Ozone-Induced Acceptability of Yellow-Poplar and Black Cherry to Gypsy Moth Larvae[1]

Anton G. Endress,[2,3] Michael R. Jeffords,[3] Laurie J. Case,[3] and Lane M. Smith II[3]
Department of Horticulture, University of Illinois
and
Illinois Natural History Survey
1005 Plant Sciences Laboratory
1201 S. Dorner Drive
Urbana, IL 61801

Abstract

The feeding behavior of 3rd instar gypsy moth (*Lymantria dispar* L. [Lepidoptera: Lymantriidae]) was examined on foliage from black cherry (*Prunus serotina* L.) and yellow-poplar (*Liriodendron tulipifera* L.) seedlings exposed to 71 ± 31, 212 ± 37, and 337 ± 31 $\mu g\ m^{-3}$ ozone (O_3) for 70 hours to gauge the effect of O_3 stress on host acceptability. Normally, black cherry is a suboptimal food source and yellow-poplar is unacceptable. With feeding preference assays conducted in the laboratory using feeding arenas, the leaf area consumption of black cherry control foliage (exposed to ambient air containing 71 $\mu g\ m^{-3}$ O_3) by starved larvae was approximately twice that of yellow-poplar control foliage during the first 4 hours. By 8 hours, the leaf area consumed was the same for both species. O_3-treated leaves of both species were preferred by the larvae relative to leaves exposed to ambient concentrations. The effect was pronounced for yellow-poplar, where consumption of ozonated foliage was more than twice that of the control, and its acceptability was enhanced to a level approximating that of black cherry.

Index words: ozone, oxidant, insect-plant interactions, gypsy moth, *Lymantria dispar*, black cherry, *Prunus serotina*, yellow poplar, *Liriodendron tulipifera*

Significance to the Nursery Industry

Generally there is little information about the cultural requirements and performance of trees in community and urban areas, particularly with respect to their tolerance of air pollutants or susceptibility to pests. Although air pollutants are found in both rural and urban areas, air pollution problems are generally greater in urban areas. Municipalities and other consumers should plant tree species and cultivars that best tolerate the urban environment. Some growers and consumers consider the direct impact of air pollutants on plant performance when making plant selections, but few are aware of the indirect and potentially significant impacts of air pollution. Air pollutants and other sources of stress in the urban environment may enhance plant susceptibility to pests, rendering otherwise desirable species or cultivars unsuitable. In documenting the enhanced acceptability of air pollutant-stressed tree species to a major herbivore in North America, the research presented in this paper illustrates that diseases affecting urban trees, and costs to maintain them, may increase as air quality deteriorates.

Introduction

Ozone (O_3) is considered responsible for most of the vegetation injury caused by ambient air pollution on a regional scale in the U.S.A. (7). While O_3 can cause overt structural damage in plants, it more typically elicits subtle changes in basic metabolic processes or in cellular and subcellular structures when at concentrations greater than 120 $\mu g\ m^{-3}$ (15).

One of the most far-reaching consequences of plant explosure to O_3 is that the quantity and distribution of both carbohydrates and nitrogenous compounds are altered. Depending on plant species examined, O_3 has been shown to reduce photosynthesis, alter patterns of photosynthate allocation, and increase concentrations of free amino acids, soluble proteins, glutathione, and reducing sugars (9, 18). Research has also documented that subtle physiological or biochemical changes in plants often affect insect herbivore development and behavior (3, 17, 20, 23). Jeffords and Endress (13) reported a preference by gypsy moth (*Lymantria dispar* L.) larvae for ozonated foliage excised from white oak (*Quercus alba* L.). In a later study, Endress and Post (5) demonstrated that the Mexican bean beetle (MBB) (*Epilachna varivestis* Mulsant) preferred to feed on excised soybean foliage injured by O_3. Soybean defoliation by the MBB has also been shown to increase with increasing O_3 concentration (1). Exposure to O_3 has also been shown to override the resistance to herbivory in soybean that had been induced by the feeding of soybean looper (*Pseudoplusia includens* Walker) larvae (16). In the most detailed of the O_3 studies to date, Trumble et al. (22) showed higher survival of tomato pinworm (*Keifera lycopersicella* Walsingham) larvae and faster development on tomato plants injured by O_3 than on plants not subjected to O_3. O_3 exposure was associated with changes in the concentrations of soluble proteins and several amino acids.

