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ESTIMATING MAXIMUM HORIZONTAL AREA OF PHEROMONE PLUMES

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Abstract—Graphs and simple Gaussian plume equations are presented for estimating the maximum horizontal area within a pheromone plume. In its simplest form the area, A_R, for a given scaling factor, $R = Q/(Ku)$, is $A_R = A_1 R^{\beta}$, where Q is the release rate, K is a specified concentration threshold, u is the wind velocity, and β is an atmospheric stability index. Estimates of A_1 and β are given for several atmospheric stability typing schemes applicable to field and forest habitats.

Key Words—Atmospheric diffusion, chemical communication, Gaussian plume model, isopleth area, pheromone, plume, plume area.

INTRODUCTION

In the past decade much attention has been directed towards theoretical and empirical studies of pheromone dispersal within the atmosphere. Among these are theoretical studies which examine mating and trapping within insect populations (e.g., Hartstack et al., 1976; McClendon et al., 1976; Geiszler et al., 1980) and empirical studies designed to determine the active space or communication distance associated with a pheromone plume (e.g., Farkas and Shorey,

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1974; Aylor et al., 1976; Nakamur and Kawasaki, 1977; David et al., 1982; Baker and Kuenen, 1982). These works range from qualitative discussions of the characteristics of a plume to detailed mathematical analyses of plume structure, and all include attempts to describe the dimensions and structure of a plume. Many of these investigations assumed that the plume was described by its time-averaged concentration profile and were concerned with the magnitude of the horizontal area (i.e., area within a concentration isopleth in the horizontal plane) of the plume at the source height (e.g., Hartstack et al., 1976; Geiszler et al., 1980). However, none of them present solutions that are both simple and applicable to a wide range of environmental conditions.

The goal of this paper is to present simple equations based on the Gaussian plume model for estimating the horizontal plume area at the source height which are applicable to field and forest conditions. The only information required is knowledge of (1) the atmospheric stability, (2) the pheromone release rate, (3) the concentration threshold defining the boundary of the plume, and (4) the mean wind velocity.

The first equation is developed from a slight modification of the elliptical approximation approach used by Nishiwaka (1959) and Hartstack et al. (1976). The second equation is derived directly from the properties of the elliptical approach and is much less mathematically complex. A third set are special cases of the first and second equations applicable primarily to short plumes. All of the equations are parameterized to be consistent with two widely used atmospheric turbulence typing schemes.

METHODS AND MATERIALS

Plume Model. The Gaussian atmospheric diffusion model in the form presented in Fares et al. (1980) was used to describe the pheromone concentration within a plume. This model represents the time-averged concentration profile of pheromone within a fully developed plume. The Gaussian plume model is mathematically simple and has achieved reasonable success (Slade, 1968; Hanna et al., 1982) in explaining a wide variety of observed plume concentration patterns.

The model assumes that at each point downwind the pheromone is distributed around a centerline in both the horizontal and vertical directions according to normal distributions. The standard deviations for each direction increase with distance downwind and the instability of the air. Unstable air exhibits a large amount of turbulence which causes rapid dilution of the pheromone.

To implement the plume model, a Cartesian coordinate system is used to represent the spatial arrangement of the plume and its source. The positive x axis represents the downwind distance from the source. The y axis represents the horizontal dimension, and the z axis represents the vertical dimension. The pheromone source is assumed to be at the point (0, 0, H) in the coordinate system.

Since a proportion of the pheromone that contacts the ground may be reflected or carried back into the air, the model assumes that there is an identical virtual source at the point (0, 0, −H) below the plane representing the ground. The aboveground portion of this plume is multiplied by the proportion being reflected (i.e., not adsorbed) and is added to the aboveground plume.

The Gaussian plume model for the concentration at the point (x, y, z) downwind for a source at height H with the proportion α being reflected from the ground can be written as

$$C(x, y, z; H) = \frac{Q}{2\pi\sigma_y(x)\,\sigma_z(x)\,u} \exp\left[-\frac{1}{2}\left(\frac{y}{\sigma_y(x)}\right)^2\right] \cdot \left\{\exp\left[-\frac{1}{2}\left(\frac{z-H}{\sigma_z(x)}\right)^2\right] + \alpha \exp\left[-\frac{1}{2}\left(\frac{z+H}{\sigma_z(x)}\right)^2\right]\right\} \tag{1}$$

where Q is the emission rate of the pheromone source, u is the average wind velocity, and $\sigma_y(x)$ and $\sigma_z(x)$ are the standard deviations for the pheromone concentration in the horizontal and vertical directions, respectively (Fares et al., 1980). Collectively, $\sigma_y(x)$ and $\sigma_z(x)$ are called the "dispersion parameters," since they alone determine the rate at which the plume spreads out downwind. The units associated with each parameter depend upon the system under study, but must be consistent throughout the equation.

