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Dispersal and its impact on the population dynamics of the gypsy moth in the United States of America^{1, 2}

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Wind-borne dispersal of first instar larvae is the primary means by which populations of the exotic gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae), spread in North America. Deposition of these larvae has been poorly understood. Tests of models which estimate numbers of larvae available for dispersal, and deposition of these larvae in relatively level terrain as influenced by wind speed and direction as well as atmospheric turbulence, are reviewed. Results demonstrate that dispersal is a short-range process, that most larvae are deposited downwind within some hundreds of meters of the source, and that the probability of dispersal over long distances is exceedingly small.

Two special conditions, pertinent to the northeastern United States, are considered. The «sea breeze» effect, which concentrates larval deposition in a band ca 10–20 km inland, has been observed in the last decade in the coastal state of New Jersey. Wind flow in a «ridge and valley» system, such as occurs in the state of Pennsylvania, has not been suitably modelled. Modification of the basic dispersal model by assuming an elliptical rotor of wind to occur between ridges predicts larval deposition concentrated in a band just short of the opposite ridge; such a pattern has been observed frequently in Pennsylvania.

Under normal conditions, air-borne dispersal of larvae occurs as a series of short hops; even in ridge and valley situations, dispersal normally occurs over only a few kilometers, and is important in maintaining an area-wide outbreak of the insect. Dispersal does not appear as important in either the innocuous phase of the population or in its decline. These conclusions have major implications for proposed applied programs designed to retard the geographic spread of the gypsy moth in North America.

Dispersal of the gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae), is not at all well-understood. The insect was introduced into North America in 1869, accidentally escaping from a laboratory colony in Medford, Massachusetts. For most of its first century in the new world, the gypsy moth spread rather slowly from the point of introduction, but in the last decade or so it has exploded especially to the south and west (fig. 1). Early in the North American experience, the insect was in an area characterized by relatively level or gently rolling terrain. It has now reached what is referred to as the ridge and valley system in Pennsylvania, and as it continues to move south and west it will enter even more mountainous terrain. Such topography is very different from that with which the gypsy moth has been confronted historically in North America. The rate of expansion of the generally-infested area has increased, and the role of dispersal in population dynamics and spread will increase tremendously in the future.

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In North America, the female moth is considered to be flightless, although rudimentary flight over short distances has been reported on rare occasions (SANDQUIST *et al.*, 1973); we have no records of migratory movements of males such as reported by MIKKOLA (1971) in continental Eurasia. Consequently, movement of populations must occur during the egg, larval or pupal stage. Eggs and pupae are non-locomotory, and any movement is completely passive; young larvae actively place themselves in position for passive dispersal by wind. Both movement and mixing of populations over relatively short distances within the generally-infested area, and the gradual expansion of the geographic range of the gypsy moth, are accomplished primarily by this wind-blown dispersal of young larvae.

One of our major problems is accidental movement of one or another of the life stages into uninfested areas. The first federal insect quarantine, enacted in the United States in 1912, was directed at countering such movement; we retain today a prohibition on transportation of commodities such as logs, quarry stone, Christmas trees, and mobile homes from hazardous to non-infested areas without

