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Dynamics of Airborne Conidia of the Gypsy Moth (Lepidoptera: Lymantriidae) Fungal Pathogen *Entomophaga maimaiga* (Zygomycetes: Entomophthorales)

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Airborne conidia of *Entomophaga maimaiga*, a fungal pathogen of gypsy moth (*Lymantria dispar*), were sampled during 1992 and 1993 within forest canopies hosting gypsy moth populations. Conidia were occasionally abundant in the air in a site beginning the 1992 season with >20,000 egg masses/ha, but were almost undetectable when the resident gypsy moth population had declined to <100 egg masses/ha at the beginning of the 1993 field season. From third instar to pupation, presence of conidia in the air was episodic and infection in the resident gypsy moth population increased only after the first peak of abundance in airborne conidia. Conidial flux was positively associated with leaf wetness at lags of 5–14 and 16 h. Infection among larvae caged at 0.5 m above the ground was associated with leaf wetness, suggesting that moisture is critical for conidial survival and infection. Larvae caged on the ground (therefore, exposed to both resting spores and conidia of *E. maimaiga*) became infected throughout the field season, while, in comparison, larvae caged at 0.5 m (exposed only to airborne conidia) were infected sporadically during 1992 and virtually never during 1993. During 1992, infections of ground-caged larvae were initiated by both resting spores and conidia.

Key Words: **entomopathogenic fungi; *Lymantria dispar*; Lymantriidae; airborne conidia; epizootiology; biological control.**

INTRODUCTION

The fungal pathogen *Entomophaga maimaiga* Humber, Shimazu and Soper was first found causing epizootics in gypsy moth, *Lymantria dispar* (L.), populations in seven northeastern states (Massachusetts, Connecticut, New Hampshire, Vermont, eastern New York, northeastern Pennsylvania, and New Jersey) of the United States in 1989 (Andreadis and Weseloh, 1990; Hajek *et al.*, 1990b). During 1990, *E. maimaiga* spread beyond its 1989 distribution and was found in three additional states (Maine, Delaware, and northeastern Maryland) as well as central New York and central Pennsylvania (Elkinton *et al.*, 1991). Distributional surveys were not conducted in 1991 when *E. maimaiga* was introduced to locations along the leading edge of gypsy moth spread in Virginia, West Virginia, Maryland, and Pennsylvania where it did not previously occur (Hajek *et al.*, 1996). The fungus was recovered from the majority of 1991 introduction sites and spread up to 350 m from plot centers during 1991. During 1992, *E. maimaiga* seemed to simultaneously appear throughout northern Virginia gypsy moth populations for the first time (Hajek *et al.*, 1996) and thereafter has occurred throughout most of the contiguous northeastern distribution of gypsy moth.

E. maimaiga produces two types of spores; resting spores (azygospores) are produced predominantly within late instar cadavers, and conidia (asexual spores) are produced externally on cadavers, predominantly of early instars (Hajek and Shimazu, 1996). While resting spores provide overwintering survival, the conidial stage is critical to disease transmission within the same season, which is important for development of epizootics (Hajek *et al.*, 1993). After host death, cadavers of larvae killed by *E. maimaiga* generally remain attached to twigs, branches, or tree trunks (Hajek *et al.*, 1998), and conidia are actively ejected from cadavers under humid conditions (Hajek *et al.*, 1990a; Hajek and Soper, 1992). Weseloh and Andreadis (1992b) documented *E. maimaiga* infections among gypsy moth larvae within cages suspended from branches at 2 m; these caged larvae were infected presumably by airborne conidia. Although we know that conidia are discharged from cadavers and are assumed to infect

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larvae, little is specifically known about the survival, activity, or abundance of airborne conidia of *E. maimaiga*.

Rapid spread by fungal plant pathogens has frequently been attributed to aerial dispersal of spores (Gregory, 1973; Zadoks and Schein, 1979; Campbell and Madden, 1990). Conidia of insect pathogens in the Entomophthorales are actively ejected and have previously been shown to travel on the wind (see Wilding, 1970; Harper *et al.*, 1984; Steinkraus *et al.*, 1996). While the mechanism for the rapid spread of *E. maimaiga* between 1989 and 1992 is not known, we hypothesize that wind-dispersed conidia might have played a central role.