The plume, specified by the concentration levels downwind (equation 1), is defined as the set of all points at which the concentration is greater than or equal to a threshold level K. This implies that the boundaries of the plume occur at $C(x, y, z; H) = K$. In most applications to date (e.g., Hartstack et al., 1976), K has been set to the behavioral response threshold of the receiver. Further, since the mode of the vertical concentration distribution is at the source height, the greatest area on a horizontal plane through the plume also occurs at the source height.

Wall et al. (1981) demonstrated both chemically and electrophysiologically that significant levels of (E, E)-8,0-dodecadien-1-yl-acetate, the sex attractant of the pea moth, *Cydia nigricana*, were adsorbed to wheat leaves when released from attractant-baited traps. Because incorporating pheromone reflection for elevated sources does not allow the area to be calculated using the technique to be presented and significant adsorption of pheromone has been demonstrated, we assume that there is no reflection of pheromone from the ground for elevated sources. We do present simple adjustments to obtain the areas for ground-level sources. Accordingly, the boundaries at the source height, whether elevated or at ground level, for a plume without reflection (i.e., $z = H$ and $\alpha = 0$) are constrained to

$$K = \frac{Q}{2\pi\sigma_y(x)\ \sigma_z(x)\ u} \exp\left[-\frac{1}{2}\left(\frac{y}{\sigma_y(x)}\right)^2\right] \tag{2}$$

The boundaries for a ground-level plume with the proportion α being reflected are constrained to equation 2 with $Q^* = (1 + \alpha)Q$ substituted for Q.

Dispersion Parameters. The standard deviations associated with the horizontal and vertical plume concentration distributions depend upon the degree of air stability. Turbulent eddies, caused by mechanical obstructions and convection, carry pheromone away from the path associated with the mean direction of the wind. The mean wind speed and eddy size determine the downwind pheromone dispersal rate. Accordingly, the dispersion parameters will differ for different terrain types and vegetation conditions. Theoretical and empirical studies (Slade, 1968; Hanna et al., 1982) of atmospheric diffusion show that at short distances downwind ($x <$ ca. 500 m) the plume concentration standard deviations are approximately equal to the wind direction standard deviation in radians in the appropriate plane (y or z) multiplied by the distance downwind. At larger distances the standard deviations become proportional to the square root of the downwind distance.

The dispersion parameters increase with increasing sampling time (i.e., time over which the concentration is averaged) during their measurement. This is a result of the effects of larger eddies becoming measurable as the sampling interval increases. Because these eddies carry the pheromone greater distances across or above and below the centerline, the average concentration at any point decreases. This decrease is expressed as an increase in the magnitude of the dispersion parameters. Although this occurs in both directions, the primary influence of sampling time is on the horizontal coefficient in the first few hundred feet from the ground (Hanna et al., 1982). Crude estimates (Hanna et al., 1982) for the horizontal dispersion parameter, $\sigma_y(x)$, for a sampling time T can be obtained from the coefficient $\sigma_y^*(x)$ measured over a sampling time of T^* using the relationship

$$\sigma_y(x) = \sigma_y^*(x)\ (T/T^*)^q \tag{3}$$

where $q = 0.2$ for 3 min $< T <$ 1 hr and $q = 0.25$–0.30 for 1 hr $< T <$ 100 hr.

A variety of schemes have been used to categorize atmospheric turbulence into stability classes and to describe dispersion downwind within a class (Gifford, 1976). A simple scheme that is widely used because it has produced satisfactory results in most cases (Hanna et al., 1982) was developed by Pasquill (1961). He divided atmospheric stability into six categories according to observed wind speed, cloud cover, and insolation levels. These categories and the conditions with which they are associated in open field and forest habitats are presented in Table 1. Pasquill also presented graphs describing the lateral and

Table 1. Pasquill[a] and Fares Stability Categories Associated with Habitat Types and Weather Conditions[b]

Low crops and open terrain:

Surface wind speed (m/sec)	Daytime insolation			Nighttime conditions	
	Strong	Moderate	Slight	Thin overcast or $\geqslant \frac{4}{8}$ cloudiness[c]	$\leqslant \frac{3}{8}$ cloudiness
<2	A	A–B	B	F[d]	F[d]
2	A–B	B	C	E	F
4	B	B–C	C	D	E
6	C	C–D	D	D	D
>6	C	D	D	D	D

Open Forests:

Category	Temperature profile[e]	Corresponding Pasquill categories	Identifier[f]
Inversion	$\Delta T > 1.5$	F	I
Intermediate	$0 \leqslant \Delta T \leqslant 1.5$	D, E	J
Buoyant	$\Delta T < 0$	A, B, C	
(a) upward			K
(b) downward			I

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[a] Pasquill stability categories [σ_θ = wind direction SD]: A = Extremely unstable conditons [$\sigma_\theta = 25°$], B = Moderately unstable conditions [$\sigma_\theta = 20°$], C = Slightly unstable conditions [$\sigma_\theta = 15°$], D = Neutral conditons (applicable to heavy overcast day or night) [$\sigma_\theta = 10°$], E = Slightly stable conditions [$\sigma_\theta = 5°$], F = Moderately stable conditions [$\sigma_\theta = 2.5°$].

[b] After Slade (1968) and Fares et al. (1980).