CURRENT DISTRIBUTION AND RATE OF SPREAD OF GYPSY MOTH

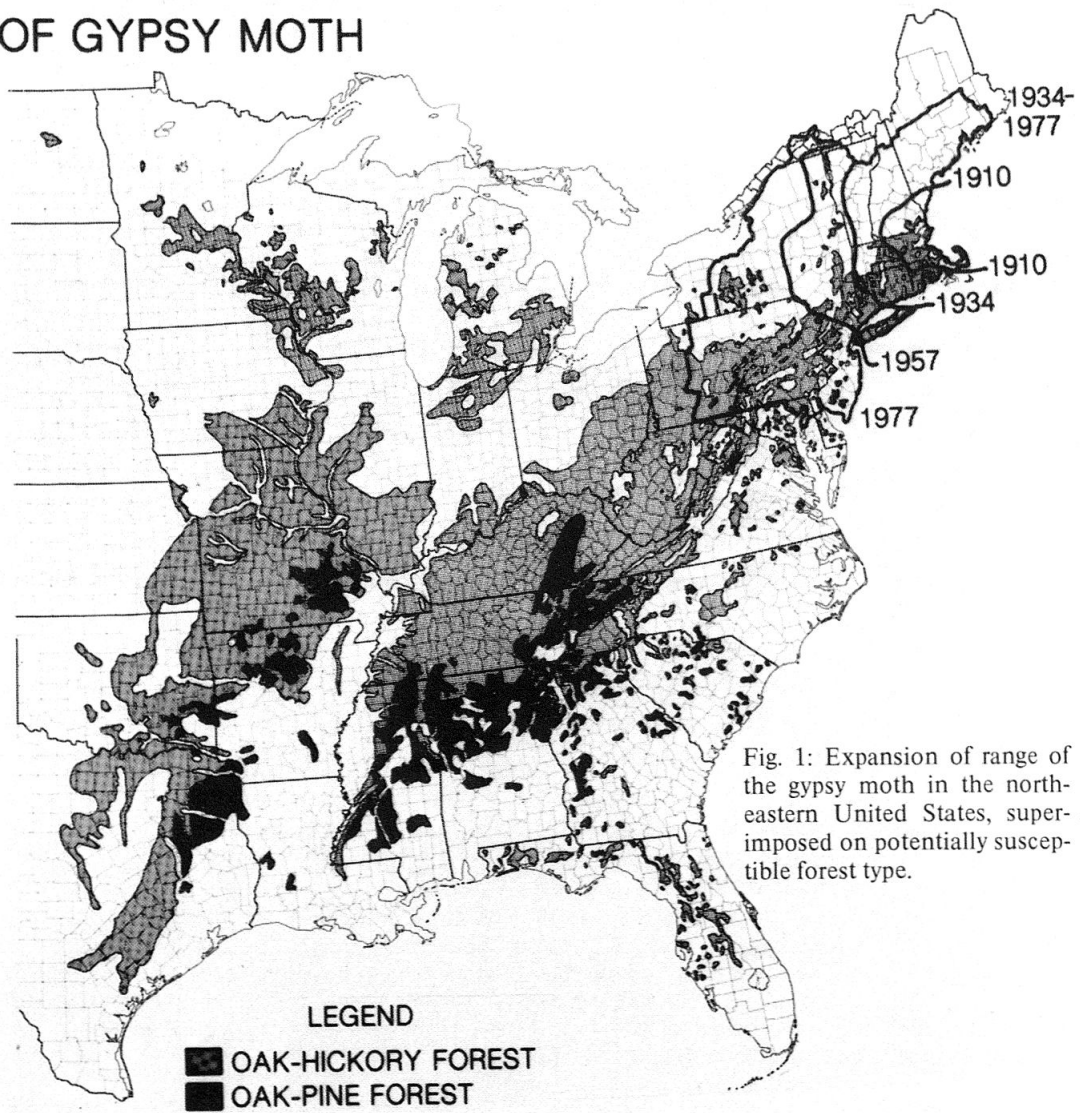


Fig. 1: Expansion of range of the gypsy moth in the northeastern United States, superimposed on potentially susceptible forest type.

inspection and, if necessary, treatment. In spite of our best efforts, small and highly localized infestations do appear periodically in remote locations, although with the exception of a widespread infestation in the state of Michigan, none of these has so far expanded into a major infestation. It appears, certainly, that the infestations outside the generally-infested northeastern United States and some adjacent parts of Canada have grown as a result of buildup of local populations. This is excellent evidence of a *lack* of long-distance wind-borne dispersal of young larvae.

Dispersal has been defined by ELTON (1927) as the movement away from a populated place resulting in the scattering of at least some of the original population. Recently McMANUS (1978) selectively reviewed the literature on dispersal in insects, and discussed the many factors which affect this process. MASON & McMANUS (1978) recognize the importance of dispersal in the population dynamics of all arthropod species, but note that, «with few exceptions, the intricate mechanisms involved are poorly understood, and the role of dispersal in the population dynamics of species has been only grossly estimated.»