In studies of the impact of other pollutants in insect/plant interactions, Hughes et al. (10), demonstrated that MBB exhibited a feeding preference for pinto bean (*Phaseolus vulgaris* L.) foliage exposed to sulfur dioxide (SO_2). Subsequent studies showed that MBB larvae reared on soybeans exposed to SO_2 developed faster, grew larger, laid more

[1]Received for publication April 17, 1991; in revised form July 22, 1991. This research was supported in part by a contract from the Illinois Department of Energy and Natural Resources. Their support is appreciated.

[2]Professor of Horticulture, University of Illinois.

[3]Associate Entomologist, Assistant Research Biologist, and Assistant Research Biologist (respectively), Illinois Natural History Survey, Urbana, IL.

eggs than those reared on control plants (11, 12), and that the feeding preference appeared to relate to the foliar content of glutathione (2). Dohmen et al. (4) also recorded enhanced performance of the black bean aphid (*Aphis fabae* Scop.) on *Vicia fabae* (L.) exposed to SO_2, nitrogen dioxide, and ambient London air. These observations imply that O_3 and other gaseous air pollutants may act as economically important modifiers of insect/plant interactions.

Gypsy moth larvae consume foliage of over 400 species of herbaceous, broadleaf, and coniferous plants during outbreaks (6). However, feeding preference studies have shown that some plant species are preferred (19). For example, white oak is an optimal (preferred) host, black cherry (*Prunus serotina* L.) is suboptimal, and yellow-poplar (*Liriodendron tulipifera* L.) is unacceptable. In field situations where larvae are starved because of massive defoliation of surrounding trees, yellow-poplar remain foliated and virtually untouched (M. Jeffords, personal communication). The purpose of this study was to determine whether O_3 stress alters acceptability of suboptimal and unacceptable plant species to gypsy moth larvae. Expanding the gypsy moth feeding range as a result of O_3 stress may have important implications for gypsy moth population dynamics and defoliation incidents.

Materials and Methods

Thirty six (36) black cherry and 36 yellow-poplar seedlings were each planted in containers of equal parts of loam, sand, peat moss, and vermiculite (1:1:1:1 by vol.). Plants were maintained in a greenhouse throughout the study, and their position on benches was regularly shifted to minimize position effects.

Seedlings were exposed to O_3 treatments, in the greenhouse, in 2 m^3 (2.6 yd^3) continuously stirred tank reactor (CSTR) chambers (8). Air exchange within the CSTRs was 4.5 m^3 min^{-1} (5.9 yd^3 min^{-1}). Ozone was generated from dry air by electric discharge with a Welsbach O_3 generator and dispensed to the chambers through rotameters. Concentrations were monitored on a time-share basis with a Dasibi Model 1003-AH O_3 analyzer calibrated against an Illinois Environmental Protection Agency transfer standard. Random number tables were used to assign plants to treatments and treatments to CSTRs. Ambient concentrations of sulfur dioxide (SO_2) in the CSTRs were measured using a Beckman Model 953 SO_2 analyzer. During the pollutant exposure segment of the experiment, the temperature and relative humidity in the CSTRs ranged from 21.3 to 42.0 C. (30.4 C. average), and from 29 to 70% (52% average), respectively.

Three O_3 treatments were used: ambient air, ambient air augmented with a constant addition of 155 $\mu g\ m^{-3}$ (0.08 ppm) O_3, and ambient air augmented with a constant addition of 270 $\mu g\ m^{-3}$ (0.14 ppm) O_3. One ppm O_3 is equivalent to 1960 $\mu g\ m^{-3}$ O_3 at standard temperature and pressure. An O_3-free treatment was not utilized because plants do not normally experience this condition. As the O_3 content of ambient air fluctuated throughout each day and week, so did that of all the treatments. Exposures were initiated when the first leaves were fully expanded (30 days after planting). Twelve trees of each species for each O_3 concentration were exposed to ambient air or ambient air supplemented with O_3 for 2 weeks, 5 days per week. Each of the 10 exposures was 7 hr. in duration for a total exposure time of 70 hr. The achieved 7-hr. mean (arithmetic mean $\pm$ standard deviation) O_3 concentrations for the treatments were 71 $\pm$ 31, 212 $\pm$ 37, and 337 $\pm$ 31 $\mu g\ m^{-3}$ (0.036, 0.108, and 0.172 ppm O_3, respectively). The peak 1-hr. O_3 concentrations were 167, 298, and 414 $\mu g\ m^{-3}$ (0.085, 0.152, and 0.211 ppm), respectively, for the 3 treatments, with all occurring during the sixth hr. of the fifth exposure. The background SO_2 concentration was 39 $\pm$ 12 $\mu g\ m^{-3}$ (0.014 ppm).

