A Tracer Investigation Of Pheromone Dispersion In A Lodgepole Pine Forest Canopy

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Abstract

To improve our understanding of the transport of insect pheromone through a forest canopy, tracer experiments were conducted in 2000 amid a lodgepole pine (Pinus contorta) forest in Montana. Six tests were analyzed to visualize relationships between wind direction and plume behavior for downwind distances of 5, 10, and 30 m. Time series of sulfur hexafluoride showed intermittent plume events with peak-to-mean ratios as high as 81 at the 10-m arc. Average dispersion coefficients ranged approximately 4-8 m at the 5-m arc, 9-17 m at the 10-m arc, and 27-45 m at the 30-m arc. In addition, a simple empirical equation was developed to estimate average plume spread on these scales as a function of standard turbulence statistics and travel time. Predicted dispersion coefficients were within a factor of 2, or better, of observed values for 95% of the cases, and the average predicted-to-observed ratio was 1.07 for the dataset of 158 plume profiles. Results from this field campaign were site-specific, but they were part of a larger effort by the United States Department of Agriculture (USDA) Forest Service to characterize dispersion in a variety of forest types.

Key words: average plume spread, concentration fluctuations, dispersion coefficients, peak-to-mean ratios, pheromones, tracer experiments

Introduction

Bark beetles are native species, and they play important roles in forest ecosystems. Dramatic infestations, however, are currently causing decreased lumber sales and increased fire danger in western regions of the United States, Canada, and elsewhere. Between the years 1995-1999, bark beetles resulted in mortality of more than 7 million trees in the Rocky Mountains alone, and the species causing the most damage in this region are mountain pine beetles (*Dendroctonus ponderosae*) and Douglas-fir beetles (*dendroctonus pseudotsugae*) (USDA Forest Service 2000).

Because bark beetles and other insects communicate via fine-tuned systems of semiochemicals known as "pheromones," the USDA Forest Service and others have been developing methods of pest management involving application of natural and synthetic pheromones as alternatives to traditional insecticides (Suckling 2000). Effectiveness, however, depends on in-depth knowledge of transport and diffusion of pheromones in the atmosphere (Aylor 1976, Aylor et al. 1976, Elkinton et al. 1984, Farrell et al. 2002). An insect reacts instantly to pheromone concentrations above a threshold level, so short-term diffusion of pheromone plume dictates immediate behavior of the insect. Over time, however, the zone of influence affecting multiple insects is characterized in terms of average dispersion patterns.

In regulation and modeling of air pollution from industrial sources, dispersion patterns are of interest also, but on much larger scales. Concentrations at distances up to 50 km downwind of a smoke stack, for example, are normally estimated using computer algorithms based on a formula known as the Gaussian plume equation (Turner 1969):

$$C_{xyz} = \frac{Q}{2\pi\sigma_y\sigma_z U} e^{\frac{-y^2}{2\sigma_y^2}} \left[e^{\frac{-(z+H_e)^2}{2\sigma_z^2}} + e^{\frac{-(z-H_e)^2}{2\sigma_z^2}} \right] \quad (1)$$

where C_{xyz} is concentration at a receptor with coordinates x,y,z; Q is mass release rate of the contaminant; H_e is effective stack height; U is mean wind speed, and σ_y and σ_z are dispersion coefficients in the y and z directions, respectively. Dispersion coefficients in Equation (1) represent standard deviations of the average horizontal and vertical concentration distributions in the plume (assumed to be Gaussian), and they are calculated using empirical equations that are functions of downwind distance (x) and atmospheric stability class (Gifford 1959).

Because regulatory models using the Gaussian plume approach only predict mean concentrations with averaging times between 1 hr and 1 yr, we have been studying near-instantaneous plume diffusion to characterize variability and peak concentrations on time scales similar to human breathing rates. Short-term peak concentrations are important because acute exposures may pose health risks for some toxic air pollutants and for chemical agents such as nerve gases. To study this, we have been 1) conducting field experiments using tracer technologies amid a variety of terrain types and meteorological conditions, 2) analyzing tracer concentration data in terms of instantaneous and average plume spread, and 3) using the field results to develop and to test air diffusion models (Peterson and Lamb 1992, 1995, Peterson et al. 1990, 1999, 2003).

Because of tracer technologies, we now know much more about instantaneous and average plume spread of air pollutants than we did 20 years ago, but many of the same uncertainties exist about how insect pheromones move through crops or forest canopies with complex micrometeorological conditions. This is not a new issue; almost three decades ago, Aylor (1976) stressed the importance of transport and diffusion processes on instantaneous and average time scales for pheromone research. Aylor et al. (1976) conducted an eloquent set of field experiments in a forest using gypsy moths (*Lymantria dispar L.*) to try to characterize disparity between instantaneous and average dispersion. While recording wind speed from a set of 1- and 2-dimensional anemometers, they released disparlure pheromone from a 1-mm orifice at a rate of 9.6 pg s^{-1}. Male gypsy moths in small mesh cages were located at downwind distances of 1.2, 2.5, and 5 m from the pheromone source, and pheromone response was quantified by counting the number of moths/cage showing rapid wing fanning during 1-min intervals. To account for plume meander, they moved cages as necessary to coincide with a plume of tufted cattail seeds that were released sequentially near the pheromone source. Results inferred peak concentrations up to 25 times higher than time-averaged concentrations.

Although research of Aylor (1976) and Aylor et al. (1976) was state-of-the-art for their time, they did not have the ability to resolve actual concentrations of pheromone. More recently, a technique called electroantennography (EAG) was developed to measure insect pheromones in the field (Van der Pers and Minks 1993, Thorpe and Tcheslavskaia 2001). In these studies, EAG devices measured changes in electrical signal for insect antennae in the presence of pheromone. The EAG signals, however, are difficult to quantify because of variability in dynamic response characteristics of antennae, and it is not yet possible to convert to absolute concentrations units.