[c] The degree of cloudiness is defined as that fraction of the sky above the local apparent horizon that is covered by clouds.

[d] F suggested, however, A–F can occur in these conditions. Selection should be based on σ_θ.

[e] ΔT is defined as the temperature change in °C between 0.5 and 8.0 m from the floor of the canopy.

[f] Arbitrarily selected letters used to identify the categories for which Fares et al. (1980) supplied parameter estimates.

vertical spreading of a plume with distance downwind in terms of the 10% points of plume concentration relative to the mean centerline value for open, level terrain. Gifford (1961) expressed these graphs in terms of $\sigma_y(x)$ and $\sigma_z(x)$ to produce the set of widely used curves now called the Pasquill–Gifford (PG) curves. A second set of widely used curves, also presented in equation form, was developed by Briggs (1973). These curves are similar to the PG curves, but they incorporate information from other studies. Although the PG curves and Briggs formulas are two of the most widely used dispersion typing schemes, the equations describing these curves over their entire range unfortunately do not allow the development of simple equations for plume area.

In many investigations the observed plume standard deviations have been described using simple power functions (e.g., Cramer et al., 1958; Fares et al., 1980). Accordingly, the equations for the dispersion parameters for a given stability class are

$$\sigma_y(x) = ax^b \tag{4}$$

and

$$\sigma_z(x) = cx^d \tag{5}$$

As we will show, these formulas allow the development of simple area equations, but their general limitation is that no single power function can fit diffusion data over all downwind distance ranges (Gifford, 1976). However, Tadmor and Gur (1969) demonstrated that power functions approximated the PG curves well for downwind distance less than 5 km. For distances less than 500 m Briggs formulas are accurately approximated by simple lines (i.e., $b = d = 1$). In this case a and c are approximately equal to the wind direction standard deviations in the horizontal and vertical directions, respectively. Since most pheromone plumes are less than 500 m in length, power function approximations to the PG and Briggs curves will allow the accurate calculation of plume areas associated with these two popular stability classification schemes.

Equations 4 and 5 will be used to describe the dispersion parameters in this study. Estimates of a, b, c, and d for the open field conditions associated with the PG curves for each stability category were taken from Eimutis and Konicek (1972) and are presented in Table 2. The values for $\sigma_z(x)$ are for downwind distances less than 100 m. These values were selected here for $\sigma_z(x)$ since a majority of the events in pheromone communication occur within 100 m of the source. For estimates of Briggs' formulas, a and c were assigned the value of the coefficient in the numerator of his equations, and b and d were set equal to one (Table 2). The maximum relative error at 500 m over all stability classes incurred by using these estimates is 2.5% for $\sigma_y(x)$ and 32.3% for $\sigma_z(x)$. Values of a, b, c, and d for open, pine forest conditions were taken from Table 6 in Fares et al. (1980) (Table 2). As presented here, equation 5 will underestimate $\sigma_z(x)$ for inversion conditions is forests, since it does not include the height of the inversion layer.

The Pasquill and Briggs estimates are applicable to 10-min sampling times and the values for the Fares estimates are based on 15-min sampling times. The horizontal parameters for other sampling periods can be estimated using equation 3. These parameter sets are based on data collected in open, level terrain and open pine forest conditions, and dispersion parameter constants for other habitat types could be different. Further, it must be noted that none of the

TABLE 2. POWER FUNCTION CONSTANTS DEFINING DISPERSION PARAMETERS IN GAUSSIAN PLUME MODEL

	Power function constants[b]						
	Horizontal		Vertical				
Stability category[a]	a	b	c	d	$F^{c,d}$	$A_1^{c,d}$	β
A (P)	0.37	0.90	0.19	0.94	0.74851	1.11688	1.03261
(B)	0.22	1	0.20	1	0.73057	0.99736	1
B (P)	0.28	0.90	0.16	0.92	0.74851	1.35798	1.04396
(B)	0.16	1	0.12	1	0.73057	1.66226	1
C (P)	0.21	0.90	0.12	0.90	0.74851	1.88670	1.05556
(B)	0.11	1	0.08	1	0.73057	2.49339	1
D (P)	0.15	0.90	0.08	0.88	0.74851	3.02401	1.06742
(B)	0.08	1	0.06	1	0.73057	3.32452	1
E (P)	0.10	0.90	0.06	0.87	0.74851	4.29713	1.07345
(B)	0.06	1	0.03	1	0.73057	6.64904	1
F (P)	0.07	0.90	0.05	0.81	0.74851	6.08839	1.11111
(B)	0.04	1	0.016	1	0.73057	12.46694	1
I	0.007	1.4	1.51	0.2	0.65759	0.34878	1.50000
J	0.007	1.4	0.99	0.42	0.65759	0.39696	1.31868
K	0.007	1.4	0.47	0.6	0.65759	0.70135	1.20000

[a] B = Approximation to Briggs (1973) formulas. P = approximation to the Pasquill–Gifford curves.