We report findings from a study of airborne conidia of *E. maimaiga* during which we examined conidial densities in the air. Associations between conidial presence in the air and weather variables were investigated. To determine whether airborne conidia were infective, gypsy moth larvae were caged adjacent to spore sampling equipment and infection levels were associated with densities of airborne conidia.

MATERIALS AND METHODS

Sampling site. From 11 June through 31 August, 1992, spore sampling equipment was continuously operated in a red oak (*Quercus rubra* L.) woodlot in Yellow Barn State Forest, central New York, where an *E. maimaiga* epizootic had occurred during 1991. During 1993, spore sampling equipment was continuously operated from 20 April through 9 August at the same site.

Sampling gypsy moth populations. Gypsy moth populations were sampled during the 2 years of aerial sampling. Egg mass densities were estimated by completely counting egg masses in three 0.01-ha plots separated by 30 m (Kolodny-Hirsch, 1986). After the first instar, on a weekly basis, 30 gypsy moth larvae were collected and reared in individual 29.6-ml plastic cups containing high-wheat-germ diet (Bell *et al.*, 1981) in an outdoor insectary. If the collected larvae died, cadavers were placed on 1.5% water agar at 20°C and 14:10 (L:D) and were checked daily for 3 days to detect potential production of conidia by *E. maimaiga*. Cadavers were subsequently dissected to detect any production of *E. maimaiga* resting spores within cadavers. Season-long infection levels were calculated as in Hajek *et al.* (1990b).

Sampling airborne conidia. Two different types of aerial spore samplers were used. To sample conidia across time, a 7-day recording, battery-powered volumetric spore trap (Burkard Manufacturing Co., Rickmansworth, Herts., UK) was operated. Particles are impacted onto plastic tape coated with sticky silicone, supported on a clockwork-driven drum that rotates at 2 mm/h past a 2 × 14-mm orifice. The trap faces into the wind, a pump pulls air through the orifice, and the air impacts the adhesive tape at 10 liters/min (=0.6 m^3/h) with a collection efficiency of approx 70 ± 20% (technical data available from Burkard Manufacturing Co.). Conidia in the sampled air adhere to the tape. The spore trap orifice was 0.5 m above ground level. During 1992, sampling began June 11, when third instars were abundant.

To sample conidia at vertical locations in the forest canopy, Rotorod spore samplers (Sampling Technologies, Minnetonka, MN) were positioned at 0.5, 1.5, and 3.0 m of height within the woodlot. Two plexiglass rods were covered with a sticky layer of silicone and attached to each Rotorod unit. These rods rotate around the unit, collecting particles from 2.72 m^3 air/h, resulting in a collection efficiency of approx 100% (technical data available from Sampling Technologies). Rotorod samplers at the different heights were operated simultaneously for hourly intervals at differing times of day. For each sampling period, two Rotorod samplers were operated at each location and data were averaged.

Morphological criteria were used to identify *E. maimaiga* conidia collected by spore samplers on Plexiglass rods or plastic tape. The characteristic pear shape of *E. maimaiga* conidia, as well as their relatively large size (approximately 21 × 27 μm) compared with much of the material adhering to tapes and rods, aided in visual identification (Fig. 1). Meteorological equipment recorded temperature, leaf wetness, and wind speed (Omnidata, Logan, UT) at the study site locations while spore samplers were being operated.

Bioassays. Gypsy moth eggs were obtained from the USDA, APHIS, Otis Methods Development Center, Otis Air National Guard Base, Massachusetts. After hatch, larvae were reared on high-wheat-germ artificial diet (Bell *et al.*, 1981).

As a method for evaluation of airborne conidial infectivity, gypsy moth larvae were caged within 3 m of spore samplers. Thirty early fourth instars were placed in groups within 23 × 31-cm cages made of 20 × 20-mesh stainless steel screening that was folded and stapled along the edges. Each cage contained a cube of artificial diet so that these cages, which would normally be flat, were approximately 3–4 cm high in the center, allowing some space for larvae to move within the cage. For each bioassay, six cages were used, placing three cages at each of two locations: ground level and the height of the Burkard spore sampler orifice. Resting spores in the soil at the bases of trees within the woodlot averaged 2968 ± 159 resting spores/g dry soil at the beginning of the season in 1992 and 1914 ± 343 resting spores/g dry soil at the beginning of the season in 1993 (Hajek and Wheeler, 1994). Therefore, larvae in cages at ground level were exposed to resting spores as well as airborne conidia that had fallen to the ground.