To address these uncertainties, we have been studying dispersion of insect pheromones using tracer methods and equipment previously developed to study behavior of air pollution on larger scales. Our work has been part of a multi-institutional effort with the USDA Forest Service to characterize dispersion in a variety of forest types (Thistle et al. 2002a, 2002b, 2004). Overall goals are to 1) improve insight into the nature of turbulent dispersion through plant canopies, and 2) develop tools for forest managers to predict pheromone plume spread. This paper describes one field campaign to characterize instantaneous and mean plume diffusion in a lodgepole pine (*Pinus contorta*) forest.

Potomac Field Experiments

During 19-28 July 2000, we conducted a set of field experiments amid a forested area in western Montana, approximately 16 km (10 mi) east of Missoula. Elevation of the Potomac field site (46°54'19"N, 113°126'45"W) was 1207 m above sea level, and lodgepole pine was the dominant vegetation with an average height of 30 m and a density of 1521 stems/ha. Equipment for the campaign included 1) a tracer release system, 2) an array of air samplers, 3) a fast-response tracer analyzer, and 4) meteorological sensors. Each unit is described as follows, and Figure 1 shows the field layout.

Throughout the experiments, we released sulfur hexafluoride (SF_6) as a tracer gas to simulate a generic insect pheromone. For more than two decades, we have used SF_6 to study average and near-instantaneous behavior of air pollutants for downwind distances ranging from 0.05 to 3.6 km (Peterson and Lamb 1992, 1995, Peterson et al. 1990, 1999, 2003), but this was one of the first intensive tracer experiments conducted in a forest canopy for pheromone research. Sulfur hexafluoride is an inert gas that is non-toxic, non-radioactive, colorless, and odorless, and SF_6 can be measured at very low concentrations, i.e., parts/trillion (ppt). In the Potomac field campaign, we released a 1-percent mixture of SF_6 and air from a gas cylinder through a mass flow controller. Release height was 1.2 m above the ground, and release location was the center of a sampling array.

Our sampling array consisted of syringe samplers arranged in three concentric circles with radii of 5, 10, and 30 m. Samplers were based on the design of Krasnec et al. (1984). Over a period of 4.5 hrs/day, each sampler sequentially collected nine air samples in 30-cc syringes with an averaging time of 30 min/syringe. In a typical test, we positioned samplers at a height of 1.2 m above the ground to characterize horizontal dispersion patterns. Time-averaged concentrations of SF_6 in the syringes were determined each day via subsequent analysis using a calibrated, fast-response analyzer based on the design of Benner and Lamb (1985) with an operational range on the order of 30 to 15,000 ppt.

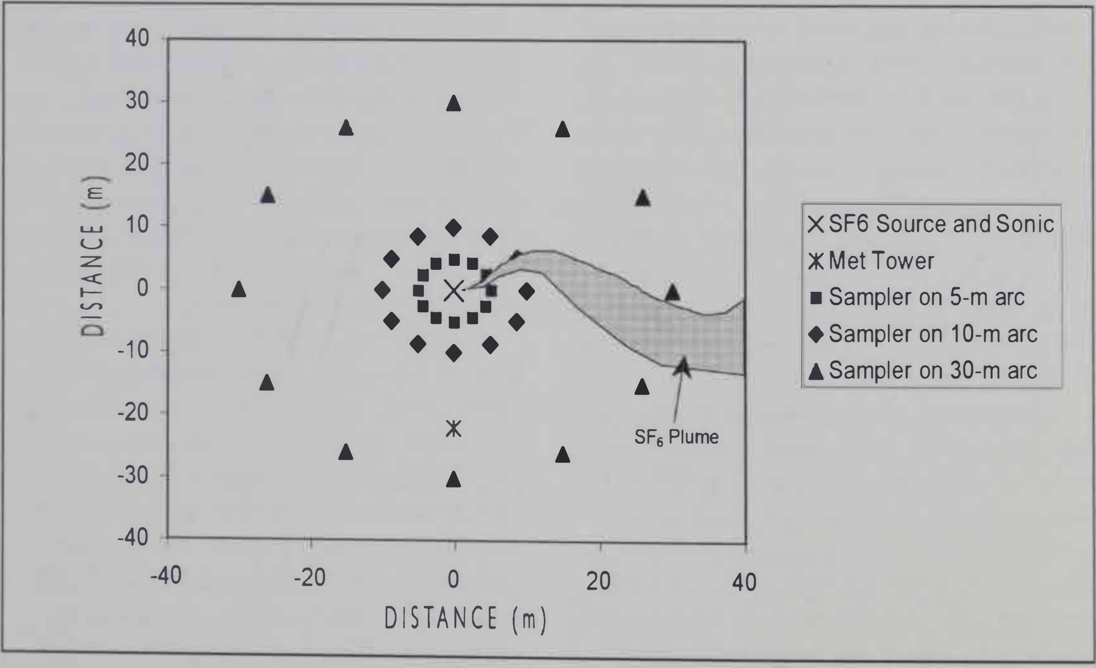

Figure 1. General layout of equipment during the Potomac field campaign.

In addition to time-averaged concentrations in the syringes, we measured near-instantaneous concentrations with a fast-response SF_6 analyzer positioned within the sampling array along the 10-m arc. Response time of this instrument was 0.6 s; the sampling rate was 1 Hz; and the sampling inlet was positioned at a height of 1.2 m.

For meteorological sensing, we equipped a tower with 3-dimensional sonic anemometers at heights of 1.5, 14.5, and 24.9 m above the ground. In addition, a sonic anemometer was located at the center of the sampling array with the tracer release system. The sampling rate of all anemometers was 10 Hz.

Results And Discussion

We describe conditions for six tests performed during morning hours when the average wind speed at the Potomac site was between 0.19 and 0.58 m s^{-1} (Table 1). Standard deviation of wind speed is a measure of turbulence, and during these tests, standard deviation in the horizontal u direction (σ_u) and standard deviation in the horizontal v direction (σ_v) varied between 0.04 and 0.44 m s^{-1}. Standard deviation of the vertical wind component, however, only ranged between 0.04 and 0.16 m s^{-1}. Average ambient temperatures were 282.3-293.3 K, and barometric pressures were 882-889 mb. Mass release rates of SF_6 were 102-110 µg s^{-1}.