At the end of the last O_3 exposure, trees were randomly selected and assigned to one of 12 groups for each species for feeding preference assays. Each group consisted of three trees, one from each O_3 treatment. None of the leaves expressed any visual symptoms of O_3 injury. The third leaf was removed from each tree and a disc of 1.1 cm^2 (0.17 in^2) was removed from each with a cork borer. Each feeding preference assay was conducted in a 14 cm (5.5 in) glass petri dish arena containing a thin layer of paraffin covered by filter paper saturated with distilled water. Leaf discs were placed on the perimeter of the arena and secured with map tacks. Each arena contained three discs, one from each of the O_3 treatments. Six arenas were prepared for each group of three trees, for a total of 72 arenas for each tree species. A single 3rd instar gypsy moth larva, from a genetically homogeneous laboratory colony reared on an artificial diet for more than 30 generations, was starved for 6 hr. and placed in the center of each arena. Third instars were used because this is the stage at which the broadening of host acceptance occurs (19).

The arenas were placed in the dark at 27°C (80°F), the optimum growth temperature for gypsy moth larvae (19). Each arena was photographed at hourly intervals until 50% of the total leaf area was consumed. The experiment was terminated after 24 hr. regardless of the amount of leaf area consumed. On completion of the experiment, the resulting 2×2 transparencies were projected on a wall, and the profiles of the partially eaten discs were traced on paper. The paper discs were then excised and their areas measured using a leaf area meter. An ANOVA indicated no significant effect of individual trees of the same species on the amount eaten so data from each tree of a given species were pooled.

Feeding preference for each disc pair (71 vs 212 $\mu g\ m^{-3}$, 212 vs 337 $\mu g\ m^{-3}$, and 71 vs 337 $\mu g\ m^{-3}$) in each arena were calculated using the formula $C = 2A/M+A$ (14), where C is the preference index, A is the leaf area consumed on the test plant (or highest O_3 concentration), and M is the leaf area consumed on the control plant (or lowest O_3 concentration). The C index measures the relative amount of feeding on the two treatments on a scale of 0 to +2. A C value of 1 indicates no preference; a C value >1 indicates preference for the test plant; a C value <1 indicates preference for the control plant.

Results and Discussion

Field observations and research results have demonstrated that gypsy moth larvae prefer black cherry foliage over yellow-poplar (19). During the present investigation, the feeding arenas did not contain leaf discs from both black cherry and yellow-poplar, thus it was not possible to directly verify that gypsy moth larvae preferred black cherry foliage to that of yellow-poplar. Assuming that this feeding preference response is based on properties of the host tissue, not simply on tissue availability, and that our larval pop-

ulation was fairly homogeneous, then feeding on black cherry control foliage should exceed that on yellow-poplar. The *in vitro* consumption of black cherry control foliage (exposed to ambient air containing 71 μg m^{-3} O_3) on an area basis by starved 3rd instar larvae was approximately twice the yellow-poplar leaf area consumed during the first 4 hours of the feeding tests (Fig. 1). The initial feeding on black cherry was rapid and then slowed during the latter one-half of the test period. In contrast, feeding on yellow-poplar was initially low and then accelerated, so that by 7–8 hours, the total leaf area consumed was essentially the same for both host species. When total leaf area consumed per host species was compared across the three O_3 treatments, species-based differences of the quantities of foliage consumed were markedly less apparent. Feeding was essentially linear over time on both species, and by 8 hours, 13% more yellow-poplar than black cherry had been consumed (Fig. 2). The close similarity of total area consumption of the two host species suggests that both black cherry and yellow-poplar were equally acceptable. When non-ozonated (control) foliage consumption only was compared, black cherry was more acceptable as a host than was yellow-poplar (Fig. 1). Taken together, exposure of yellow-poplar to O_3 enhanced its acceptability to a level approximating that of black cherry (Fig. 2).