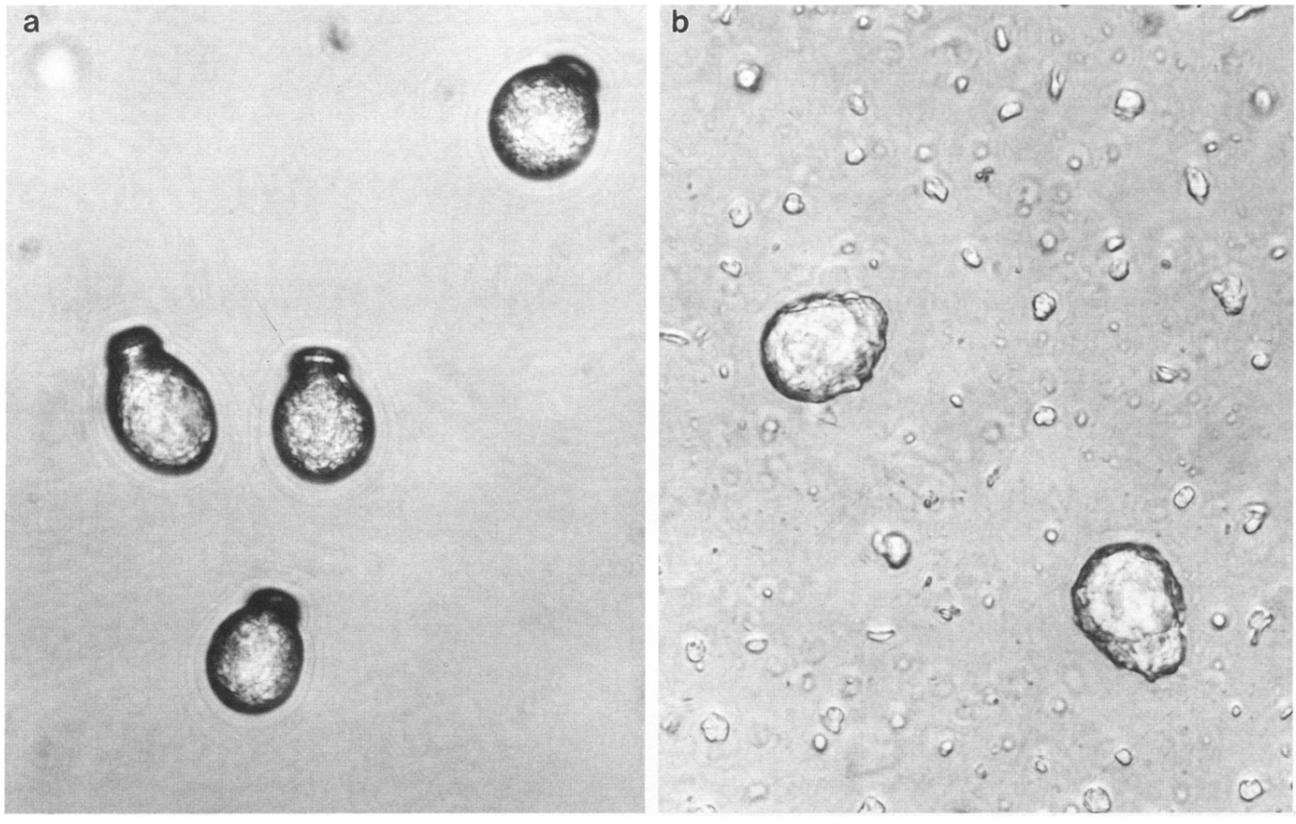

FIG. 1. Characteristic pear-shaped conidia of *Entomophaga maimaiga*. (a) Discharged onto a microscope slide without a coverslip. (b) Embedded in silicone on a plastic tape from a 7-day recording volumetric spore sampler. Conidia are approximately 21 × 27 μm.

In contrast, we assume that larvae in cages at 0.5 m were exposed only to airborne conidia.

Larvae were caged in the field for 3 days in an attempt to obtain infection during each sampling period. After 3 days, larvae were returned to the laboratory where they were removed from cages and placed in groups of 10 into 236-ml plastic cups containing artificial diet. Larvae were reared at 20°C, 14:10 (L:D) and were checked daily for mortality for 10 days. All caged larvae that died were examined for *E. maimaiga* infections as described above for larvae sampled from field populations. Field bioassays were conducted 14 times between 12 June and 31 July, 1992 and 18 times between 7 May and 8 July, 1993.

