter System (Model PM-910A, Delta-T Devices LTD, Cambridge, UK) before and after each bioassay. The difference between the two measurements represented the leaf area consumed by ELB. Leaf consumption per ELB pair and number of eggs per females were calculated for each tree and analyzed as in 1986. Leaf consumption and fecundity data were also subjected to linear regression analyses.

Results

1986 Experiment

Ozone fumigation had no significant effect ($F=2.0$; DF=1,100; $P=0.16$) on leaf nitrogen content (Fig. 1). Nitrogen content was highest in '970' foliage while 'Homestead' had significantly more nitrogen than 'Pioneer' (Fig. 1). Within each hybrid there were no significant relationships between leaf nitrogen content and ELB fecundity. But when data for all hybrids were pooled, there was a significant relationship ($r^2=0.31$; n=106; $P<0.01$) between percent nitrogen content and fecundity (Fig. 2).

Ozone fumigation had no significant effect ($F=0.8$; DF=1,100; $P=0.37$) on leaf water content (Fig. 3). Water content was significantly higher in hybrid '970' than in either 'Pioneer' or 'Homestead'. When the data were pooled for all hybrids, there was a weak but significant relationship between leaf water content and ELB fecundity ($r^2=0.04$; n=106; $P<0.05$) (Fig. 4).

For each hybrid, female beetles fed ozone-fumigated leaves laid significantly fewer ($F=4.1$; DF=1,100; $P=0.04$) eggs than females fed CFA-fumigated leaves (Table 1). A higher percentage of females fed '970' oviposited than did the other two hybrids. Moreover, females laid significantly more ($F=40.6$; DF=2,100; $P<0.01$) eggs on '970' than on the other two hybrids (Fig. 5).

There were no significant differences in mortality of males or females among the three hybrids and/or the fumigation treatments.

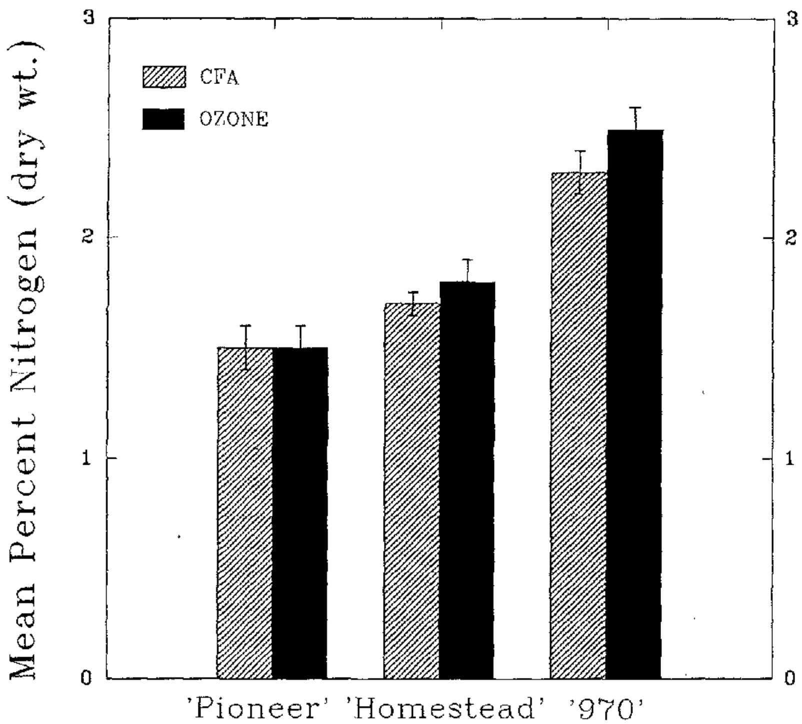

Figure 1.—Mean percent leaf nitrogen content (dry weight) from three elm hybrids fumigated with 15 pphm ozone or charcoal-filtered air (CFA) for 12 weeks in 1986.