Figure 2 illustrates of the nature of the wind fields during the six example tests. We graphed time series of wind azimuth on 2-dimensional, radial grids to show horizontal wind angle during each 30-min period with time (t) increasing from t = 0 s at the origin to t = 1800 s at the outer rings. In some of the tests, a dominant wind direction is obvious. Figures 2d and 2e, for example, indicate dominant wind flows to the west-northwest (WNW) and south-southwest (SSW), respectively. In other tests, such as Figures 2a and 2f, winds appear to blow with two or three main bearings during distinct directional shifts. Lastly, Figures 2b and 2c contain a wide range of short-term shifts in wind direction covering all angles of the compass.

In Figure 3, concentration time series depict measurements from the fast-response SF_6 analyzer on the 10-m arc where analyzer positions correspond to specific receptor angles (Fig. 2). As expected, a variety of exposure patterns are identified. Distinct, dramatic concentration events in Figures 3a, 3d, and 3f corresponded to the tracer plume passing over the analyzer during major wind shifts, while the plume meandering back-

Table 1. Subset of Potomac Field Experiments - Test Conditions

Test	Date	Start Time	U	σ_u	σ_v	σ_w	T	P	Q_{SF6}
	(D-M-YR)	(MDT)	(m s-1)	(m s-1)	(m s-1)	(m s-1)	(K)	(mb)	(µg s-1)
P724P2	07-24-00	0700	0.24	0.06	0.06	0.05	282.3	889	110
P724P7	07-24-00	0930	0.57	0.26	0.23	0.11	291.7	889	106
P724P8	07-24-00	1000	0.58	0.37	0.44	0.16	293.2	889	106
P725P4	07-25-00	0800	0.19	0.04	0.06	0.04	290.6	884	102
P725P5	07-25-00	0830	0.51	0.17	0.15	0.10	293.3	884	102
P727P6	07-26-00	0900	0.29	0.10	0.09	0.06	287.9	882	107

Test duration - 30 min
U - average wind speed
σ_u - standard deviation of horizontal wind speed in the u direction
σ_v - standard deviation of horizontal wind speed in the v direction
σ_w - standard deviation of vertical wind speed in the w direction
T - ambient temperature
P - ambient pressure
Q_{SF6} - release rate of tracer gas

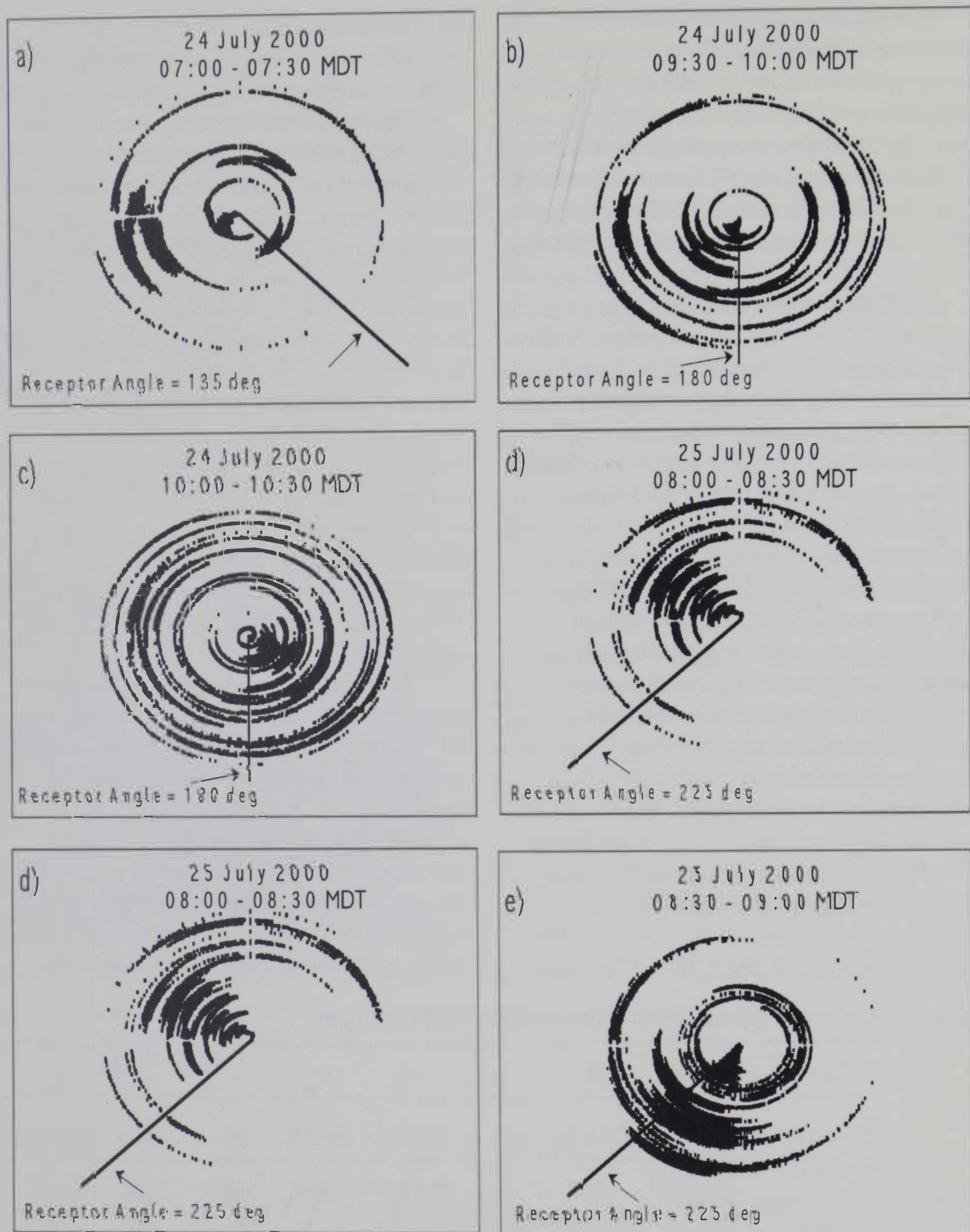

Figure 2. Radial time series of wind direction for: a) Test P724P2, b) Test P724P7, c) Test P724P8, d) Test P725P4, e) Test P725P5, and f) Test P727P6.

and-forth caused intermittent concentrations as illustrated in Figures 3b, 3c, and 3e.