Data analysis. Because the Burkard spore sampler draws in air at a constant rate, hourly conidial counts were converted to flux (number conidia/m^3 air/h · m/s air speed). Tobit models were used to evaluate associations of weather variables with conidial flux and bootstrap procedures were used to derive standard errors (Stata, College Station, TX). For the tobit model, we used data between 12 June and 9 July because this is the period from the 1992 initiation of spore sampling until the last sampling interval during which larvae were collected. Based on previous findings of a lagged association between moisture and fungal performance (Hajek and Soper, 1992), we tested for autocorrelations of flux with lagged flux and cross correlations of flux with leaf wetness and temperature. Graphical examination of correlations was used to choose 18 h as the maximum lag tested. For each variable, lags were tested independently against flux due to multicollinearity. For associations between flux and each type of weather variable and for autocorrelations, results were considered as part of one comprehensive evaluation and for each pair of variables, an overall α of 0.05 was partitioned by 18 so that individual lagged comparisons were each tested at $\alpha = 0.00278$.

RESULTS

Although spore samplers were operated over 2 years, airborne conidia were detected in abundance only during 1992, when the gypsy moth population averaged 23,013 egg masses/ha (SE = 3993) at the beginning of the field season. During the period that larvae were present, this area received near-average rainfall (May, 8.05 cm; June, 9.47 cm) (NOAA, 1992). Rainfall during May was fairly frequent (16 days > 0.025 cm) while June rainfall was less frequent (11 days), although near normal (June 30 year average = 12 days of rain).

Season-long *E. maimaiga* infections in the resident gypsy moth population totalled 97.5%.

In 1993, the gypsy moth population had declined to 59 egg masses/ha (SE = 59) and the season-long *E. maimaiga* infection level was 12.6%. May, 1993 was dry (3.94 cm rain over 14 days) while June received above-average rainfall (11.71 cm over 12 days) (NOAA, 1993). Airborne conidia were barely detected in the presence of the lower density 1993 gypsy moth populations. Possibly, when the host population was low, cadavers of larvae dying from *E. maimaiga* were not abundant enough to produce densities of conidia that could be detected with the equipment used.

During 1992, aerial sampling began when third instars were abundant. Two main periods of higher densities of airborne conidia occurred when fourth and fifth instars were present (daily sums of flux presented in Fig. 2). Conidial flux was >1/h for 13 h on 20 June (maximum flux/h = 3.9) and for periods that were 14–16 h long on each day of 3–5 July (maximum flux/h = 29.3). Concurrent larval sampling in the field demonstrated that *E. maimaiga* infections in larval populations increased only after the first increase in airborne conidia that we detected.

Between June 12 and July 9, leaf wetness was associated with conidial flux for lags of 5–14 and 16 h. Associations between flux and simultaneous leaf wetness or leaf wetness at lags of 1–4 h were close to significant (range for $P = 0.0049$–0.0109; critical value for each test = 0.00278). For independent tests of lagged temperature, no associations were found, although the general trend was a negative association. When autocorrelations were tested, lags of flux from 1 to 3 h were significant, with associations for lags of 5–7 h still quite high ($P = 0.0339$–0.0099). An overall model using the lags with highest associations demonstrated significantly positive associations between conidial flux and flux with a 1-h lag, leaf wetness with a 5-h lag, and simultaneous wind speed and a negative association of conidial flux with temperature at a 6-h lag (Table 1).

We investigated the time of day that conidia were most abundant in the air. Throughout the period of 12 June–9 July, conidial flux of 1 was more frequent between 0700 and 1900 h than between 1900 and 0700 h ($\chi^2 = 14.76$; $P < 0.05$). However, we saw no sharply defined period of high conidial density associated with photoperiod.