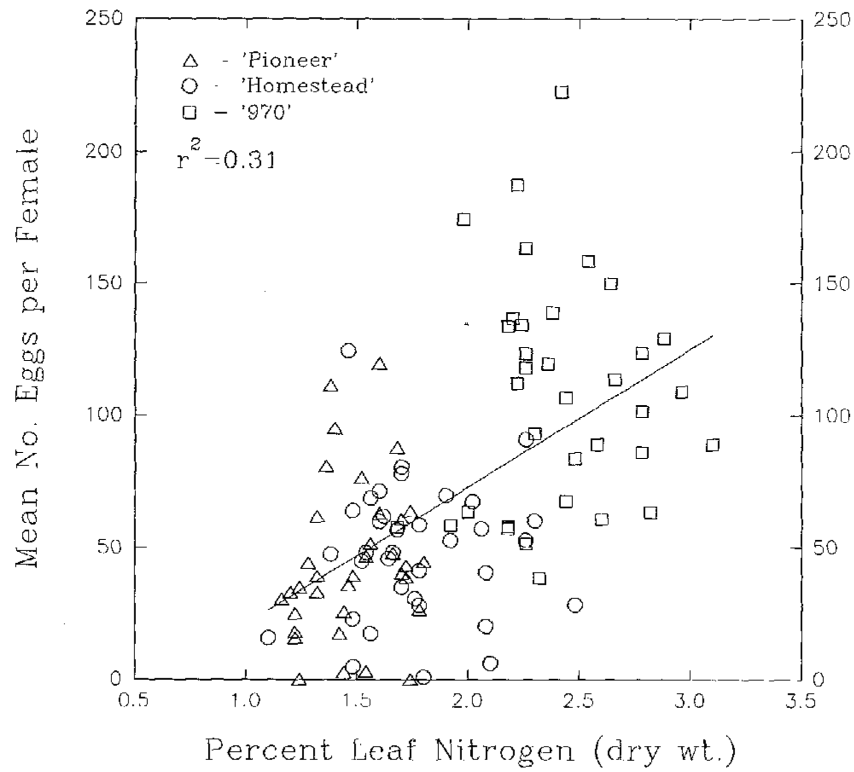

Figure 2.—Relationship between percent nitrogen content per unit dry weight of leaves and mean number of eggs laid in two weeks by ELB on leaves of three elm hybrids fumigated with 15 pphm ozone or charcoal-filtered air (CFA) for 12 and 13 weeks, respectively, in 1986.

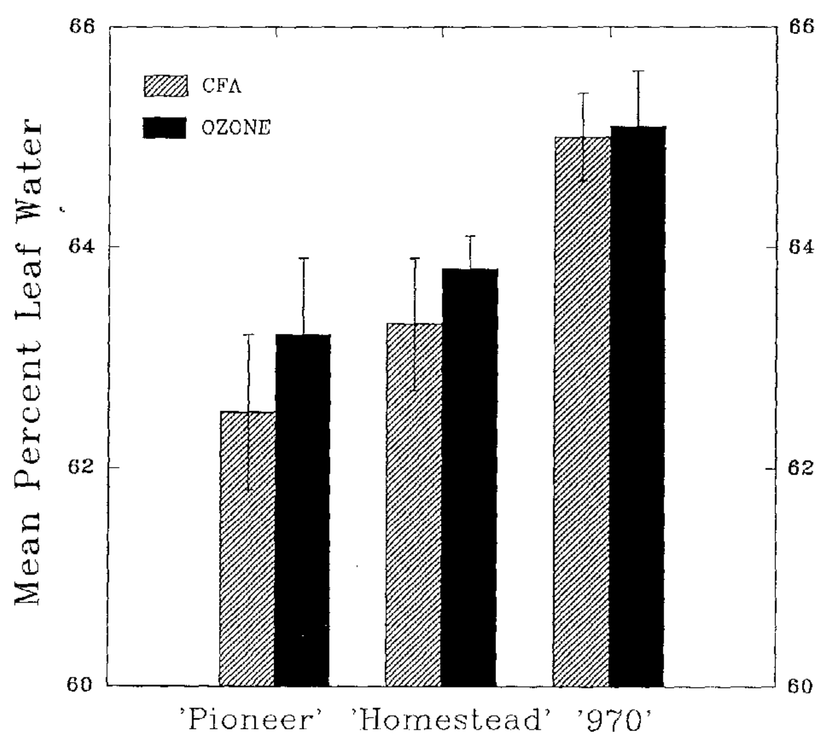

Figure 3.—Mean percent leaf water content from three elm hybrids fumigated with 15 pphm ozone or charcoal-filtered air (CFA) for 12 weeks in 1986.