Much of the literature on gypsy moth dispersal draws conclusions based on inference rather than critical studies (see MASON & McMANUS, 1978, for a review). Once it was determined that larvae could be dispersed by wind, the emphasis of studies shifted to attempts to determine «how far». Claims of dispersal of 30–48 km over water were made by COLLINS (1917); NICHOLS (1961) credited airborne dispersal of larvae with initiation of an infestation 56 km from its presumed source population. Generally overlooked was the report by MINOTT (1922) indicating that most dispersal from a woodland onto a cranberry bog was actually short-range: 76% of the 1110 larvae trapped in that study were captured within 75 m of the woodland edge.

During the late 1960's and early 1970's, LEONARD (1967, 1970, 1971) reported on investigations of early larval behavior, silking behavior, and dispersal. McMANUS (1973a) extended these studies of behavior of the newly-hatched larvae, concluding that all newly-hatched larvae are predisposed to disperse *even in the presence of preferred foliage*. CAPINERA & BARBOSA (1976) agreed, and noted that larger larvae tend to disperse repeatedly. With the growing recognition that dispersal was a complex phenomenon, McMANUS (1973b) presented a conceptual model to describe the component elements and functional relationships which, if quantified, would allow prediction of the magnitude of gypsy moth larval dispersal from a known egg mass population (fig. 2).

DISPERSAL MODEL

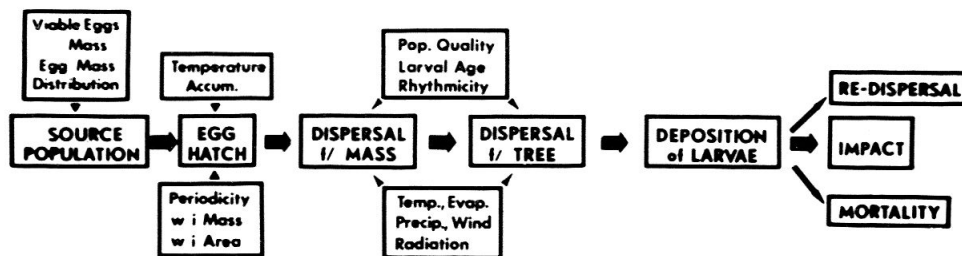


Fig. 2: Conceptual model for larval dispersal (after McMANUS, 1973b).

Reasonably good information concerning the gypsy moth was available or could be obtained for several of the major elements of the model. For example, egg masses per unit area times average number of viable eggs per mass gives an estimate of source population; egg hatch is a function of accumulated day degrees over a threshold temperature, probably near 5°C; dispersal from the egg mass is a function of both biological and physical factors, as is dispersal from a source tree. The greatest void of knowledge was in deposition of larvae. Once larvae land, they may 1) initiate feeding on a suitable host; 2) re-disperse from an unsuitable (or suitable) host; or, 3) die because they have landed in an unsuitable area – such as an open field, lake, paved area, etc. – from which they cannot redisperse. Mortality is likely to be high at times during this dispersal phase, although good estimates of its magnitude are simply not available. Perhaps the closest approximations are losses of from 23–70% attributed by CAMPBELL (1969, 1978) to «dispersion, etc.» during instars I–III. From his data, however, there is no way of separating loss during dispersal from the «etcetera», since there were no measurements of populations from the time that eggs were examined until larvae had reached instar IV. Factors unrelated to dispersal *per se* could account for little or much of the mortality during this time period.

Let us return to the element «deposition of larvae» in the dispersal model. A source function model to estimate the number of larvae that leave the tree-top dispersal sites is available (EDMONDS, 1974; MASON, 1975). The passive transport of larvae by the atmosphere should be describable by a deterministic atmospheric dispersion model which would describe the dispersion pattern of particles (larvae) entrained in the atmosphere, given meteorological data on wind speed and direction, and turbulence. If such a model can be adapted successfully, quantitative predictions of the range of wind-blown dispersal will be possible.