The best indication of an O_3-induced feeding preference was provided by the calculation of a consumption ratio. The ratio of ozonated foliage consumed per unit of control foliage consumed (calculated as [total host area eaten - control host area eaten]/control host area eaten), showed that the O_3-treated leaves of both species were preferred, i.e., consumption ratio >1. The effect was particularly pronounced for yellow-poplar (Fig. 3), where consumption of ozonated foliage area was usually more than twice that of the control.

Gypsy moth larvae consumed more total leaf area from O_3-treated black cherry leaf discs compared to the 71 μg m^{-3} control treatment (Fig. 4a); there was 50% more ozonated foliage available (both low and high treatments). Throughout the first six hours, total consumption was greatest on the control leaf tissue, intermediate for the 337 μg m^{-3} treatment, and least for the 212 μg m^{-3} treatment. By 8 hours, there were no differences between the 3 O_3 treatments. Conversely, cumulative consumption of yellow-poplar leaf discs (Fig. 4b) was greatest for the 337 μg m^{-3} O_3 treatment throughout the entire 8 hour observation period. Consumption of leaf discs from trees exposed to 71 or 212 μg m^{-3} O_3 were equivalent. The apparent switch in acceptability of yellow-poplar foliage, as a consequence of exposure to O_3 during the 8 hour feeding period resulted from very high consumption rates during the first 2 hours (Fig. 5b). The initial feeding rate favored the control treatment, but by the second hour, the rate of feeding on ozonated foliage was quite high. During the subsequent 6 hours, the rate of feeding on leaf discs from the 212 μg m^{-3} O_3 treatment returned to a low, sustained level. This reduced feeding co-occurred with an observed increase in the rate of feeding on yellow-poplar leaf discs exposed to high O_3, suggesting that gypsy moth larvae preferred the latter.

On black cherry, gypsy moth larvae tended to select control foliage for initial feeding (Fig. 5a). After 2 hours, there was a decline in the feeding rate on control tissue coupled with an increase in the feeding rate on leaf discs taken from plants exposed to 337 μg O_3 m^{-3}. The consumption rate on tissue from the 212 μg O_3 m^{-3} treatment was at a low and constant level. The rate of consumption of control tissue

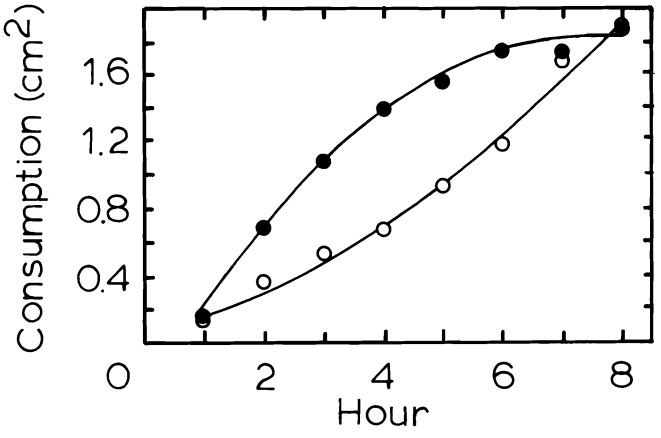

Fig. 1. Cumulative consumption of *Prunus* (●) and *Liriodendron* (○) control (71 μg m^{-3} O_3) leaf discs by starved 3rd instar *Lymantria* larvae. The values illustrated are the means and standard errors of the means. Results of regression analyses are *Prunus*: $\hat{Y} = -0.35 + 0.58x - 0.04x^2$; $R^2 = 0.995$; *Liriodendron*: $\hat{Y} = 0.08 + 0.08x + 0.02x^2$; $R^2 = 0.992$.

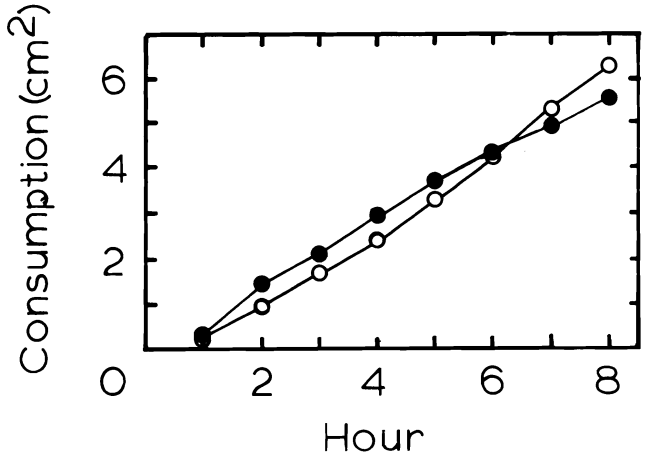

Fig. 2. Cumulative consumption of the combined O_3 treatments for *Prunus* (●) and *Liriodendron* (○) leaf discs by starved 3rd instar *Lymantria* larvae.