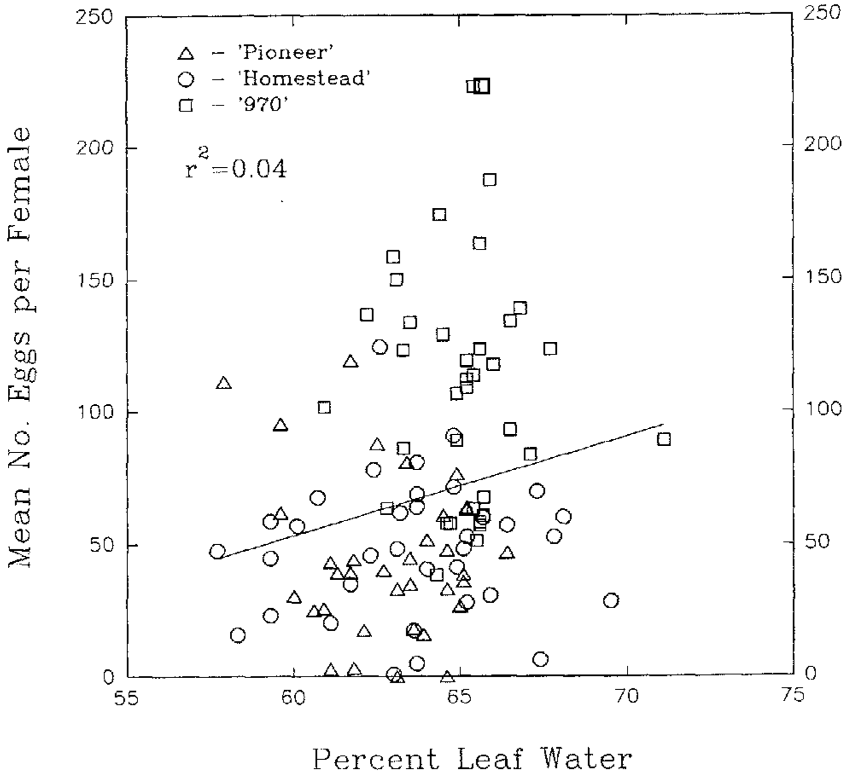

Figure 4.—Relationship between percent water content of leaves and number of eggs laid in two weeks by ELB on leaves of three elm hybrids fumigated with 15 pphm ozone or charcoal-filtered air (CFA) for 12 and 13 weeks, respectively, in 1986.

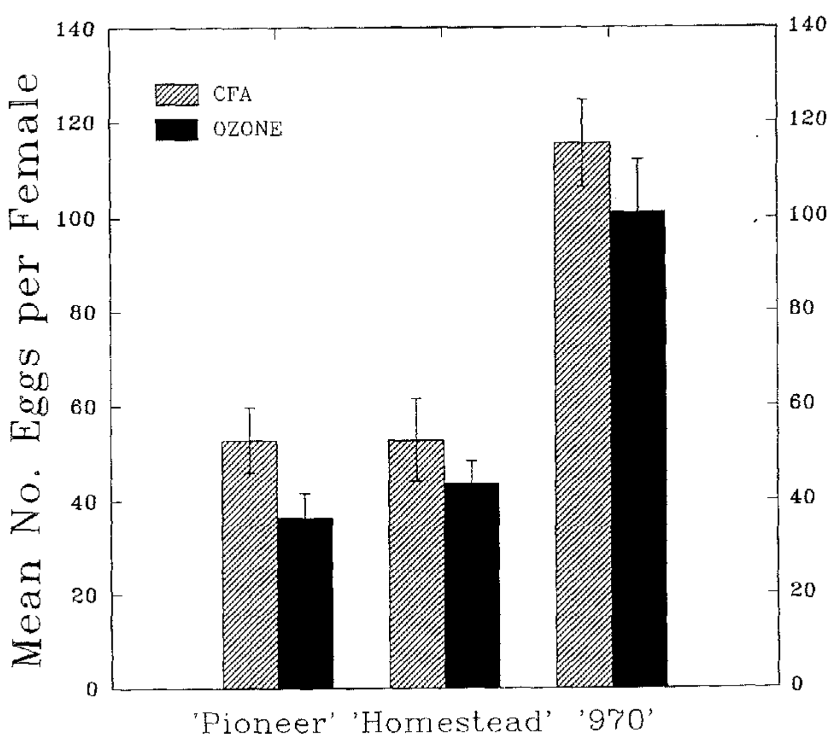

Figure 5.—Mean number of eggs laid per female by ELB on leaves from three elm hybrids fumigated with 15 pphm ozone or charcoal-filtered air (CFA) for 13 weeks in 1986.