Larvae caged at the ground level (potentially infected by both conidia and resting spores) were always infected at higher levels than larvae at 0.5 m (infected principally by conidia) (Fig. 3). Gypsy moth larvae at ground level became infected throughout the season until late instars were present during both 1992 and 1993. In contrast, larvae caged at 0.5 m were infected sporadically during 1992, presumably due to the sporadic occurrence of conidia in the air and were almost never infected during 1993. Percentage infection among gypsy moth larvae caged at 0.5 m averaged 8.1 ± 5.1% (range 0.0–48.0%) and was positively associated with hours of leaf wetness during the 3-day period of exposure but not with conidial flux or average temperature ($F = 11.38$; $P < 0.05$). In analyzing infections among caged larvae, we included only results from bioassays through 13 July because after this time only pupae were detected during population sampling. We continued to cage larvae after this time and, surprisingly, infections occurred through 24–27 July. Conidia were also detected with the spore sampler through this time,

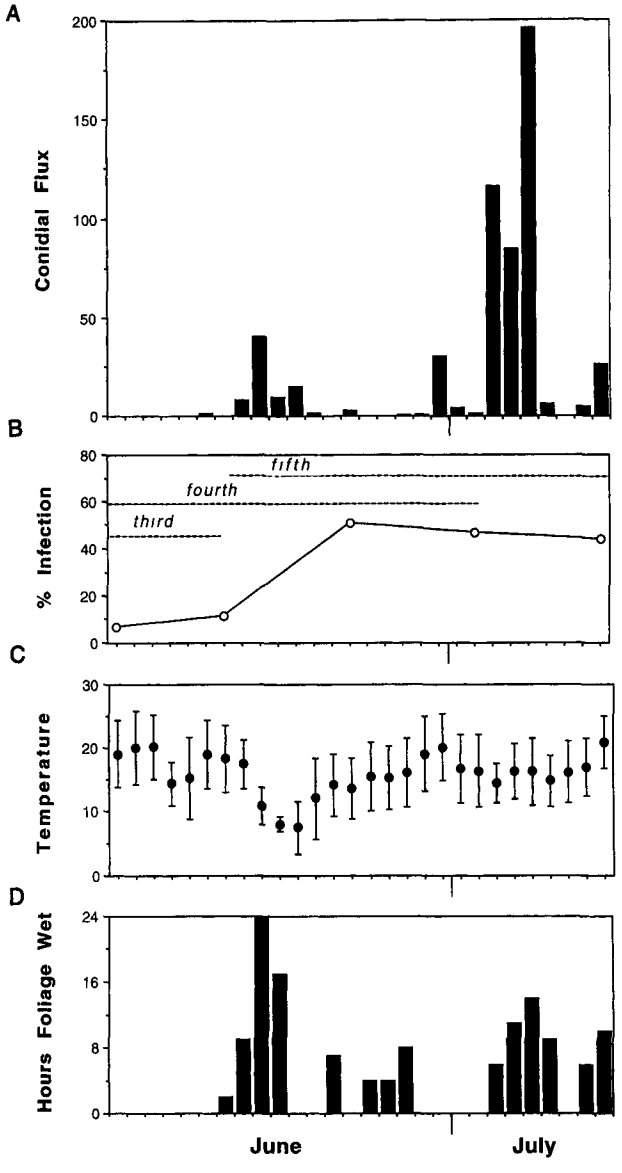

FIG. 2. (A) Daily sum of conidial flux calculated from collections from a Burkard spore sampler adjusted by wind speed (mps) in central New York, 1992. (B) Gypsy moth larval instar and *Entomophaga maimaiga* infection levels during weekly sampling at study sites. (C) Maximum, minimum, and average temperatures measured daily at the study site. (D) Hours of leaf wetness measured daily at the study site.

TABLE 1

Tobit Model of the Association between the Flux of Airborne Conidia of *Entomophaga maimaiga* and Weather Variables

	Coefficient	95% Confidence interval
Flux lag, 1 h	0.903	0.712–1.094
Leaf wetness lag, 5 h	2.874	0.655–5.092
Temperature lag, 6 h	−0.131	−0.250–−0.012
Windspeed (mps)	1.527	0.275–2.780

Note. All variables included are significant.

although at lower densities. Therefore, cadavers remaining in the field were probably rehydrating and discharging conidia for several weeks after susceptible host stages were absent or conidia were discharged at extremely low densities as the last of the late instars died.

Across the 1992 season, infections of larvae caged on the soil and at 0.5 m frequently resulted in production of both resting spores and conidia. During 1992, at ground level an average of 38.2% (SE = 7.2, range 1.4–64.7%) of infections between June 19 and July 20 produced resting spores; these infections must therefore have been initiated by conidia because only infections initiated by conidia discharged from cadavers can result in resting spore production (Hajek, 1997).