[b] Pasquill coefficients extracted from Tables 1 and 3 in Eimutis and Konicek (1972). Numerator coefficient for Briggs formulas taken from Table 4.5 in Hanna et al. (1982). Forest coefficients taken from Table 6 in Fares et al. (1980).

[c] Based on Simpson's rule approximation of the actual areas using 10,000 subintervals and double-precision arithmetic.

[d] Values represent the averages for R equaling 1, 10^2, 10^4, 10^6, and 10^8. The actual deviation between any two observed values within a stability category was $<10^{-6}$ in every case.

atmospheric diffusion data from which these dispersion parameters were estimated were directly concerned with pheromone communication systems. They are only used here due to lack of alternatives.

Derivation of Plume Area Equations. Nishiwaka (1959) observed that the area of an ellipse closely approximated the plume area when the plume's length is used as the ellipse's length and its maximum width is used as the ellipse's maximum width. Hartstack et al. (1976) also used this approach to estimate the plume area. The length (Length), width as a function of distance downwind [$W(x)$], distance downwind at which the width is greatest (XW_{max}), and the

TABLE 3. EQUATIONS DESCRIBING DIMENSIONS OF TIME-AVERAGE PLUME (AREA WITHIN CONCENTRATION ISOPLETH) AT SOURCE HEIGHT FOR GAUSSIAN PLUME MODEL[a]

Dimension	Equation[b]	No.
Length	$\text{Length} = \left(\dfrac{R}{2\pi ac}\right)^{1/(b+d)}$	(T3.1)
Width at downwind distance x	$W(x) = \{8a^2x^{2b} \log_e [R/(2\pi acx^{b+d})]\}^{1/2}$ for $0 < x \leqslant \text{Length}$	(T3.2)
Downwind distance of maximum width	$XW_{\max} = (\text{Length}) \exp[-1/(2b)]$	(T3.3)
Maximum width	$\text{Width} = 2a \exp[-1/2]\,[(b+d)/b]^{1/2}\,(\text{Length})^b$	(T3.4)
Area	$A_R = (F)\,(\text{Length})\,(\text{Width})$	(T3.5)
	$= A_1R^{\beta}$	(T3.6)
	where	
	$F = (\pi/4) \exp\{-0.0847b + 0.0044b^2$ $- 0.1602 \log_e(b) - 0.1320 [\log_e(b)]^2\}$	(T3.7)[c]
	$\beta = (b+1)/(b+d)$	(T3.8)

[a] Dispersion parameters: $\sigma_y(x) = ax^b$ and $\sigma_z(x) = cx^d$.

[b] $R = Q/(Ku)$ for elevated or ground-level sources with complete pheromone adsorption to the ground. $R = (1 + \alpha)\,Q/(Ku)$ for ground-level sources which reflect the proportion α of the pheromone contacting the ground back into the air.

[c] F is accurate to within $0.01\pi/4$ over the range $0.1 \leqslant b \leqslant 10.0$.

maximum width (Width) are given in Table 3 by equations T3.1–T3.4, respectively. These equations can all be derived directly from equation 2 and are expressed as functions of the scaling factor, $R = Q/(Ku)$. This factor represents an adjustment of the ratio (Q/K) of the release rate to the response threshold identified by Bossert and Wilson (1963) as the primary measure describing olfactory communication. Because the wind speed determines the time which a volume of air has to pick up the pheromone being released as it passes the source, there will be less pheromone in the volume of air at higher wind speeds than at lower speeds. Accordingly, Q/u represents the apparent release rate when monitoring the concentration in a volume of air, which could be quite different from the biologically meaningful pheromone flux rate (see Elkinton and Cardé, 1984), and R could be thought of as the effective communication ratio.

Using the dispersion parameter constants in Table 2, plume area estimates calculated using the area of an ellipse [i.e., π(Length) (Width)/4] were compared to the actual plume areas. The maximum absolute relative error incurred by using the area of an ellipse was 4.7% for Pasquill's categories and 16.3% for

Fares' forest stability categories. This error was similar to that observed by Nishiwaka (1959). Actual plume areas were obtained here and for subsequent parameter estimations by integrating equation T3.2 using Simpson's rule with 10,000 subintervals and double-precision arithmetic on a PRIME 400® computer. In determining the error associated with approximating plume area by the area of an ellipse, it was observed that for a given stability category the relative error was constant over all values of R. A small variation of the order of 10^{-6}–10^{-8} was observed, but this was assumed to be due to the truncation and round-off error associated with the Simpson's rule estimation. This belief is based on the observation that the variation consistently decreased as the number of integration subintervals used increased. This implied that precise values of the plume area at the source height for a given set of dispersion parameters and value of R could be obtained by multiplying the area of the ellipse by a constant correction factor, f. Sensitivity analysis showed that the correction factor f depended solely upon the value of b.

Using these observations, formulas for the plume area base on correcting the area of the equivalent ellipse were derived through simple algebraic substitution and simplification. An approximation for the correction factor as a function of b was obtained using multiple linear regression on transformed data using exact values of f calculated over a range of b between 0.1 and 10.0.