1988 Experiment

In general, fecundity of ELB was negatively influenced (F=7.66; DF=3,76; P<0.01) by ozone fumigation of the host plant '970' (Fig. 6). A Student-Newman-Keuls multiple comparison test showed a significant ozone effect on fecundity but only at 45 pphm, the highest concentration tested (Table 2).

Mean leaf consumption by ELB fed ozone-fumigated leaves was greater than leaf area consumed by ELB fed CFA-fumigated leaves, but there was no significant relationship between ozone concentration and leaf area consumed (r^2=0.0001; n=80; P=0.9) (Table 2).

The relationship between fecundity and leaf consumption is shown in Figure 7 for all treatments combined. There is a statistically significant positive linear relationship between ELB fecundity and leaf area consumed (r^2=0.16; n=80; P<0.01).

There were no significant differences in mortality of males or females among any of the fumigation treatments.

Table 1.—1986 mean fecundity of ELB fed leaves, leaf nitrogen content per unit dry weight, and leaf water content of elm trees fumigated in open-top chambers with charcoal-filtered air (CFA) or 15 pphm ozone

	'Pioneer'		'Homestead'		'970'	
Variable	CFA	Ozone	CFA	Ozone	CFA	Ozone
No. trees/hybrid	17	18	19	16	18	18
No. eggs/female[a]	52.8(±8.7)[c]	36.6(±4.7)	52.8(±6.9)	43.7(±5.0)	115.5(±9.1)	101.1(±11.0)
Nitrogen[b]	1.5(±0.0)	1.5(±0.1)	1.7(±0.1)	1.8(±0.1)	2.3(±0.1)	2.5(±0.1)
Percent water	62.5(±0.6)	63.2(±0.3)	63.3(±0.7)	63.8(±0.7)	65.0(±0.4)	65.1(±0.5)

[a]Five females were fed on each tree.
[b]Percent dry weight.
[c]Values are the mean ±SEM.

Table 2.—1988 mean fecundity and mean leaf area consumed by ELB fed excised foliage of the elm hybrid '970' fumigated in open-top chambers with charcoal-filtered air (CFA) or one of three concentrations of ozone

Variable	CFA	15 pphm ozone	30 pphm ozone	45 pphm ozone
No. of trees	20	20	20	20
Fecundity[a]	221.5(±15.1)a[c]	226.4(±14.1)a	186.1(±13.6)a	142.2(±12.2)b
Leaf area consumed[b]	244.2(±6.2)a	264.5(±11.4)a	257.6(±15.3)a	244.4(±14.6)a

[a]Five pairs of ELB were fed on each tree.
[b]In mm^2 per beetle pair.
[c]Values are the mean ±SEM. Means in rows followed by the same letter are not significantly different according to Student-Newman-Keuls multiple comparison test at the 0.05 level.