During the past two decades, we have used a set of standard statistics to characterize time series of near-instantaneous exposure of air pollutants (Peterson et al. 2003). Statistics included: average concentration (C); standard deviation (σ_c); concentration fluctuation intensity (IN), where intensity is the ratio of standard deviation to the mean concentration; intermittency factor (I), where intermittency is the fraction of time non-zero concentrations are recorded at a receptor, and peak-to-mean ratio (P/M).

Concentration fluctuation statistics for the six Potomac tests were highly variable even though the SF_6 release rates were

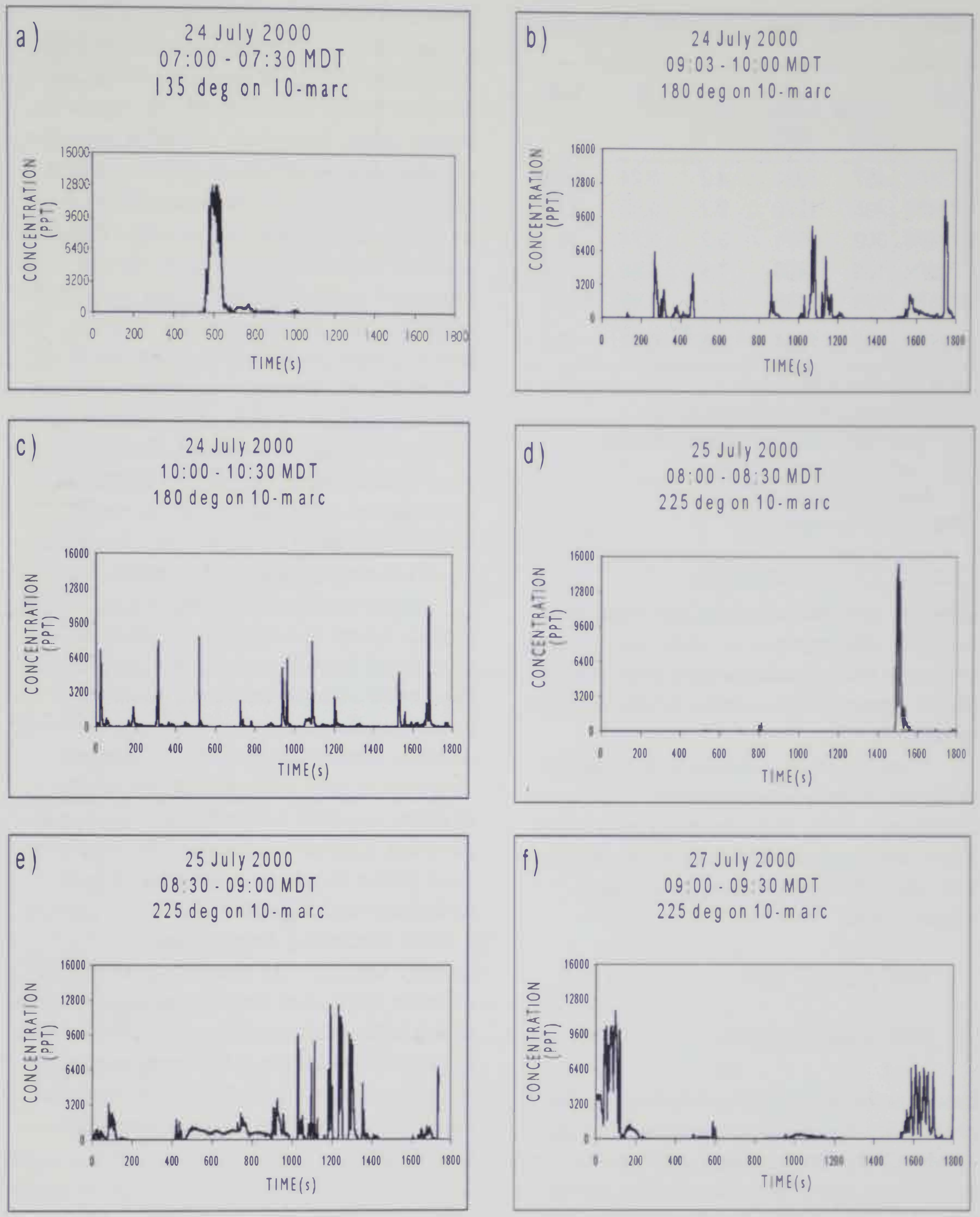

Figure 3. Time series of instantaneous concentration for: a) Test P724P2, b) Test P724P7, c) Test P724P8, d) Test P725P4, e) Test P725P5, and f) Test P727P6.

almost the same, and downwind distance was 10 m in all cases (Table 2). The 30-min mean concentration ranged 189-755 ppt, and standard deviation of concentration was between 971 and 1954 ppt. Standard deviation (σ_c) was always greater than the mean concentration (C) because exposure consisted of intermittent plume events separated by periods of zero concentration. Intensity ($IN = \sigma_c/C$) varied from 2.2 to 7.4; intermittency factor ranged 0.08-0.74; and peak-to-mean ratio was between 15.4 and 80.7. Low intensity, high intermittency, and low peak-to-mean ratio corresponded to exposures where the plume blew toward the analyzer more than away from it. High

Table 2. Concentration Fluctuation Statistics

Test	C (ppt)	σ_c (ppt)	IN	I	P/M
P724P2	457	1931	4.2	0.24	27.8
P724P7	465	1270	2.7	0.48	24.0
P724P8	302	971	3.2	0.74	36.9
P725P4	189	1409	7.4	0.08	80.7
P725P5	699	1538	2.2	0.59	17.6
P727P6	755	1954	2.6	0.47	15.4

Test Duration = 30 min
C - arithmetic mean concentration
σ_c – standard deviation of concentration
IN – concentration intensity
I – intermittency factor
P/M – peak-to-mean ratio

intensity, low intermittency, and high peak-to-mean ratio represented cases where winds primarily blew in another direction, but the plume impacted the receptor briefly during a wind shift.