Although Rotorod samplers were operated for 5 h in 1992 and 31 h in 1993, sufficient numbers of conidia for comparisons by height were collected only in 1992. Conidia were equally abundant at 0.5 (mean ± SE = 22.7 ± 12.1 conidia/2.72 m^3 air), 1.5 (24.1 ± 11.6), and 3.0 m (24.1 ± 8.9) height (nonparametric ANOVA; $P > 0.05$). The highest density of conidia was collected during the only sampling period with high moisture levels both during sampling and throughout the 12 h prior to sampling.

DISCUSSION

Conidia of *E. maimaiga* were abundant in the air during sporadic intervals in 1992, a year during which gypsy moth larvae were abundant. Interestingly, even during 1992, *E. maimaiga* conidia were not as regularly abundant in the air as recorded during epizootics of *Neozygites fresenii* (Nowakowski) Remaudière and Keller (Steinkraus *et al.*, 1996) and *Pandora gammae* (Weiser) Humber (=*Entomophthora gammae*) (Harper *et al.*, 1984). In the present study, the densities of conidia in the air remained low for extended periods of time between occasional episodes of abundance. Airborne conidia were virtually absent during 1993 when gypsy moth populations were scarce. In agreement, at sites of low gypsy moth density (500–800 egg masses/ha) in Virginia, in 1992 we found no airborne conidia (A.E.H., unpubl. data).

When conidia were present in the air, conidial flux was positively associated with the leaf wetness 5–14 and 16 h before. In the laboratory conidia are discharged only under humid conditions (Hajek *et al.*, 1990a) and in the field an association was demonstrated between leaf wetness and localized conidial discharge in experimental microcosms, with a lag of 1–3 h (Hajek and Soper, 1992). Results from the present study demonstrate a longer lagged association between environmental moisture and the flux of conidia in the air. In fact, during 1992, the episodes of high conidial flux occurred during extended stormy periods.

Weseloh and Andreadis (1992b) found that infection among larvae caged in the understory was significantly

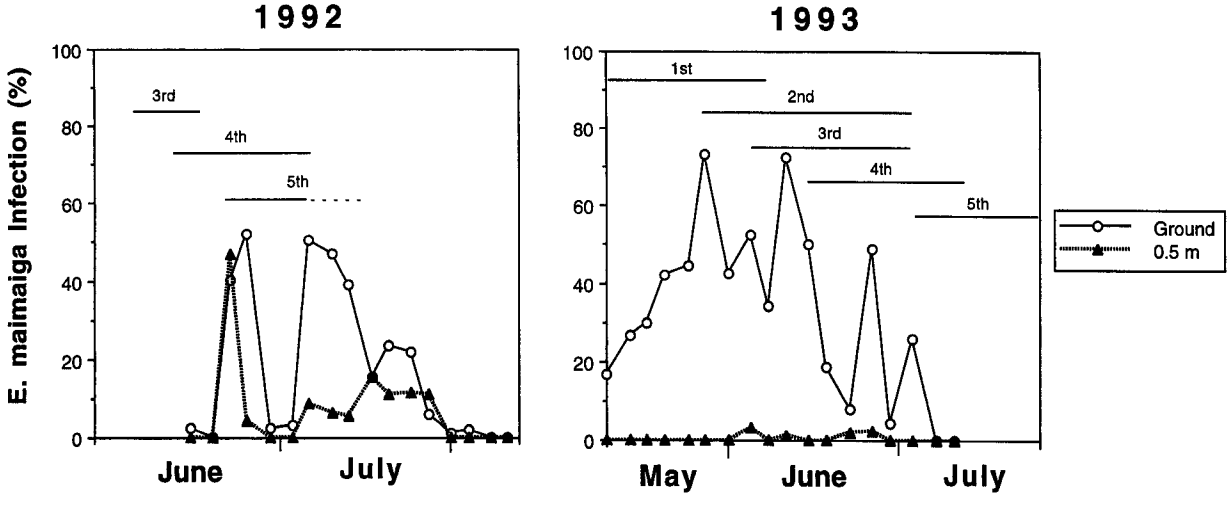

FIG. 3. Levels of infection by *Entomophaga maimaiga* in gypsy moth larvae caged at ground level (ground infection) and 0.5 m (aerial infection), Yellow Barn State Forest, New York, 1992 and 1993. Sampling for instar distribution ended each year around the beginning of pupation; therefore, during 1992 fifth instar larvae and pupae were present, producing conidia, after sampling ended.

positively associated with daily rainfall, although the r of 0.241 was not high. In agreement, we found that infections among larvae caged at 0.5 m were associated with leaf wetness rather than conidial flux. These results suggest that, although conidia are present in the air, moisture level has a stronger association with the ability of *E. maimaiga* to infect than does conidial flux.