Approximation Accuracy. To compare the agreement of these approximations to the true areas associated with plumes defined by the actual PG and Briggs dispersion parameters, the correct areas were plotted along with the approximations in the same graph. Actual areas calculated with PG curves for a ground-level source with complete reflection were determined graphically by Hilsmeier and Gifford (1962) for R greater than 100. These values were adjusted to correspond to plumes without reflection using equation 11 (see below). Numerical integration, using Simpson's rule with 2000 subintervals, was used to obtain the actual areas associated with Briggs formulas as the dispersion parameters. Because the forest diffusion parameters were given as power functions, the estimates are exact for the intended model in all cases except the inversion conditions. Excluding inversion conditions, the only error is the discrepancy between the model and a real plume. Under inversion conditions, the approximation will increasingly overestimate the plume area as the height of the inversion layer increases.

RESULTS

Plume Area Equations. Based on the analytical observations in the methods section, very precise areas within a concentration isopleth at the source height for a plume without reflection from the ground can be calculated as

$$A_R = (F)(\text{Length})(\text{Width}) \tag{6}$$

where A_R is the area for a given R, $F = f\pi/4$ is the modified correction factor, and Length and Width are equations T3.1 and T3.4, respectively, in Table 3. Exact values of F for each set of dispersion parameters are given in Table 2. The approximation of F as a function of b is given in Table 3 as equation T3.7. This function predicts within $0.01(\pi/4)$ of the true value over the range $0 \leq b \leq 10.0$.

Substitution of the equations for Length and Width into equation 6 allows A_R to be calculated directly from the dispersion parameter constants, F and R, as

$$A_R = 2Fa \exp\,[-1/2][(b + d)/b]^{1/2}\left(\frac{R}{2\pi ac}\right)^{(b+1)/(b+d)} \tag{7}$$

A simpler equation than 6 or 7 can be obtained by factoring R out of equation 7 and recognizing that the value of the terms not including R equals A_1, i.e., the area of a plume having $R = 1$. Accordingly, the plume area can be calculated by a simple power function as

$$A_R = A_1 R^{\beta} \tag{8}$$

where $\beta = (b + 1)/(b + d)$. Equation 8 states that within a stability category the area for any plume can be obtained by scaling the area of a plume with $R = 1$. Thus, under the Gaussian plume model with power function dispersion parameters, the accuracy of A_R is solely dependent upon the accuracy of A_1. Exact values of A_1 are presented for each stability category in Table 2.

In cases where the exponents of the dispersion parameters equal one (i.e., $b = d = 1$), as with the estimates to Briggs formulas or short plumes where the wind direction standard deviations can be used for a and c, equations 7 and 8 simplify greatly. They become, respectively,

$$A_R = FR/[c\pi(0.5 \exp\,[1])^{1/2}] \tag{9}$$

$$A_R = A_1 R \tag{10}$$

Both equations are simple lines passing through the origin with slope A_1 when A_R is plotted against R. This simplicity allows rapid calculation of accurate estimates of plume area when the short plume estimates of Briggs formulas are used.

To calculate the plume area associated with a ground-level source for which the proportion α of the phermone contacting the ground is reflected back into the atmosphere,

$$R^* = (1 + \alpha)R \tag{11}$$

is substituted for R into equations 6 through 10. Unfortunately, this substitution does not hold for elevated sources. To illustrate the use of equation 11 for ground-level sources, the effect of adsorption on the plume area associated with the dermestid *Trogoderma glabrum* will be examined. Shapas and Burkholder (1978) estimated the average peak release rate of 14-methyl-8-hexadecenal by females as $Q = 3.2 \times 10^{-2}$ ng/sec and the threshold for response by 50% of the males as 1 ng/m^3. At a wind velocity of 0.50 m/sec, $R = 3.2 \times 10^{-2}/[(0.50)(1)] = 0.0640$ m^2. If this occurred in the open under moderate-to-slight insolation (Pasquill category B), the area of a female's plume using Briggs coefficients (which may be poor estimates for such small plumes) and equation 10 would be $A_{0.0640} = (1.66226)(0.0640) = 0.106$ m^2, assuming that all pheromone contacting the ground is adsorbed. However, if only 25% of the pheromone is adsorbed, $R^* = (1 + 0.75)(0.0640) = 0.1120$ m^2 and the resulting plume area is $A_{0.1120} = 0.186$ m^2. Although this is not a dramatic increase, it does illustrate the importance of adsorption on plume area.

Approximation Accuracy. Graphs of the plume area associated with the PG curves for each stability category plotted against R, as predicted by equation 8, are presented as the broken lines in Figure 1. The solid lines in the graph are the areas calculated by Hilsmeier and Gifford adjusted to remove reflection. The numbers in parentheses are the lengths of each plume at R equal to 10^4 calculated using equation T3.1. Like the areas, these values demonstrate the importance of turbulence in the rapid dilution of pheromone. The plume for the most stable category, F, is almost nine times as long as the plume in the least stable category, A. As shown, the approximations based on the dispersion parameter values in Table 2 agree well with the Hilsmeier and Gifford areas even for plumes greater than 100 m in length. The approximation for F deviates the greatest from the Hilsmeier and Gifford areas, and is consistently lower than the Hilsmeier and Gifford predictions. However, the maximum difference in the range graphed is only 25% and should cause little problem in application.

