On the Transport of Nematodes by the Wind

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Abstract: The possible effectiveness of atmospheric transport of nematode forms (dry larvae or eggs) as a means for introducing new species to a given environment is examined. Given the measured sedimentation velocities for a range of forms ($0.1 \geqq W_s \geqq 0.6$ mps), the necessary conditions on the wind speed required for natural erosion are defined. With these results scenarios for lofting, transport, and diffusion of these forms are examined using relevant gaussian plume models. Results indicate that on rare occasions individuals can be deposited up to 40 km from their original location. Redepositions up to 5 km per erosion event should be fairly common occurances when dry loose soil conditions or dry tillage operations combine with optimal atmospheric conditions and the presence of significant numbers of nematodes at the surface. *Key words:* wind dissemination, terminal velocities, model calculations.

An important question regarding the population dynamics of nematodes is how species can be introduced into new environments. One mechanism which has received little attention, but which has long been suspected as a factor determining nematode distribution (2,3), is that of airborne transport. It has been established (7,11) that a wide range of soil-born nematodes, including plant parasitic forms, can tolerate dust dry conditions amendable to air transport. This paper reports an examination of processes that could lift individual larval or egg stage nematodes into the air and uses simple transport models to predict where such individuals are likely to be deposited. This work was conducted in three parts: determining the terminal velocity of various forms in still air, defining the natural and anthropogenic processes or events that would cause them to be carried aloft, and estimating their concentration as a function

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of distance downwind using the appropriate dispersion model and atmospheric conditions.

Two classes of processes can lift individuals from the soil surface into the air: natural aeolian erosion processes and mechanical lofting due to anthropogenic activities such as vehicular traffic and tillage operations. The first process requires that the wind speed near the ground be sufficiently strong that the wind stress on the surface particles exceeds a threshold value. When this stress is exceeded, the surface particles smaller than the critical size move downwind with a bouncing motion (saltation), rebounding into the air and dislodging other particles on impact. If the air flow is sufficiently turbulent, the fluctuating vertical component will exceed the terminal velocity of particles less than the critical size and a major fraction of the saltation particles will be carried upward.

The threshold saltation stress is usually expressed as the critical friction velocity (u_{*c}) and is dependent on the soil particle size, density, wetness, and adhesion properties (4,5). The actual stress (u_*) at any time depends on the wind speed, surface roughness, and hydrostatic stability of the air near the ground. The threshold friction velocity for various sized soil particles is shown in Table 1. For significant lofting of particles to occur, the actual stress must exceed the threshold value by at least a factor of two. The actual stress can be estimated using equation 1, given that the wind speed at a height z, the surface roughness, and the stability are known.

$$u_* = \frac{u(z) \cdot k}{\ln (z/z_0)} \phi \qquad (1)$$

where: k = a constant (0.4),
ϕ = stability correction (unity for neutral conditions),
z = height of the u measurement, and
z_0 = the roughness parameter.

The ratio of $u(z)/u_*$ for neutral conditions and surface textures of importance to this problem are shown in Table 2.

TERMINAL VELOCITIES

Since the erodibility of a particle depends on its terminal velocity, it was necessary to experimentally determine this velocity for various nematode forms. Terminal velocities for dry larval, egg, and cyst forms for a number of species were measured by timing their fall through the lower 2 m of a 3.5-m vertical plexiglas tube, 10 cm in diameter. The average fall time among 40 like forms was used to calculate the mean terminal velocity (W_s). In addition, the average weight for the individuals was determined by dividing the measured total sample weight by the number of individuals in the sample.

The terminal velocity determinations are summarized in Table 3. With the exception of the cysts, it can be seen that terminal velocities of 0.1, 0.3, and 0.6 m per second (mps) represent the range among forms, and these are the values used in the calculations reported below.

Comparing these terminal velocities with those fo soil particles listed in Table 1, it is clear that these nematode forms are more erodible than soil particles, that their threshold friction velocity is less than 0.15 mps, and natural lofting of these forms (if

Table 1. Threshold friction velocity versus equivalent size (diameter) of erodible soil particles and their terminal velocities (after Gillette et al., 1974).

u_{*c}	Equiv. diam. (cm)	Terminal velocity W_s (m/sec)
0.15	0.013	.74
0.30	.024	1.01
0.45	.031	1.15
0.60	.045	1.38
0.75	.060	1.60
0.90	.070	1.72

Table 2. Ratio of u (z) to u_* for neutral stability (from Eqn. 1).

z (m)	u (z)/u_*		
	z_0 = 0.5 cm	z_0 = 1 cm	z_0 = 2 cm
1	13.2	11.5	9.8
2	15.0	13.3	11.5
3	16.0	14.3	12.5
4	16.7	15.0	13.2
5	17.3	15.5	13.8

z_0 ~ 0.5 cm = snow or smooth fine grain soil.
z_0 ~ 1 cm = smooth soil.
z_0 ~ 2 cm = flat open country.

Table 3. Measured time for 2-m fall (T), terminal velocity (W_s), and weight (M) of one nematode larva, cyst, or egg mass. Averages of 40 trials.