Previous tracer campaigns to study air pollution at downwind distances up to 1 km (Hanna 1984, Peterson and Lamb 1995) found that intensity and peak-to-mean ratio were described by the following simple relationships:

$$IN = [(2\,I^{-1}) - 1]^{1/2} \qquad (2)$$

$$P/M = [\ln(100\,I)]\,I^{-1} \qquad (3)$$

based on the assumption of an exponential probability distribution. As shown in Figure 4, when Potomac data were compared to Equations (2) and (3), observed intensities were 1.4-2.5 times higher than predicted by Equation (2), and peak-to-mean ratios were 1.9-6.3 times higher than predicted by Equation (3). Thus, narrow plume events measured 10 m downwind from the source in a forest were sharper than observed in air pollution studies, and while the assumption of an exponential probability distribution worked well in other conditions, it underestimated maximum concentrations within instantaneous plumes in this canopy.

Although Figures 3 and 4 addressed instantaneous plume diffusion, we depicted patterns of mean plume dispersion in addition to best-fit Gaussian curves for the 5-m, 10-m, and 30-m arcs in Figure 5. Again, in the field of air pollution, modelers use dispersion coefficients (σ) to describe plume spread for downwind distances out to 50 km and beyond. In the case of insect pheromones in a forest canopy, we are interested in mean plume spread on much smaller scales, but because the average concentration profiles (Fig. 5) tended to be approximately Gaussian in shape, we were able to calculate average dispersion coefficients at each arc. Dispersion coefficients at the 5-m arc ranged from 3.9 to 7.7 m (Table 3); along the 10-m arc, σ_y values varied between 8.5 and 17.0 m; and results for the 30-m arc were between 27.2 and 44.8 m.

Figure 6a shows how our average tracer plumes spread as a function of distance downwind from the source. We could have developed a simple empirical equation describing the slope of σ_y versus downwind distance from these data, but the relationship may or may not apply for dispersion in forest canopies with other tree types and densities. Logically, spread of the time-averaged plume should be a function of local turbulence and travel time ($T = x\,U^{-1}$, where x is the downwind distance and U is the average wind speed); hence, Figure 6b contains the dispersion coefficients as a function of the horizontal turbulence statistics (σ_u and σ_v) times travel time. A linear regression of the data resulted in the following empirical equation to predict an average dispersion coefficient:

$$\sigma_y = 2.06\,(\sigma_u^2 + \sigma_v^2)^{1/2}\,X\,U^{-1} \qquad (4)$$

where $R^2 = 0.69$, and predicted dispersion coefficients from Equation (4) were within a few meters of observed values (Table 3).

Because Equation (4) was developed using a subset of data, it was necessary to test the method with independent dispersion measurements. In Figure 7, predicted σ_y from Equation (4) was compared to observed σ_y for 158 profiles within the Potomac dataset. Approximately 99 percent