Approximations using equation 10 (broken lines) and numerically integrated areas using Briggs formulas show excellent agreement between the two sets of curves (Figure 2). As before, the only significant deviation between the approximation and the areas actually defined by Briggs formulas occurs in category F. At $R = 1$ there is less than 0.5% error, and the error goes from ca. 15% at $R = 1000$ to 50% at $R = 10^4$. Note that the areas associated with Briggs formulas agree well with Hilsmeier's and Gifford's estimates for all stability categories, except A. The areas for A associated with Briggs formulas are approximately 40% smaller than Hilsmeier's and Gifford's areas. This is to be expected since Briggs defined $\sigma_z(x)$ for category A to represent more unstable conditions than defined by the PG curves.

For both the PG curves and Briggs formulas the area associated with the most stable category, F, is approximately 10 times that of the least stable cate-

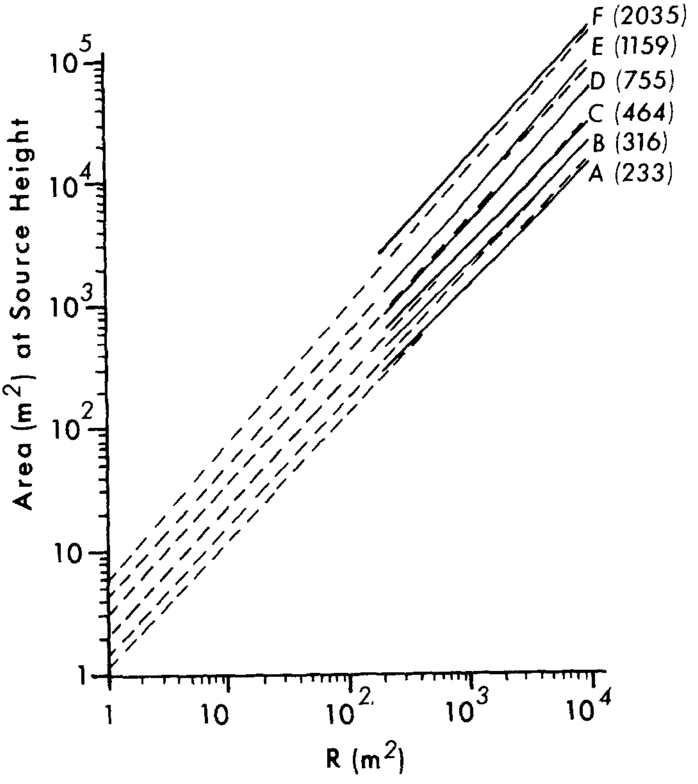

FIG. 1. Areas for plumes without reflection defined by the Plasquill-Gifford diffusion parameters. Solid lines represent the adjusted Hilsmeier-Gifford estimates, and the broken lines are the approximations given by equation 8. Plume lengths for $R = 10^4$ are in parentheses.

gory, A. In general the approximations based on the PG curves are smaller than those for Briggs formulas for small R and larger than those for large R. The greatest deviation occurs between the approximations in category F. For $R = 10^4$, the PG area is only ca. 25% greater than the Briggs area approximation. However, at $R = 1$, the Briggs area is twice that predicted for the PG curves. The estimate associated with the PG curves is probably more reliable since the tabled dispersion parameter values are for plumes less than 100 m in length. For both sets of approximations, little error will be accrued in categories A, B, and C when using the approximations for several orders of magnitude above $R = 10^4$. However, for categories E and F for the PG curves and D, E, and F for the approximations to Briggs areas, the approximations will underestimate the mean plume area for values of $R > 10^4$. Except for very large values of R (e.g., 10^6), this error will be less than an order of magnitude.