MASON & McMANUS (1978) have described in detail how the Gaussian plume model described the bivariate normal distribution of a theoretical plume of larvae released from an elevated point source over level ground (fig. 3). This

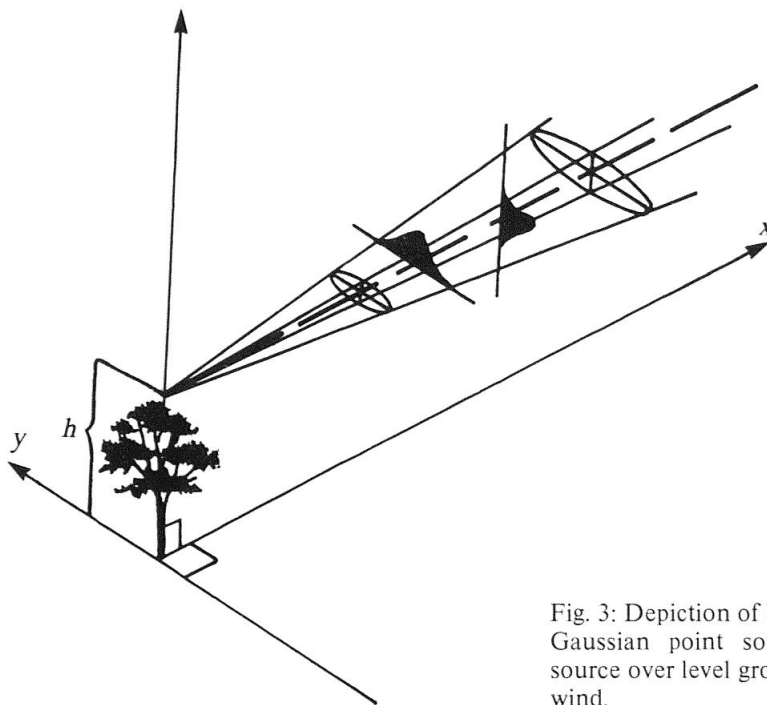


Fig. 3: Depiction of bivariate normal distribution in a Gaussian point source plume from an elevated source over level ground. X-axis is direction of mean wind.