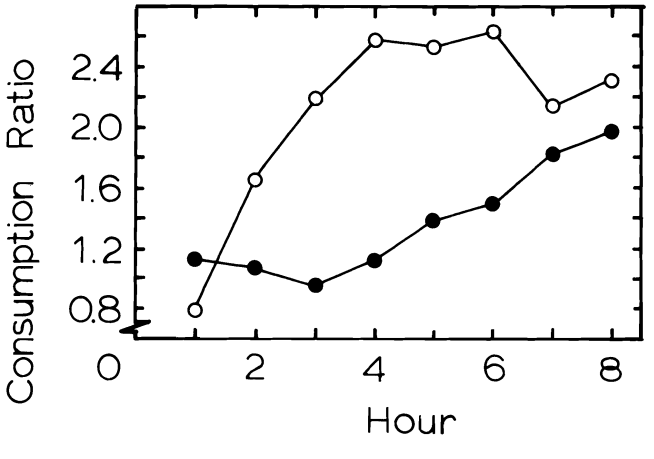

Fig. 3. Consumption ratio of ozonated to control leaf area for *Prunus* (●) and *Liriodendron* (○) leaf discs by starved 3rd instar *Lymantria* larvae.

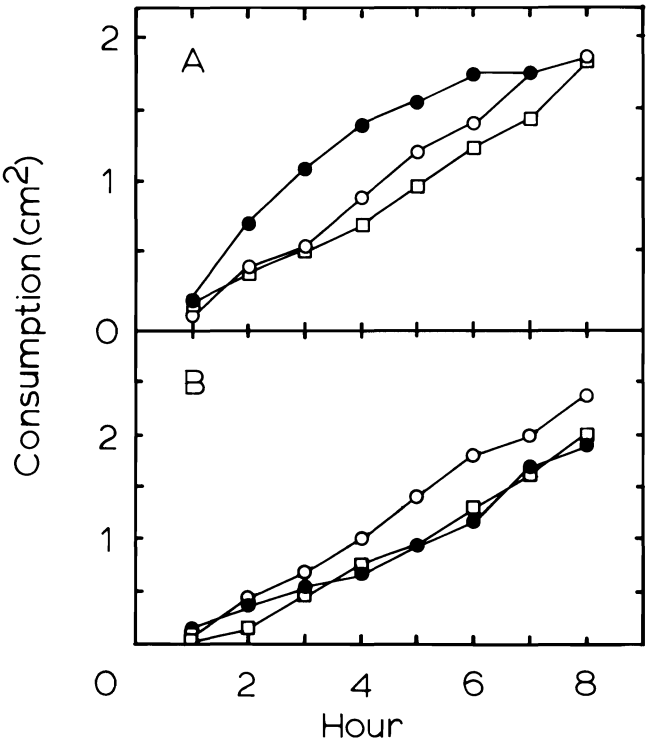

Fig. 4. Effect of O_3 on the cumulative consumption of *Prunus* (A) and *Liriodendron* (B) leaf discs by starved 3rd instar *Lymantria* larvae. O_3 treatments: 71 μg m^{-3} (●); 212 μg m^{-3} (□); 337 μg m^{-3} (○). The values illustrated are the means and standard errors of the means. The results of regression analyses for *Prunus* (A) are: 71 μg m^{-3} O_3 treatment: $\hat{Y} = -0.35 + 0.58x - 0.04x^2$; $R^2 = 0.993$; 212 μg m^{-3} O_3 treatment: $\hat{Y} = 3.5 \times 10^{-3} + 0.13x + 0.01x^2$; $R^2 = 0.995$; 337 μg m^{-3} O_3 treatment: $\hat{Y} = -0.23 + 0.29x - 2.9 \times 10^{-4}x^2$; $R^2 = 0.990$; The results of regression analyses for *Liriodendron* are: 71 μg m^{-3} O_3 treatment: $\hat{Y} = 0.08 + 0.08x + 0.02x^2$; $R^2 = 0.987$; 212 μg m^{-3} O_3 treatment; $\hat{Y} = -0.17 + 0.16x + 0.01x^2$; $R^2 = 0.997$; 337 μg m^{-3} O_3 treatment: $\hat{Y} = -0.24 + 0.32x + 7.2 \times 10^{-4}x^2$, $R^2 = 0.994$.