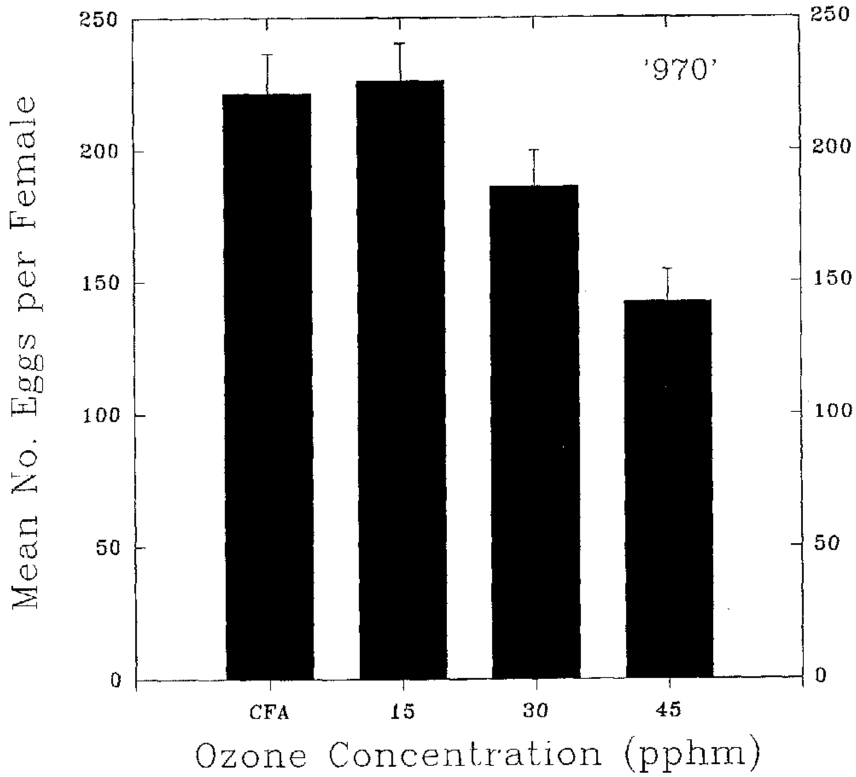

Figure 6.—Mean number of eggs laid per female by elm leaf beetles on leaves from elm hybrid '970' fumigated with three concentrations of ozone or charcoal filtered air (CFA) for 13 weeks in 1988.

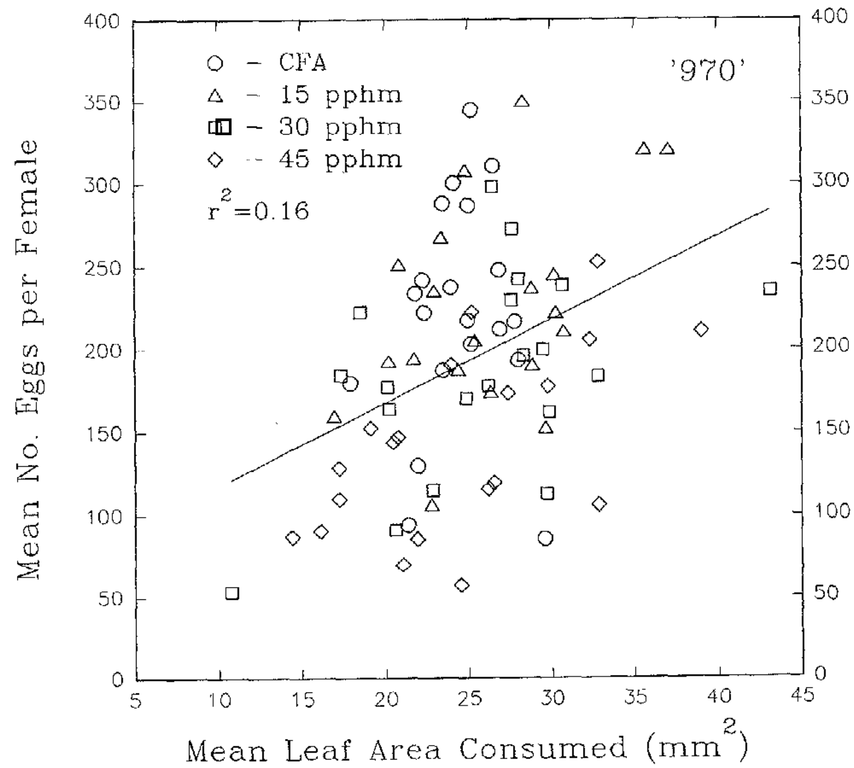

Figure 7.—Relationship between mean number of eggs per female laid in two weeks and leaf area consumed by ELB fed leaves of the elm hybrid '970' fumigated with three concentrations of ozone or charcoal-filtered air (CFA) for 13 weeks in 1988.

Discussion

We used excised leaves rather than attached leaves to test for differences in herbivory and fecundity because we were able to maintain greater accuracy and proficiency in the bioassays and because the ELB is a known specialist. It is generally recognized and accepted that the feeding preference of an insect specialist is strongly directional. Thus we believed it unlikely that subtle changes in leaf chemistry due to harvesting (artificial defoliation) would override a strong directional feeding and ovipositional preference (Risch 1985; Hall 1986). We also believed that any harvesting effects on leaf chemistry would be similar for all treatment bioassays. Further, some studies have shown that the remaining leaves on certain insect-defoliated plants contain increased levels of various feeding deterrents (Schultz and Baldwin 1982; Karban and Carey 1984), or, conversely, contain increased levels of feeding stimulants (Chambliss and Jones 1966; Carroll and Hoffman 1980). Still other studies have demonstrated that the remaining leaves on artificially defoliated plants are less likely to be chemically affected than the remaining leaves on plants defoliated by herbivores (Capinera and Roltsch 1980; Karban and Carey 1984).