PROJECTED DOWNWIND CONCENTRATION FROM AN ELEVATED POINT SOURCE

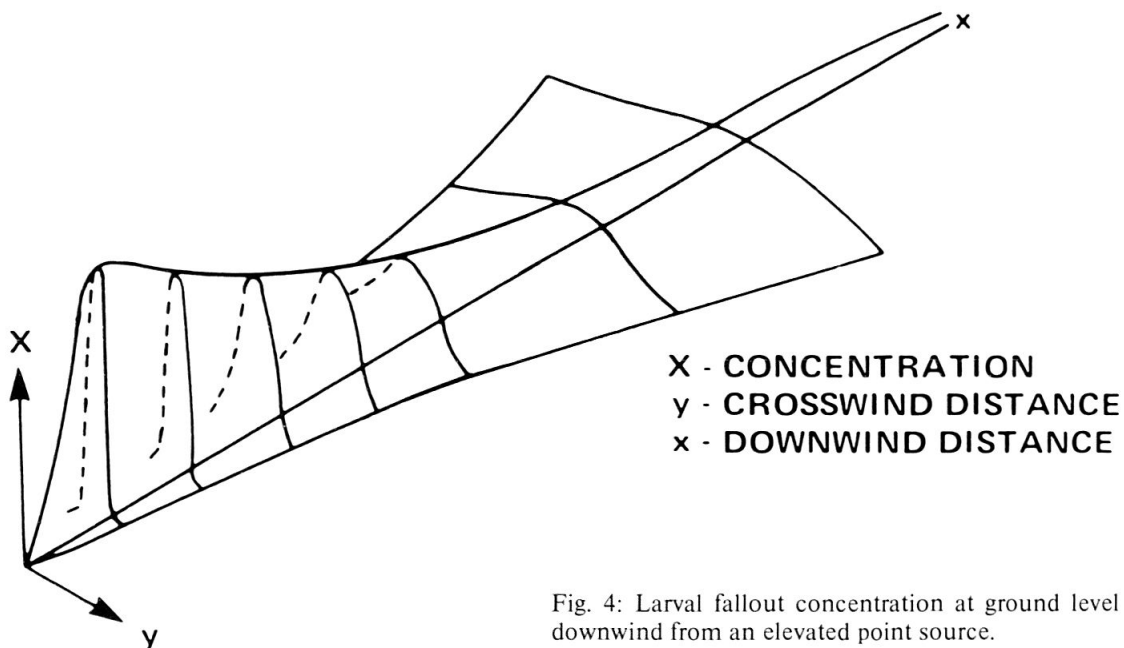


Fig. 4: Larval fallout concentration at ground level downwind from an elevated point source.

model predicts peak fallout concentration of larvae to occur some distance downwind (not at the source itself) (fig. 4), and dispersion coefficients are included in the equation to account for variation in atmospheric turbulence, distance from the source, sampling time (or duration over which concentration measurements are averaged), and terrain characteristics. The larvae (or «biological particulates») would be released from the atmosphere at a calculable rate. This rate is based on their settling velocity, and is calculated as the interaction of horizontal and vertical movements which combine to allow an estimation of particle trajectory (table 1).

The limits of the basic Gaussian plume model – that is, applicability to a situation in which the entrainment rate of organisms in the atmosphere is constant, dispersion is over flat terrain, and wind speed and direction are unvarying – restricted its utility for describing dispersal of gypsy moth larvae. Turbulence above a forest canopy occurs, and varies during the day. To overcome these limits, MASON (1975) developed an advecting Gaussian puff model, where emission from a source is treated as a series of instantaneous puffs. Each puff undergoes Gaussian diffusion as its centre moves with the wind. Concentration for any point in space is obtained by adding the effects of successive puffs. Because of rather high terminal velocities for dispersing larvae, dispersal is generally restricted to distances of a few kilometers or less. Accepting the approximations which must be made in the model, it is suggested by MASON & McMANUS (1978) that predictions will be accurate to within a factor of about three.

Several times terminal velocity has been mentioned. This is a critical element of information needed for the model. Not only do young gypsy moth larvae have long, buoyant setae, but also they trail silk. First instar larvae, weighing 0.5 to 0.8 mg and trailing 0 to 90 cm of silk, were dropped from a height of 3 m to determine terminal velocities; these velocities ranged from 40–110 cm/sec. It was noted that larvae with 90 cm silk fell at 1/2 the velocity of those with no silk, and that if

Tab. 1: A comparison of dispersal estimates, as ground-level trap counts, for spores or larvae released from an elevated point source under different atmospheric conditions.

Slightly Unstable	Some Turbulence					
Distance (m)	0.0	80.5	161.0	322	805	1600
From Source (mi)	0.0	.05	0.1	0.2	0.5	1.0
Spores	9	190	41	19	4	1
Larvae	1200	25,300	730	140	9	1
Extremely Unstable	High Turbulence					
Distance (m)	0.0	80.5	161.0	322	805	1600
From Source (mi)	0.0	.05	0.1	0.2	0.5	1.0
Spores	28	64	21	6	1	0
Larvae	3400	7800	1900	270	43	10

Sampling Time = 1 hr

Wind Speed = 6.4 Km/hr
4 mph

Source Height = 15.2 m
50 ft

Point Source:

Terminal Velocity: Spores = .75 cm/sec
Larvae = 75 cm/sec

1,000,000 spores
1,000,000 larvae

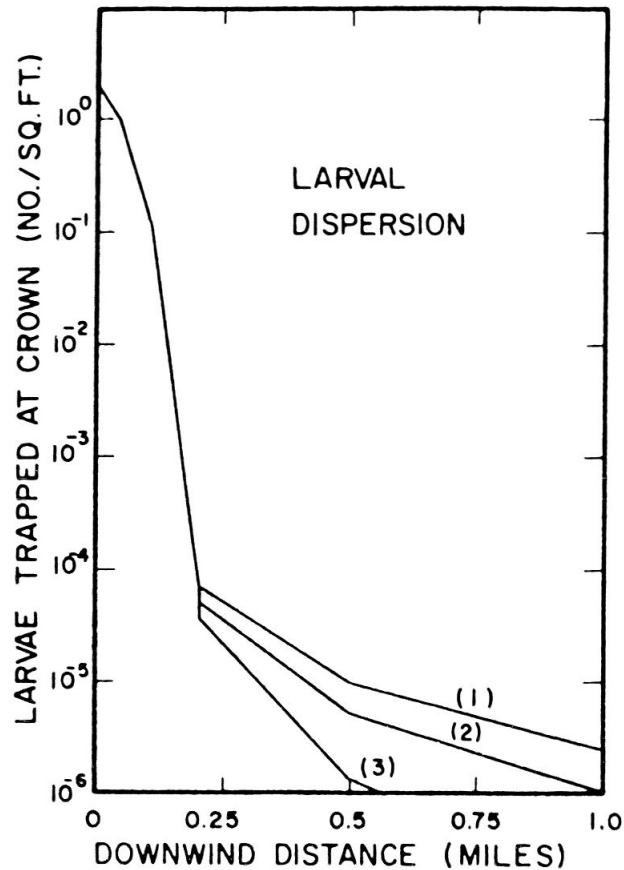
silk exceeded 40 cm, the body axis of the larva remained parallel to the ground thus increasing air resistance to falling, or «drag» (MASON & McMANUS, 1978). Substitution of numbers into a single equation which incorporates height above ground at which the larva is released, terminal velocity, and wind speed, will allow calculation of the estimated distance a larva may travel. Even the lightest larva with the longest silk thread will move only ca 116 m away from a release point 10 m above the ground in a 5 m/sec wind - a rather brisk breeze. Indeed, few gypsy moth larvae will spin silk when wind speed exceeds ca 6.7 m/sec.

In a forest, then, it becomes clear that the great majority of dispersing larvae probably travel no further than adjacent trees, regardless of turbulent intensity, before their silk becomes entangled in the canopy. The dispersal distance of 116 m just mentioned might apply only to larvae leaving trees along a woodland edge, or from an isolated tree in an open field. Redispersal may occur, but with shifting winds and turbulence in the forest the direction of movement is likely to be somewhat different. The net result is dispersal through a series of short hops (MASON & McMANUS, 1978). The probability of dispersal over long distances is exceedingly small.

So much for theory and prediction. What really happens under field conditions? After all, it is in those circumstances that the gypsy moth lives, and in which it creates problems in part by moving about.

The model predicted that, over flat land and in the absence of severe turbulence, most larvae would be deposited within 1.6 km (= 1 mi) of their origin (fig. 5). A study area was chosen on Cape Cod, Massachusetts, in which to attempt validation of the model. The site had four important characteristics: terrain was level, permitting definition of the wind profile within the study area by a single

Fig. 5: Predicted numbers of larvae which would be trapped at various distances downwind from a source under (1) extremely unstable, (2) slightly unstable, or (3) slightly stable atmospheric conditions.



meteorological tower; water bordered two sides of the study area, thus reducing the possibility of gypsy moth invasion from adjacent populations; the forest canopy was only 9-12 m high, facilitating placement and servicing of samplers above the canopy; and permanent study plots in the area provided historical gypsy moth population information.

The larval samplers were designed to meet the following criteria, among others: traps were cylindrical to project the same surface area regardless of wind direction; they could be placed at or above the top of the forest canopy; and they could be lowered readily to permit several examinations per day. Traps were constructed of 0.01 m mesh hardware cloth coated with Tack-Trap, and were 90 cm long by 30 cm diam (1974) or 60 cm long by 30 cm diam (1975). Therefore, each trap projected 0.27 m² (1974) or 0.18 m² (1975) of area into the wind. In 1975, a vertical mast fitted with a cross-arm and pulleys permitted positioning traps within or above the canopy, as well as raising and lowering as necessary; each mast supported a total of 6 individual traps, with a combined surface area of 1.08 m² presented to dispersing larvae. These samplers were placed in concentric circles 60, 120 or 180 m from the central source region, with one sampler at the centre of the source to provide an estimate of entrainment rate. Meteorological data were gathered during the tests, and dispersion coefficients were obtained from the literature. Thus all parameters in the model were accounted for.