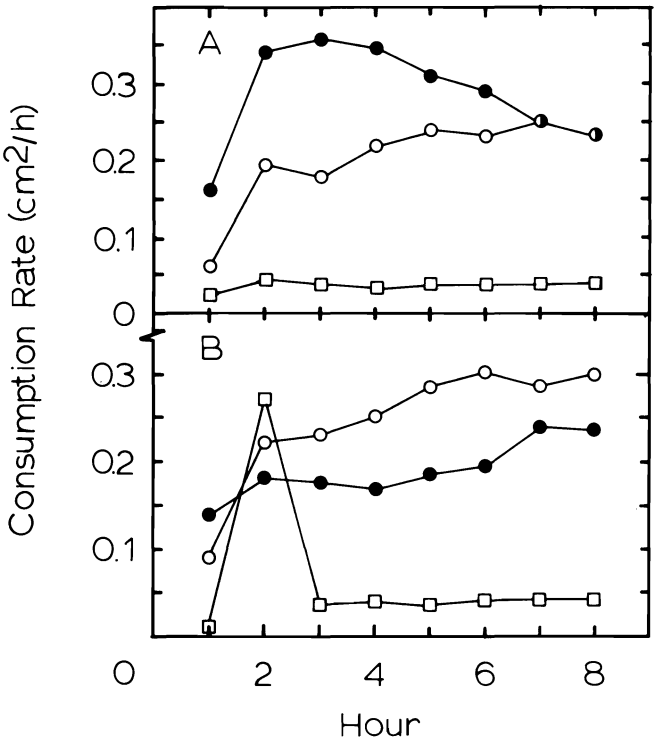

Fig. 5. Effect of O_3 on rate of leaf area consumption by starved 3rd instar *Lymantria* larvae for *Prunus* (A) and *Liriodendron* (B). O_3 treatments: 71 μg m^{-3} (●); 212 μg m^{-3} (□); 337 μg m^{-3} (○).

decreased after 2 hours, possibly because larval satiation occurred or some larvae switched from control to ozonated tissue as feeding on the latter continued to increase.

We attempted to estimate the direction and magnitude of larval switching between leaf discs from differing O_3 treatments using photographic documentation. The results are presented in Fig. 6, where the values indicate the percent of the total larvae switching from one treatment to another. Because leaf discs were arranged at equidistant intervals within the arenas, larval movement toward the alternative leaf discs should occur with equal frequency unless the properties of the discs vary (presumably due to O_3 treatment).

Larvae feeding on black cherry leaf tissue exposed to ambient greenhouse air tended to switch to leaf discs from the intermediate O_3 treatment. Switching in the reverse direction occurred less frequently. In turn, larvae feeding on tissue from moderate O_3 fumigation tended to switch to the higher O_3 tissue, rather than control tissue. For yellow-poplar, switching between the control and moderate O_3 treatment occurred with equal frequencies, but the tendency for larvae on both the control and moderate treatments to switch to the high O_3-treated leaf discs is consistent with the observation of preferred cumulative consumption for this treatment.

For each species, C index values were tabulated after 1, 2, 4, and 8 hours of feeding. To determine if the larvae were exhibiting any general preference for ozonated foliage, three contingency tables (3×3) were constructed for each tree species using the calculated C values and analyzed by chi-square for significance. This technique has been utilized previously to demonstrate feeding preferences for ozonated foliage (5, 13, 16). While trends were observed (e.g., a preference, after 2 hours for ozonated yellow-poplar foliage with a probability of $P = 0.139$ ($x^2 = 6.935$, 4 d.f.)), this technique was not sufficiently robust to identify a feeding preference for ozonated foliage in this study at a statistically significant level.