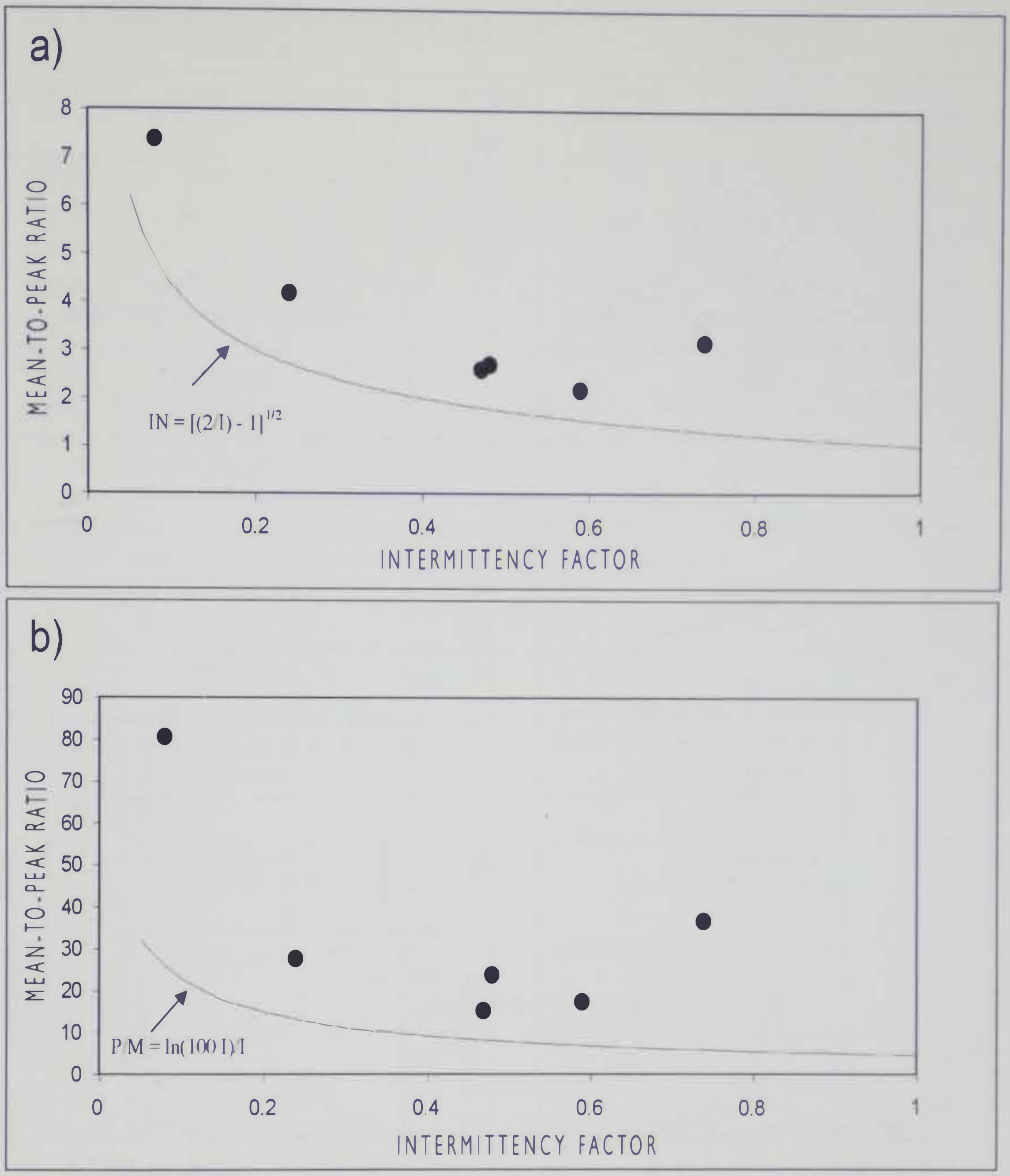

Figure 4. Relationships of a) concentration intensity and b) peak-to-mean ratio versus intermittency factor for the Potomac time series and curves from Equations (2) and (3) that assume an exponential probability distribution.

of the predicted dispersion coefficients were within a factor of 3 of the observed values, and 95 percent were within a factor of 2. The average predicted-to-observed ratio was 1.07 with a standard deviation of 0.44.

For the range of conditions tested at the Potomac site, this simple approach provided realistic estimates of average dispersion rates within 30 m of a pheromone source. In order to judge robustness of Equation (4), however, field results from additional forest settings will be considered in a follow-up paper.

Summary

Measurements of wind speed, wind direction, and tracer concentration revealed a wide range of turbulent motions resulting

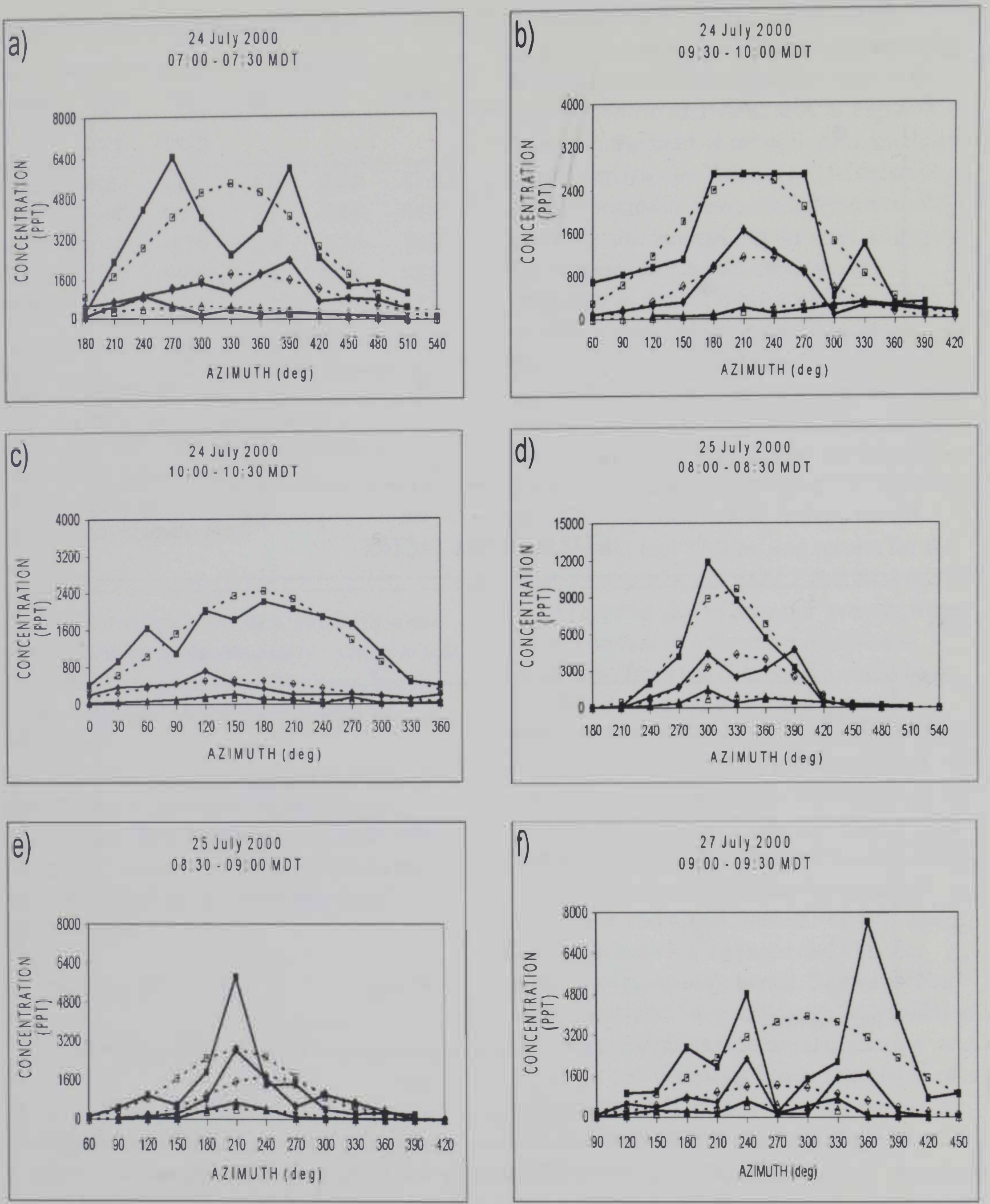

Figure 5. Average concentration profiles for: a) Test P724P2, b) Test P724P7, c) Test P724P8, d) Test P725P4, e) Test P725P5, and f) Test P727P6.

in intermittent plume exposure downwind of the SF_6 source. Peak-to-mean ratios were observed as high as 81 at the 10-m arc, and the concentration time series exhibited sharper peaks than predicted by exponential probability distributions.

Horizontal dispersion coefficients were used to develop a simple empirical equation for predicting mean dispersion as a function of the horizontal turbulence parameters and travel time. When tested against the Potomac set of 158 dispersion profiles, the method predicted within a factor of 3 for 99 percent of the cases, and within a factor of 2 for 95 percent of the data. Overall, the mean predicted-to-observed ratio was 1.07, but a variety of forest conditions must be tested before proposing it as a tool for forest managers.