A preliminary test was conducted in 1974, in which larvae hatching from a natural population of gypsy moth within the study area were used (the egg mass density was 200-1500/ha). This test showed that peak dispersal was synchronous with peak hatch but lagged by 1-2 days, and conforms with recent observations

on larval behavior. Unfortunately, however, overcast and cool weather midway through the hatch shut off dispersal. Because of the variability in resident population numbers within the test area, the potential number of dispersing larvae was highly variable. This precluded relation of numbers trapped on any individual sampler to the source population near it from which dispersing larvae could be trapped.

To overcome some of the uncontrolled elements of the 1974 test, viable eggs were collected in 1975 from naturally infested areas, dehaired, counted, and placed in mesh packets. These packets, each containing 7,000–20,000 eggs, were stapled to the boles of trees within a 20 m diameter area. During the first test, 1.2 millions eggs were used; 850,000 eggs were used in the second test. It was calculated that these would give an entrainment rate of 1000 larvae/minute for four hours/day over a 5 day hatching period. Tests were conducted during the time of normal egg hatch so weather conditions would be appropriate for hatching larvae.

Detailed data for one day are presented by MASON & McMANUS (1978). It is obvious from the results that a great majority of larvae were trapped downwind of the source. The model systematically under-estimated downwind capture, leading them to suggest significant re-entrainment and re-dispersal occurred during the period of the test. This would cause a slow migration of the source in the direction of the average wind, in effect moving these downwind samplers closer to the source population. Therefore, these factors must be incorporated into an improved model, and the proportion of re-dispersing larvae and the time interval between landing and redispersal must also be determined.

Tab. 2: Number of larvae trapped after a point-source release on oak, Cape Cod, Mass. June 1975.

Distance From Source (ft.)	No. Trap Days	Total Larvae Trapped	\bar{x} Larvae/Trap Day
0	13	5244	403
100 (30.5 m)	20	192	10
200 (61)	52	142	3
400 (122)	96	108	1
600 (183)	48	46	1

The results emphasized again that dispersal is a *short-range* process (table 2); they also demonstrated that considerable dispersal was taking place within, rather than above, the canopy: one-third to one-half of the larvae were captured on the lowest level of traps. The model assumes free dispersal. An examination of data from the top tier of traps only (i.e., those above the crown) gave excellent agreement with predicted catch. In other words, the model has been verified under field conditions.

It was noted at the outset that the gypsy moth in North America has moved south and west over the last century, and that terrain is not uniform and certainly not uniformly flat. The dispersal model would have greater utility if it could be modified to incorporate the effects of terrain features. Two modifications are appropriate for North American conditions: one would consider the «sea breeze» effect along the coast, where temperature differentials between land and a large body of water cause convective air flow patterns; the second would take into account obstruction of air flow, as well as turbulence, generated by ridges.

Sea breeze has been modelled mathematically (WILSON, 1967). It is best developed in early afternoon - which is precisely the time when many gypsy moth larvae are still dispersing. A convergence frontal zone of onshore and offshore breezes occurs about 10-20 km inland. If larval dispersal is underway simultaneously with a sea breeze, a dispersal model modified to incorporate sea breeze effects predicts that the updrafts in the frontal zone would extend the normally shortrange dispersal and bring larvae in from a larger surrounding area. Thus, a heavily infested «hot spot», which parallels the coast but ca 10 km inland, would be created. An examination of gypsy moth defoliation maps along the seacoast of the State of New Jersey during the 1970's reveals that just such a pattern does occur in several places.