Figure 3 contains the areas associated with the dispersion parameters for

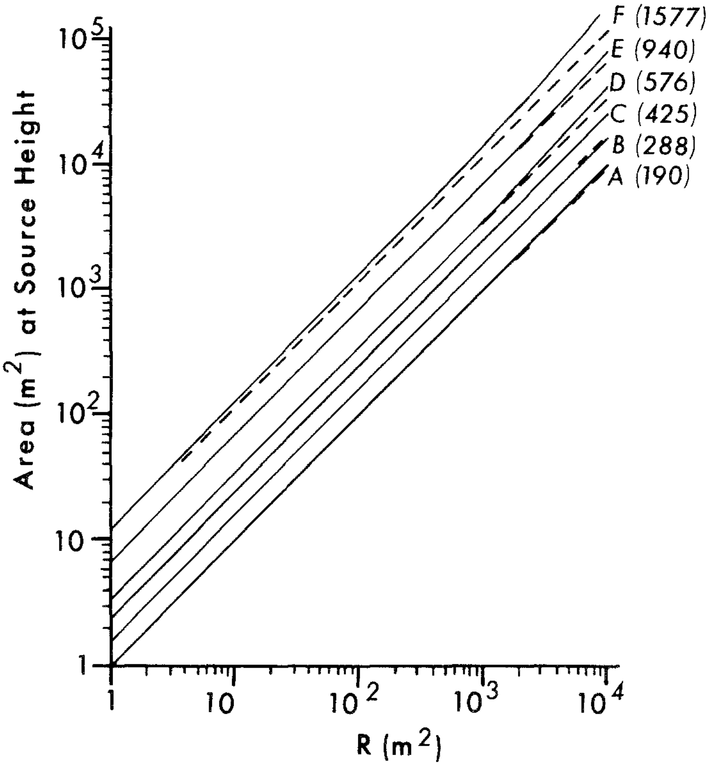

FIG. 2. Areas for plumes without reflection using dispersion parameters defined by Briggs formulas. Solid lines represent the numerically integrated plume model, and the broken-lines are the approximations given by equation 10. Plume lengths for $R = 10^4$ are in parentheses.

forest habitats in Table 2. These lines are exact for the three categories since the dispersion parameters were defined as power functions. For $R < 30$, the areas for all the categories are similar, and categories J and K are similar for the entire range graphed. At $R = 10^4$, the area associated with category J is only twice that of K, and category I, which is more stable, has an area 10 times that of K. In general, the areas associated with the forest habitat differ greatly from those associated with the PG curves and Briggs formulas for open areas, but at $R > 1000$ the areas of I, J, and K are similar to F, D, and E, respectively.

DISCUSSION

To estimate the plume areas for a given habitat and stability category, the areas can be read directly from Figures 1, 2, or 3. Adjustment for pheromone

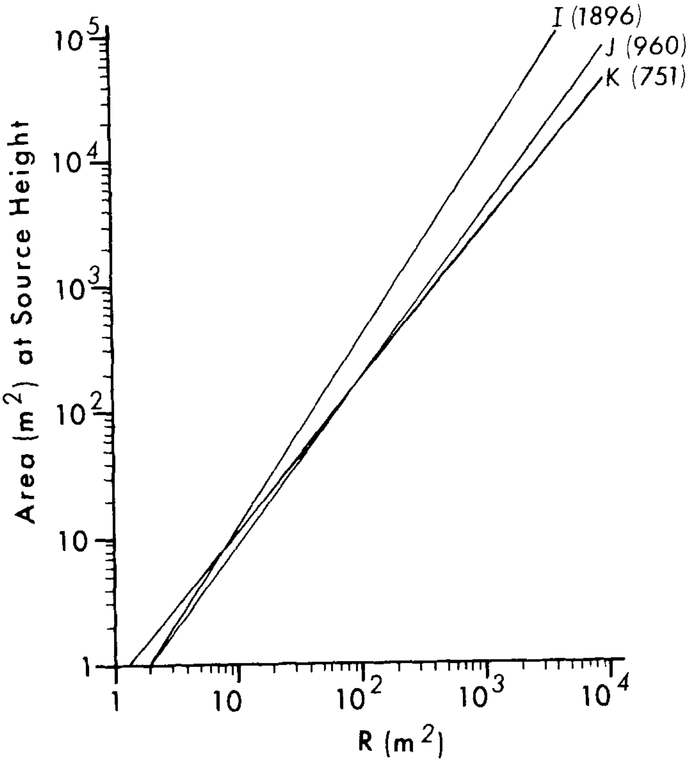

FIG. 3. Areas for plumes without reflection using the forest dispersion parameters defined by Fares et al. Plume lengths for $R = 10^4$ are in parentheses.

reflection off the ground for gound-level sources is achieved by shifting the value of R according to equation 11. However, equations 7 through 10 provide very simple formulas for calculating the areas using the parameters in Table 2. Equation 10 is especially simple as it is a line. Since Briggs formulas are generally accepted as reasonable estimates among workers in atmospheric diffusion (Gifford, 1976, Hanna et al., 1982), this equation should be a useful tool to researchers studying pheromone communication. Further, the equations developed here are immediately applicable to any stability classification scheme in which the dispersion parameters are defined or approximated by power functions. To estimate the areas for a stability class, estimate the correction factor using equation T3.7. The area A_1 for $R = 1$ is calculated using equation 7, or equation 9 if b and $d = 1$. The areas associated with a value of R can then be calculated using equation 8, or equation 10 if $d = 1$. Equation 11 can be used to adjust for reflection for ground-level sources.

A significant point in this study is that a power function of R (i.e., eq. 8) gives the plume area associated with the Gaussian plume model with the dispersion parameters defined as power functions. Elliott (1959) and Elliott and Nickola (1961) demonstrated empirically, using field data, that within a stability class the plume area can be described well by a power function of R. It is reassuring that the form of equation 8 is in agreement with previous empirical observations. Slade (1968) presents an unpublished study by Gifford in which he compares Elliott's areas to the Hilsmeier and Gifford curves. In general, the two sets of curves were in fair agreement with one another.