Table 3. Time-Average Dispersion Data

Test	σ_y-5m (m)	σ_y-5m^p (m)	σ_y-10m (m)	σ_y-10m^p (m)	σ_y-30m (m)	σ_y-30m^p (m)
P724P2	7.0	3.6	14.6	7.3	44.8	21.8
P724P7	6.5	6.3	11.3	12.5	43.3	37.6
P724P8	7.7	10.2	17.0	20.4	43.1	61.3
P725P4	3.9	3.9	8.5	7.8	29.9	23.5
P725P5	5.1	4.6	10.0	9.2	27.2	27.5
P727P6	7.6	4.8	14	9.6	36.6	28.7

σ_y-5m - Observed average dispersion coefficient along the 5-m arc
σ_y-5mp - Predicted average dispersion along the 5-m arc using Eq. (4)
σ_y-10m - Observed average dispersion coefficient along the 10-m arc
σ_y-10mP - Predicted average dispersion coefficient along the 10-m arc using Eq. (4)
σ_y-30m - Observed average dispersion coefficient along the 30-m arc
σ_y-30mP – Predicted average dispersion coefficient along the 30-m arc using Eq. (4)

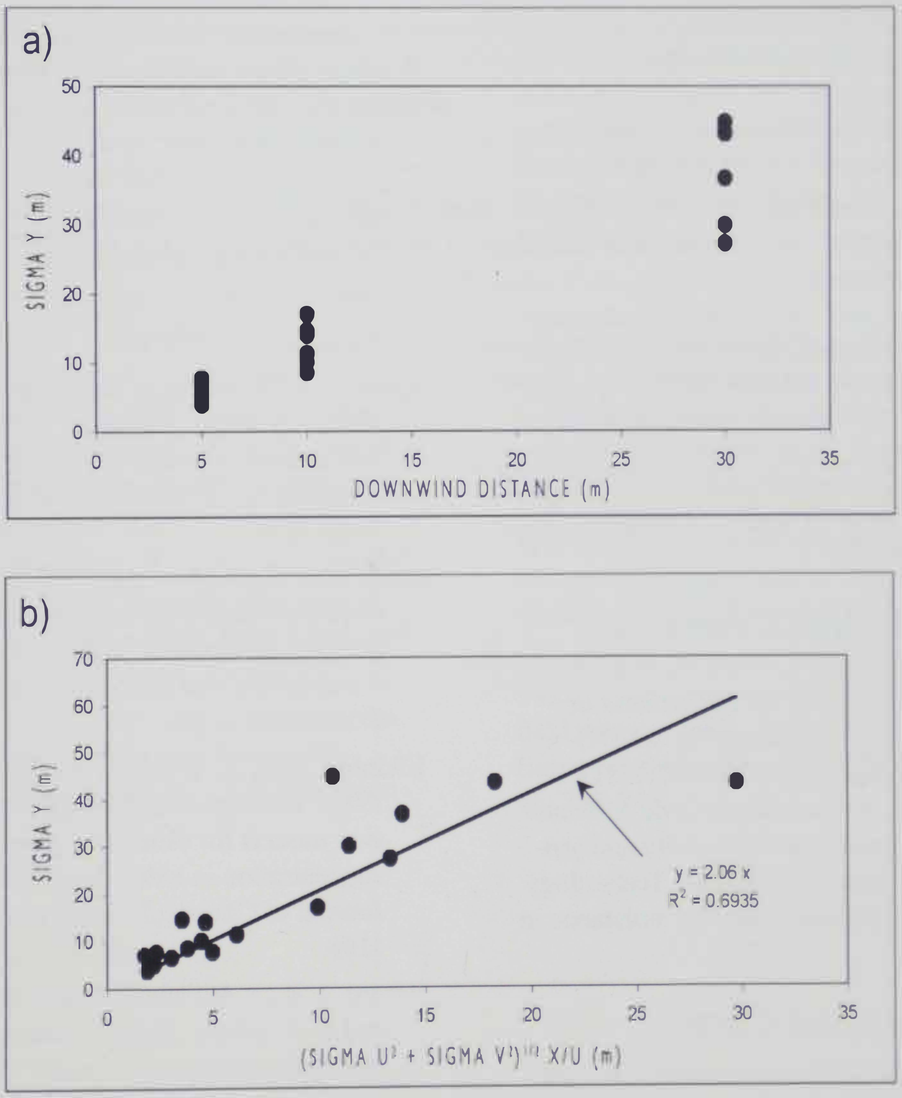

Figure 6. Average horizontal dispersion coefficient as a function of: a) downwind distance, and b) turbulence times travel time as $(\sigma_u^2+\sigma_v^2)^{1/2}$ X U.