The host range of young gypsy moth larvae is more limited than for older larvae. Rossiter (21) showed that when compared with growth and development on oaks, older gypsy moth larvae on pitch pine (*Pinus rigida*, Mill.), a suboptimal host for 3rd instar larvae, were more fecund. Hughes et al. (11, 12) demonstrated that larvae of the MBB feeding on soybean tissue previously exposed to the air pollutant sulfur dioxide developed faster and were more robust and fecund. Chappelka et al. (1) showed that with increasing O_3, MBB feeding preference, as represented by percent defoliation, increased linearly. In addition, MBB larvae tended to weigh more and develop faster on ozonated foliage. If O_3 or other ambient air pollutant exposures increase the acceptability of otherwise sub-optimal plants to gypsy moth larvae, outbreaks may be even more devastating to both commercial and community forests. The enhanced *in vitro* acceptability of yellow-poplar caused by exposure to O_3 in this study

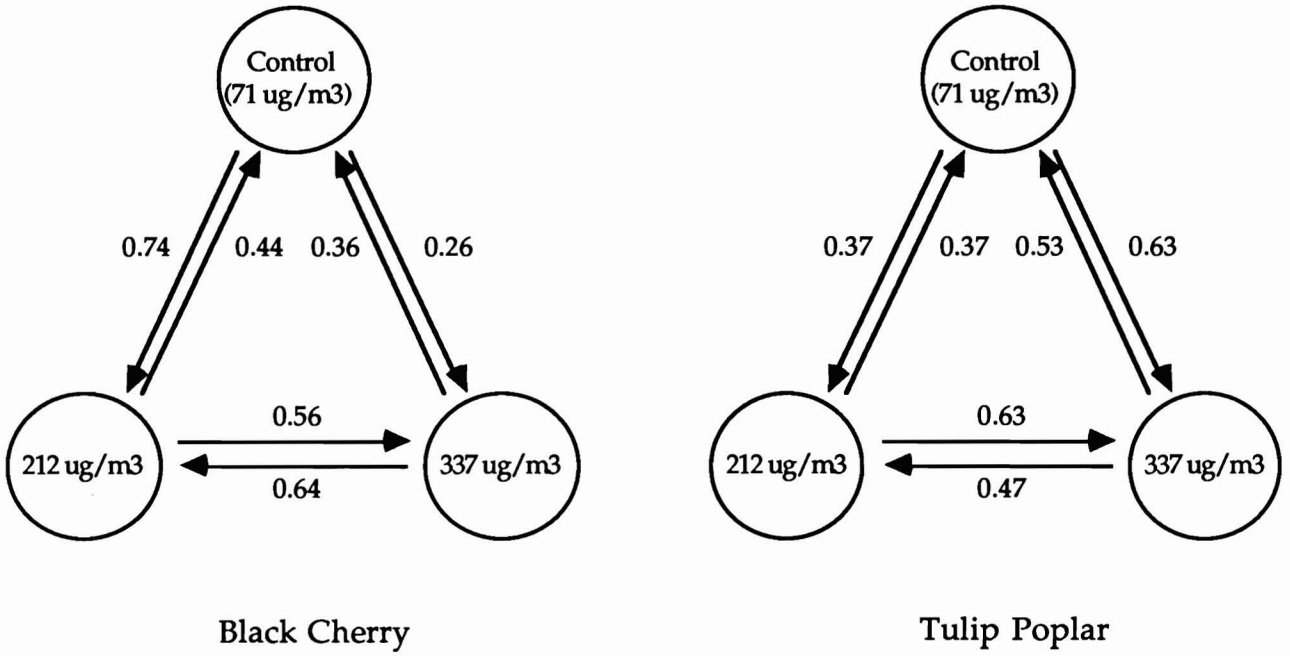

Fig. 6. Direction and magnitude of switching of 3rd instar *Lymantria* larvae between leaf discs differing in O_3 exposure concentration for *Prunus* and *Liriodendron*. The values are ratios of the total switching to each of the alternatives.

suggests the potential for expanded gypsy moth host range. It is not known whether they can complete development and reproduce following ingestion of ozonated yellow-poplar foliage.

Literature Cited

1. Chappelka, A.H., M.E. Kraemer, T. Mebrahtu, M. Rangappa, and P.S. Benepal. 1988. Effects of ozone on soybean resistance to the Mexican bean beetle (*Epilachna varivestis* Mulsant). Environ. Exp. Bot. 28:53–60.

2. Chiment, J.J., R. Alscher, and P.R. Hughes. 1986. Glutathione as an indicator of SO_2-induced stress in soybean. Environ. Exp. Bot. 26:147–152.