In 1987 we attempted to conduct ELB bioassays on attached leaves rather than excised leaves, using modified petri dishes, to minimize possible confounding effects of harvesting on leaf chemistry (Risch 1985). The caging procedures necessary to maintain ELB on the tree foliage were exceptionally labor intensive and it was difficult to maintain the proper microenvironment of caged leaves and test insects. Also, bioassayed leaves in the cages had to be harvested immediately to accurately determine both leaf area consumed and fecundity. Thus, even with this procedure we could not have prevented possible changes in leaf chemistry of the remaining attached leaves. These obscuring factors resulted in the loss of our 1987 experiment. Obviously, much research needs to be conducted on induced chemical changes in leaves as a direct result of insect herbivore defoliation compared to induced changes by indirect artificial defoliation before choosing a particular bioassay technique.

Studies by Jeffords and Endress (1984) to determine feeding preference of gypsy moth larvae (*Lymantria dispar* L.) for leaves from white oak (*Quercus alba* L.) seedlings fumigated for 77 hours with various levels of ozone showed that larvae preferred leaves from seedlings exposed to the highest ozone level tested (15 pphm). While no ozone exposures in their study were made on oak above 15 pphm, their results correspond to ours, that is, mean ELB leaf consumption also was greatest in absolute terms on trees fumigated at 15 pphm ozone. However, in our studies, mean leaf consumption decreased gradually as ozone concentration increased above 15 pphm, but consumption remained generally higher on leaves fumigated with ozone than on leaves fumigated with CFA (Table 2). Jones and Coleman (1988), found that adults and larvae of the beetle, *Plagiodera versicolora* Laich., preferred to feed on and consumed more of cottonwood leaf discs, *Populus deltoides* Bartr., that had been previously exposed to a single acute dose of ozone (20 pphm) for 5 hours compared to controls in choice experiments. In our studies, the lowest level of ozone fumigation used, 15 pphm, was considered acute and occurs infrequently under ambient conditions in the Ohio River Valley where this experiment was conducted (Pinkerton and Lefohn 1987; Lefohn and Pinkerton 1988).

We used whole leaves in our bioassays and our plants were fumigated for much longer periods (12 to 13 weeks), seven hours per day, and five days per week before being tested for ELB suitability. While our study was intentionally designed to promote ozone effects, there may be an ozone concentration threshold for herbivory near 15 pphm, the lowest level used. Leaf consumption was higher at 15 pphm than with CFA but consumption did not continue to increase proportionally with increases in ozone fumigation (Table 2). Because our ozone exposure regime did not follow ambient conditions but was delivered at constant high rates, plant acclimation processes may have occurred over our longer exposure time, allowing compensatory physiological characteristics to ameliorate the ozone effects (Sasek and Richardson 1989).

Factors other than the amount of leaf material consumed may have influenced fecundity. Results from our studies showed a significant decrease in ELB fecundity on all three ozone-fumigated elm hybrids at the 15-pphm level in 1986 (Table 1) and at the 45-pphm level for hybrid '970' in 1988 when compared with CFA (Table 2). While there was evidence that ELB may have compensated for lower quality foliage by increased herbivory (1988 study), the nutritional benefits of additional herbivory were not reflected by increased fecundity. Components of leaf chemistry and/or texture may have changed in response to the ozone fumigation (Fluckiger et al. 1988), both of which are important to insect fecundity. Qualitative or quantitative changes in nitrogenous compounds, carbohydrates, lipids, and particularly secondary compounds such as phenolics (Meyer and Montgomery 1987), or changes in respiration or transpiration have been suggested as the cause of such differences (Hughes and Laurence 1984; Hall and Young 1986). Such changes are complex and we may never be able to determine the reasons for differences observed in this study. Further, in the 1986 study, type of elm hybrid affected ELB fecundity in absolute terms more than ozone fumigation. It is apparent, however, that ozone-fumigated leaves do not meet the optimal nutritional needs of ELB.

The impact of ozone on ELB fecundity and herbivory varied depending on concentration. It is ironic that although ozone has been shown to decrease vigor and growth of trees (McLaughlin et al. 1982; Heck et al. 1986), it may actually increase insect herbivory. Such a response might be expected since many insects show compensatory consumption, i.e., eating more as host quality declines. Further studies should focus on the changes in the biochemical components of elm leaves in response to an ozone-fumigation scenario that follows constant percentages of the ambient temporal fluctuations in ozone concentration, and how these changes may affect ELB fecundity and herbivory. Additional research also is needed to determine the degree of egg viability and larval development on the ozonated foliage. While ELB was generally less fecund on fumigated foliage, egg viability and larval survival and development may increase.

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Keywords: Fecundity; herbivory; survivorship; suitability; open-top chamber

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