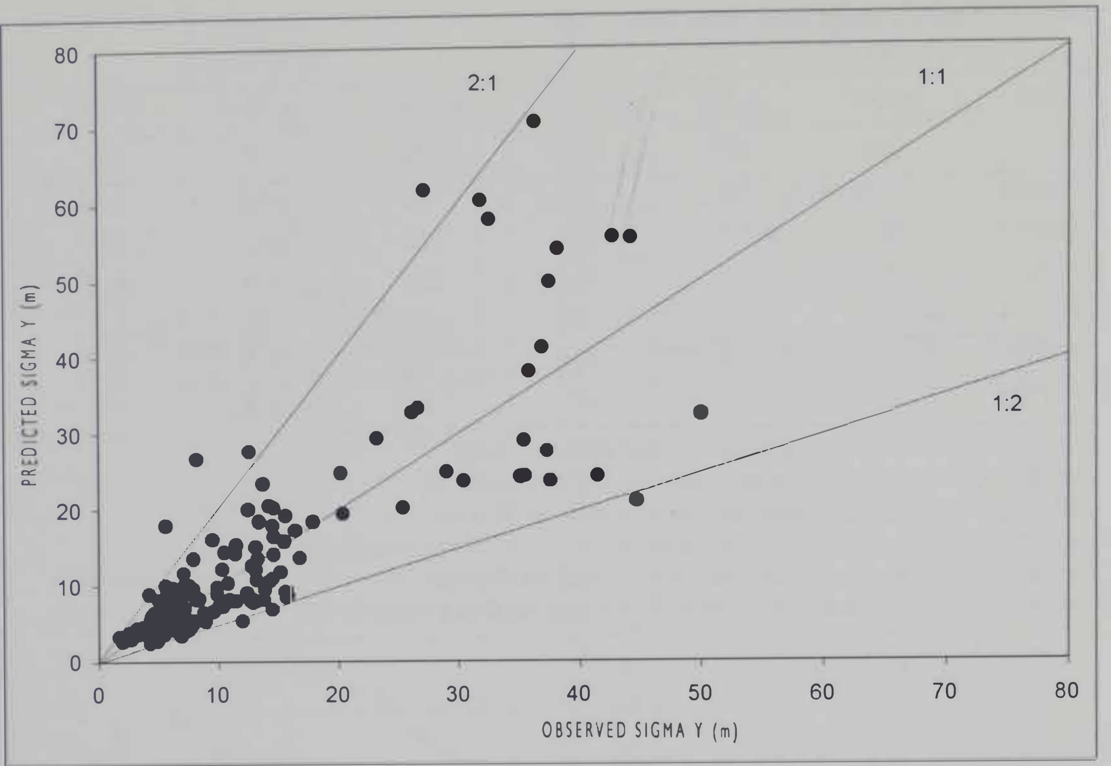

Figure 7. Predicted dispersion coefficients from Equation (4) versus observed values for the entire dataset of the Potomac field campaign. Also shown are the 2:1, 1:1, and 1:2 lines-of-correspondence.

Dispersion of pheromone through forest canopies is still not well understood. We are, however, making substantial advances via application of tracer technologies (previously used on larger scales for air pollution research) to small scales involved in pheromone transport.

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Literature Cited

Aylor, D. E. 1976. Estimating peak concentrations of pheromones in the forest. Perspectives in Forest Entomology. J. F. Anderson and H. K. Kaya eds. Academic Press, Inc. pp. 177-188.

Aylor, D. E., J. Parlange, and J. Granett. 1976. Turbulent dispersion of disparlure in the forest and male gypsy moth response. Environmental Entomology 1026-1032.

Benner, R. L., and B. Lamb. 1985. A fast response continuous analyzer for halogenated atmospheric tracers. Journal of Atmospheric and Oceanic Technolology 2:582-589.

Elkinton, J. S., R. T. Carde, and C. J. Mason. 1984. Evaluation of time-average dispersion models for estimating pheromone concentration in a deciduous forest. Journal of Chemical Ecology 10:1081-1108.

Farrell, J. A., J. Murlis, X. Long, W. Li, and R. T. Carde. 2002. Filament-based atmospheric dispersion model to achieve short time-scale structure of odor plumes. Environmental Fluid Mechanics 2:143-169.

Gifford, F. A. 1959. Statistical properties of a fluctuating plume dispersion model. Advances in Geophysics, Volume 6. Academic Press. Pp. 117-137.

Hanna, S. R. 1984. Concentration fluctuations in a smoke plume. Atmospheric Environment 12:1091-1106.

Kransec, J., D. Demaray, B. Lamb, and R. Benner. 1984. Automated sequential syringe sampler for atmospheric tracer studies. Journal of Atmospheric and Oceanic Technology 1:372-376.

Peterson, H. G., T. Donovan, S. O'Neill, and B. Lamb. 2003. Peak concentrations and plume diffusion in the atmospheric surface layer. Intermountain Journal of Sciences 9:87-100.

_____, and B. Lamb. 1992. Comparison of results from a meandering plume model with measured atmospheric tracer concentration fluctuations. Journal of Applied Meteorology 31:553-564.

_____ and _____. 1995. An investigation of instantaneous diffusion and concentration fluctuations Journal of Applied Meteorology 34:2724-2746.

_____, _____, and D. Stock. 1990. Interpretation of measured tracer concentration fluctuations using a sinusoidal meandering plume model. Journal of Applied Meteorology 29:1284-1299.

_____, D. Mazzolini, S. M. O'Neill and B. K. Lamb. 1999. Instantaneous spread of plumes in the surface layer Journal of Applied Meteorology. 38:343-352.

Suckling, D.M. 2000. Issues affecting the use of pheromones and other semiochemicals in orchards. Crop Protection 19: 677-683.

Thistle, H., G. Allwine, B. Lamb, T. Strand, H. Peterson, E. Holsten and P. Shea. 2002a. Near-field trunk space dispersion. ASAE Technical Paper #024017, ASAE, St. Josephs, MI.

_____, H. Peterson, B. Lamb, T. Strand, G. Allwine, E. Holsten and P. Shea. 2002b. Mass balance of pheromone-surrogate plumes in the canopy trunk space. ASAE Technical Paper No. 021006, ASAE, St. Josephs, MI.

_____, _____, G. Allwine, B. Lamb, T. Strand, E. Holsten and P. Shea. 2004. Surrogate pheromone plumes in three forest trunk spaces: composite statistics and case studies. Forest Science. In press.

Thorpe, K. and K. Tcheslavskaia. 2001. Portable electroantennogram (EAG) as a quality control tool to measure gypsy moth pheromone in the field. Proceedings of the 2001 Annual Gypsy Moth Review. Des Moines, IA .. Pp. 113-121.

Turner, D.B. 1969. Workbook of Atmospheric Dispersion Estimates. U.S. Department of Health, Education, and Welfare. Cincinnati, OH. Public Health Service Publication No. 999-AP-26.

USDA Forest Service. 2000. Assessment and response to bark beetle outbreaks in the rocky mountain area. Rocky Mountain Research Station. General Technical Report RMRS-GTR-62.

Van der Pers, J. N. C. and A. K. Minks. 1993. Pheromone monitoring in the field using a single sensillum recording. Entomologia Experimentalis et Applicata 68: 237-245.

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