3. Denno, R.F. and M.S. McClure [eds.] 1983. Variable plants and herbivores in natural and managed systems. Academic Press, New York. 717 pp.

4. Dohmen, G.P., S. McNeill, and J.N.B. Bell. 1984. Air pollution increases *Aphis fabae* pest potential. Nature, Lond., 307:52–53.

5. Endress, A.G. and S.L. Post. 1985. Altered feeding preference of Mexican bean beetle *Epilachna varivestis* for ozonated soybean foliage. Environ. Pollut. 39:9–16.

6. Forbush, E.H. and C.H. Fernald. 1896. The Gypsy Moth. Wright and Potter, Boston, MA. 495 pp.

7. Heck, W.W., O.C. Taylor, R. Adams, G. Bingham, J. Miller, E. Preston, and L. Weinstein. 1982. Assessment of crop loss from ozone. J. Air Pollut. Control Assoc. 32:353–361.

8. Heck, W.W., R.B. Philbeck, and J.A. Dunning. 1978. A continuous stirred tank reactor (CSTR) system for exposing plants to gaseous air contaminants: principles, specifications, construction and operation. ARS Series No. 181, U.S. Govt. Printing Office, Washington, D.C.

9. Hughes, P.R. and J.A. Laurence. 1984. Relationship of biochemical effects of air pollutants on plants to environmental problems: insect and microbial interactions, pp. 361–377. *In* M.J. Koziol and F.R. Whatley [eds.], Gaseous Air Pollutants and Plant Metabolism. Butterworths, London. 466 pp.

10. Hughes, P.R., J.E. Potter, and L.H. Weinstein. 1981. Effects of air pollutants on plant-insect interactions: Reactions of the Mexican bean beetle to SO_2-fumigated pinto beans. Environ. Entomol. 10:741–744.

11. Hughes, P.R., J.E. Potter, and L.H. Weinstein. 1982. Effects of air pollution on plant-insect interactions: Increased susceptibility of greenhouse grown soybeans to the Mexican bean beetle after plant exposure to SO_2. Environ. Entomol. 11:173–176.

12. Hughes, P.R., A.I. Dickie, and M.A. Penton. 1983. Increased success of the Mexican bean beetle on field-grown soybeans exposed to SO_2. J. Environ. Qual. 12:565–568.

13. Jeffords, M.R. and A.G. Endress. 1984. A possible role of ozone in tree defoliation by the gypsy moth (Lepidoptera: Lymantriidae). Environ. Entomol. 13:1249–1252.

14. Kogan, M. and R.D. Goeden. 1970. The host-plant range of *Lema triliniata daturaphpila* (Coleoptera: Chrysomelidae). Ann. Ent. Soc. Amer. 63:1175–1180.

15. Koziol, M.J. and F.R. Whatley [eds.]. 1984. Gaseous Air Pollutants and Plant Metabolism. Butterworths, London. 466 pp.

16. Lin, H.-C., M. Kogan and A.G. Endress. 1990. Influence of ozone on induced resistance in soybean to the Mexican bean beetle (Coleoptera: Coccinellidae). Environ. Entomol. 19:854–858.

17. Mattson, W.J., Jr. 1980. Herbivory in relation to plant nitrogen content. Ann. Rev. Ecol. Syst. 11:119–161.

18. Miller, J.E. 1988. Effects on photosynthesis, carbon allocation, and plant growth associated with air pollutant stress, pp. 287–314. *In* W.W. Heck, O.C. Taylor, and D.T. Tingey [eds.], Assessment from Crop Loss from Air Pollutants. Elsevier Applied Science, London. 552 pp.

19. Mosher, F.H. 1915. Food plants of the gypsy moth in America. US. Dept. Agricul. Bull., 250.

20. Prestidge, R.A. 1982. Instar duration, adult consumption, oviposition and nitrogen utilization efficiencies of leafhoppers on different quality food (Auchenorrhyncha: Homoptera). Ecol. Entomol. 7:91–101.

21. Rossiter, M.C. 1987. Use of a secondary host by non-outbreak populations of the gypsy moth. Ecology 68:857–868.

22. Trumble, J.T., J.D. Hare, R.C. Musselman, and P.M. McCool. 1987. Ozone-induced changes in host plant suitability: Interactions of *Keifera lycopersicella* and *Lycopersicon esculentum*. J. Chem. Ecol. 13:203–218.

23. White, T.C.R. 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. Oecologia 63:90–105.