In agreement with findings by Weseloh and Andreadis (1992b), infection levels among larvae caged at ground level were always higher than infections among larvae caged in the vegetation. Our results demonstrate that conidia produced from cadavers cause infections at ground level as well as at 0.5 m. Therefore, some airborne conidia must settle from the air onto the ground while still alive and then cause infections. During 1993, almost all infections occurred in larvae caged on the ground and only conidia were produced from resulting cadavers, as would be expected for infections initiated by resting spores.

During this study, we found no strong diel periodicity to occurrence of conidia in the air. This is surprising to some extent because studies with *N. fresenii* infecting cotton aphids, *Aphis gossypii* Glover (Steinkraus *et al.,* 1996), and *P. gammae* infecting the soybean looper, *Pseudoplusia includens* (Walker) (Harper *et al.,* 1984), have demonstrated a strong diurnal periodicity in occurrence of conidia in the air. In a study of six entomophthoralean pathogens infecting aphids on alfalfa (Milner *et al.,* 1984), three species demonstrated strong associations between mortality of infected aphids and time of day, although for the remaining three species, this association was weak. *E. maimaiga* and gypsy moth occur in shady forests rather than crops where hosts would potentially be more directly exposed to sunlight. Laboratory bioassays with *E. maimaiga* infecting gypsy moth larvae have shown no diurnal periodicity in time of death of infected hosts (A.E.H., unpubl. data). The lack of diurnal periodicity in abundance of airborne conidia of *E. maimaiga* documented during the present study is clearly in agreement with the lack of periodicity in mortality of infected hosts.

E. maimaiga conidia are actively discharged from cadavers. Cadavers of earlier instars producing conidia are rarely seen on tree trunks but have frequently been observed instead on leaves, leaf petioles, twigs, and branches (Weseloh and Andreadis, 1992a; Hajek *et al.,* 1998). It has been suggested that when hosts die in exposed locations, conidia have a better opportunity to travel substantial distances in moving air (Wilding, 1970). However, the length of time conidia are in the air and the distance they travel are only two facets of whether conidia reach hosts and infect, adding to epizootic development. The air is a viscous medium for spores that are the size and density of *E. maimaiga* conidia (Sawyer *et al.,* 1994). While conidia are continually falling, they do so in a packet of air that itself may be moving horizontally or even upward. In addition to conidial movement, dilution of conidia while in the air and conidial survival and deposition are subsequently critical to whether airborne conidia successfully infect to add to development of epizootics (Aylor, 1986).

E. maimaiga conidia were detected from 0.5 to 3.0 m height in the forest canopy. However, conidia discharged from cadavers are most certainly not all airborne. Gypsy moth larvae frequently reside on branches and trunks in groups. Therefore, larvae walking or resting next to sporulating cadavers could subsequently become infected by conidia which did not travel in the airstream. The relative contributions of short-range versus long-range dispersal by conidia to epizootic development remain unknown.

Our study cannot determine whether the airborne conidia sampled were produced within the same plot or had traveled a long distance. Long-distance aerial movement by spores of plant pathogenic fungi has been hypothesized in numerous systems (Zadoks and Schein, 1979; Campbell and Madden, 1990). During 1992, field observations suggested a seemingly simultaneous appearance of *E. maimaiga* throughout much of northern Virginia (Hajek *et al.,* 1995). The prevailing wind directions (from north to south during this time in 1992), rainfall patterns (abundant rainfall), and simultaneous occurrence of epizootics at many locations where *E. maimaiga* had not previously been recovered raise the possibility that at least part of the fungal inoculum responsible for 1992 epizootics may have traveled long distance on weather systems (see Dwyer *et al.,* 1998). Although we cannot prove the source of conidia, our study demonstrates that *E. maimaiga* conidia definitely become airborne within forest canopies and their presence in the air can be associated with infection.

While *E. maimaiga* conidia were detected in the air, in abundance at times, this does not discount the possibility of other means for spread of this pathogen. Some possibilities include (1) inadvertent movement of resting spores or conidia by vertebrates or invertebrates (e.g., in the soil on human shoe soles (Hajek *et al.,* 1995)) and (2) movement of infected larvae (either ballooning infected first instars or walking infected later instars).

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