No suitable model of wind flow in the vicinity of a ridge and valley system is available, in part, at least, because wind flow in such a situation is extremely complicated. Wind flow is affected by, among other factors, the angle at which the wind hits the ridge, wind velocity, the slope and height of the ridge, and turbulence. MASON & MCMANUS (1978) modified the dispersal model by assuming an elliptical rotor of wind to occur in the valley between parallel ridges when wind flow is across the ridges. Ridges in central Pennsylvania, where the gypsy moth is currently very active, rise about 400-500 m above the valley floor, and may be separated by about 3-5 km. The model predicts an initial lofting of dispersing larvae from a ridge top because of updrafts, transport across the valley, and fallout on the opposite ridge being concentrated just short of that ridge top. The source ridge effectively acts as a highly elevated population source; deposition always occurs downwind rather than at the base of the source. The additional effect of the updrafts in this ridge and valley situation extends the downwind distance at which the larvae fall out, and this is enhanced by the slope of the ridge falling away under the dispersing larvae - that is, they must fall farther to reach the ground as they move away from a ridge top.

Such a dispersal pattern has been observed often in Pennsylvania in recent years as populations appear to move from ridge top to ridge top. This would seem to validate the assumptions made in the model. However, actual data for air flow around ridges are not available, so the model has not really been verified.

HOUSTON & VALENTINE (1977) have studied a series of structural variables to be found on trees, such as bark flaps, holes or wounds on the lower bole suitable for use as resting or hiding places, dead branches below the live crown, dead sprout stubs, prevalence of deep bark fissures on trees, and numbers of trees with a crook or sweep. These structures are known both to influence gypsy moth behavior and to reflect the response of a tree to disturbance, or they are inherent features of species growing on adverse sites (HOUSTON & VALENTINE, 1977). Through principal components analysis ordination models, they are developing a system to predict stand susceptibility to gypsy moth. These various factors, used in conjunction with species composition of the forest (and especially the proportion of trees in gypsy moth preferred food classes) and with other factors such as site quality, soil moisture, etc., are important in the realization of population establishment or forest defoliation as a consequence of early larval dispersal.

With this much greater understanding of early larval dispersal, are we in a position to assess its impact on population dynamics? Certainly not completely! But it is obvious that some of the widely held notions of the role of dispersal must be questioned. It is clear that, along level terrain, individual larvae move only in short hops even though redispersal may occur and magnify the total distance

travelled. Even in ridge and valley situations, dispersal occurs over only a few kilometers from one ridge top to an adjacent one. It is highly improbable (although not impossible) that an individual larva will be transported over tens of kilometers; major geographic expansion of infestations in a single year are unlikely to result from dispersal of young larvae under normal circumstances.

CAMPBELL (1978) argues that «. . . individual subpopulations [of the gypsy moth] are sometimes influenced more by conditions within nearby subpopulations than by local on-site conditions». From his data, he concludes that dispersal is important in maintaining an area-wide outbreak and in its spread, but not in its initiation or the release phase. Rather, he suggests, release of innocuous populations occurs as a result of secure resting locations for individual females with high fecundity, and a temporary escape from biotic control factors such as natural enemies and especially the effects of the nuclear polyhedrosis virus. Dispersal does not seem to play a major role in either the decline of a population, or during the innocuous phase.

It is clear that we are only beginning to understand dispersal and its role in gypsy moth population dynamics. As we improve our understanding of the dispersal process itself, and develop improved models to describe what occurs under various complex situations of geography or terrain, we should be better able to incorporate this knowledge into the broader concerns of population dynamics. And of equal importance, we may be better able to predict the future rate of spread of this pest insect through the oak forests of the eastern United States.

Such predictions take on added importance in light of the current emphasis on a regional approach to integrated pest management of this major hardwood defoliator. If programs to retard the spread of the gypsy moth in the United States, now under discussion, are ever implemented, data demonstrating that larval dispersal is much shorter than many believe it to be would justify the exclusion of perhaps tens of thousands of hectares from a chemical insecticide spray program. Such practical results cannot be overlooked.

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