Despite this empirical support, the relevance and limitations of the equations and graphs presented in this paper should be considered when applying these relationships to field situations. They provide quantitative measurements of the attributes of the Gaussian plume model, but are not improvements over the Gaussian model. Discussions of the reliability of the Gaussian plume model can be found in Slade (1968), Fares et al. (1980), and Hanna et al. (1982). The Gaussian plume model is relevant to the meandering plume's average behavior in variable wind directions (David et al., 1982), since each Pasquill stability category can be associated with a specific wind standard deviation range (Slade, 1968). The equations presented in this paper will be useful for estimating the area in the field that, on the average, is exposed to at least a threshold concentration. However, because the plume model represents the long-term average concentration at a given point, the actual concentration at a given instant is likely to be much lower or greater than predicted. This was demonstrated by Aylor et al. (1976), who estimated peak disparlure concentrations 24 times greater than the predicted average at 1.2 m from the source. Accordingly, plumes defined by the Gaussian plume model will generally be wider and shorter due to the averaging than the instantaneous plumes.

A recent field bioassay by Elkinton et al.(1984) lends a further note of caution regarding the use of time-average plume models. They were able to estimate the concentration profile of time-averaged plumes using a grid of male gypsy moths, *Lymantria dispar*, set up downwind of a disparlure source in a woodlot. They observed that the qualitative behavior of the plume models was similar to that of the plumes. However, they found that the predicted average concentrations at locations where wing fanning occurred were often several orders of magnitude lower than wing-fanning response thresholds determined in wind tunnel tests. They found the best agreement using the PG dispersion parameters in which the category was selected using the lateral wind direction standard deviation. But even the "best" agreements implied response thresholds 2–4 orders of magnitude lower than those observed in the wind tunnel. Contrary to expectation, they observed the poorest agreement using the forest dispersion parameters presented in Fares et al. (1980). They did point out that their bioassay tended to overestimate the average concentration, since a brief exposure to a concentration greater than the threshold will produce a response even though the average concentration at the site is below the threshold. As they note, this is certainly a shortcoming of time-average plume models in general.

A very crude estimate in the error between the area over which a peak concentration greater than the threshold occurred sometime during the sampling interval and the area within the threshold concentration isopleth predicted by the Gaussian plume model can be obtained using the results of Elkinton et al. (1984). The former area would estimate the spatial area actually sampled for males by the plume, while the latter area represents the spatial area in which the average concentration over the interval was greater than the threshold. Elkinton et al. reported that the threshold concentration eliciting a wing-fanning response in 50% of the males in wind tunnel bioassays was $K = 1 \times 10^{-18}$ g/cm^3, and the release rate from their source loaded with 100 μg of disparlure was $Q = 296$ pg/sec in a $u = 1.32$ m/sec wind [$R = Q/(Ku) = 224.2$ m^2]. Their figures show that concentration isopleths at the source height based on a threshold of $K^* = 1 \times 10^{-20}$ g/cm^3 ($R = 22{,}424$ m^2) enclosed most stations were $\geq 50\%$ of the males responded. If we use the dispersion parameters for Pasquill category B and equation 8, assuming that isopleths based on K^* define the bounds of 50% male response, then the area sampled by the plume ($A_{22424} = 1.35798(22424)^{1.04396} = 47{,}300$ m^2) is 123 times greater than the predicted area ($A_{224.2} = 386$ m^2). This is probably an overestimate, since equation T3.1 would indicate that the time-average plume using K^* would be 493 m long. Elkington et al. only monitored response up to 80 m downwind. It is unlikely that 50% male response would be observed ca. $\frac{1}{2}$ km downwind in a woodlot, since there would be significant adsorption of pheromone to the trees. However, Figures 4 and 5 in Elkinton et al. (1984) indicate that the discrepancy in the areas is large. Assuming that the error estimate is close to the true value, then the discrepancy between the two areas is ca. 10 times greater than the relative difference between the Gaussian plume areas in the least and most stable Pasquil stability categories. This makes it clearly evident that more studies like that of Elkinton et al. are needed to assess the usefulness of the Gaussian plume model parameterized with currently available diffusion parameter estimates. These studies should help to identify where the Gaussian model is appropriate and, ultimately supply investigators with a set of dispersion parameter estimates and adjustment factors that will allow realistic estimates of the area within a concentration isopleth to be obtained.

This paper has presented simple equations and graphs for estimating the area of a pheromone plume based on the Gaussian plume model parameterized using the most commonly used dispersion parameter sets. As illustrated above, these parameter sets may not be adequate and more studies are needed. Although the Gaussian plume model may be inappropriate in purely mechanistic studies of pheromone communication, its qualitative behavior and mathematical simplicity insure its use in quantitative studies until a more precise replacement is developed. A real advantage associated with equation 8 and especially equation 10 is that they can be easily inserted into mating, trapping, and/or communication disruption models with little addition to the complexity of the models. This should promote the development of simpler models describing the population dynamics associated with pheromone communication, and help to improve our understanding of the quantitative ecology of pheromone communication.

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