Nematode	T (sec)	W_s (m/sec)	M (μg)
Pratylenchus vulnus	6.43	0.311	0.242
Ditylenchus destructor	6.19	0.323	1.67
Ditylenchus dipsaci (L_4)	6.25	0.320	1.39
Meloidogyne hapla (L_2)	18.84	0.106	0.152
Meloidogyne hapla egg mass	3.25	0.615	0.1203
Meloidogyne hapla single egg	3.40	0.588	0.0014
Heterodera schachtii cysts	1.88	1.06	23.81
Aphelenchus avenae	7.06	0.283	0.708
Cephalobus	7.00	0.286	1.70
P. silusiae	7.74	0.258	1.79
Xiphinema index	6.11	0.327	2.10
Criconemoides xenoplax	6.22	0.322	1.34

present at the surface) is possible with wind speeds (at z = 2m) greater than 3 mps.

TRANSPORT AND DISPERSION

Once carried aloft, the cloud of particles is carried on the mean wind while being diffused vertically and horizontally by the turbulent and eddying motion in the flow. Analytical models of the effect of this motion on the concentration of material in such clouds, as functions of distance downwind, source type, stability, and particle sedimentation velocity, have been developed and are routinely used in air quality studies (10). These gaussian plume models are based on a number of assumptions that are somewhat artificial and not always met in the real world. These include the constancy in time and space of the mean wind speed, mean wind direction and stability, constant source emission rates, no gain or loss of the emitted material during transport, and a gaussian distribution of the material concentration about the plume centerline in the vertical and transverse directions. While these assumptions are rather restrictive, these models can serve to provide order of magnitude estimates of concentrations downwind from different types of sources and for differing atmospheric conditions. Since our primary concern here is to determine how far downwind a finite probability exists that a sufficient number of nematode forms could be deposited and thereby develop a viable new colony, these models are judged to be a good compromise between accuracy and computational complexity.

Two forms of these models were used. The first is for an elevated point source (i.e., dust devil cases) for which the ground level concentration along the plume centerline is given by

$$c\,(x, H) = \frac{Q_o}{\pi\sigma_y\sigma_z\,u}\,\mathrm{EXP}\left[-\frac{1}{2}\left(\frac{H}{\sigma_z}\right)^2\right]$$

where: Q_o = the source strength [number of particles/unit time],
σ_y, σ_z are the diffusion parameters (functions of stability and distance downwind (x)),
$\bar{u}$ = mean wind speed [mps],
x = distance downwind [m],
H_0 = release height [m],
H = apparent release height of a plume with a finite sedimentation velocity (W_s), i.e.,
H = $H_0 - W_s x/\bar{u}$, and
EXP = exponential function; i.e., $\mathrm{EXP}\,(x) \equiv e^x$.

The second form of gaussian model used is for an infinite line source and is intended here to represent large scale wind erosion and anthropogenic sources. The ground-level, centerline concentration for such a line source is

$$c\,(x, H) = \frac{2q_o}{\sqrt{2\pi}\sigma_z u}\,\mathrm{EXP}\left[-\frac{1}{2}\left(\frac{H}{\sigma_z}\right)^2\right]$$

Here the source strength (q_o) is given in terms of particles released per unit time per unit length.

We emphasize that the concentrations predicted by these models are not of high accuracy; however, they are useful estimates of the relative transport and dispersion among cases or scenarios, and they do give useful order of magnitude estimates for each case. Of the restrictive assumptions used to derive these models, the one most inappropriate to this problem is that all emitted material must remain in the air. Obviously with finite terminal velocities, individuals will fall out during transport; therefore, predicted concentrations for the fixed site sources (dust devils and tillage cases) will be overestimates. Given the complexities of the problem, the degree of overprediction is not known, but is probably less than 50%

A second major artificiality is the presumption of a single release height. For the dust devil case this is realistic. For the others the natural event involves a vertical distribution of particles in the form of a vertical sheet rather than a horizontal line at a discrete height. Rather than attempt to simulate such a source, calculations were made with varying release heights to examine the vertical extremes to which particles are likely to be lifted in the prescribed conditions.

SOURCE SCENARIOS

As discussed above, aeolian erosion of soil and organic particles from the surface is likely if the wind speed near the ground exceeds 3 mps. Wind speeds of this magnitude occur over large regions in the presence of strong large-scale pressure gradients; they also occur locally in convective vortices such as dust devils. The regional strong-wind case is characterized by simultaneous erosion over large areas (assuming dry loose material is present at the surface). For modeling purposes we consider the release height in these situations to increase with wind speed and treat these cases as line sources rather than area sources, since we wish to consider how far the material lofted from a particular location can travel. With the strong winds, near neutral stability is required for each case.

The dust devil mechanism is most likely to be significant with light mean winds ($1.5 \leq \bar{u} \leq 3.5$ mps) during periods of strong isolation over dry bare soil (1,8). These vorticies typically have tangential speeds near the ground of 3–10 mps and vertical speeds of 0.6–2 mps, with the updrafts reaching heights in excess of 100–1,000 meters, respectively (9). Given the occurrence criteria, these cases are modeled using the most unstable category.

The anthropogenic sources are treated in a fashion similar to the large-scale strong-wind cases, except that lofting no longer requires strong winds. All cases are considered to be daytime events, as the frequency of relevant human activity is minimal at night. Therefore only unstable through neutral stability (classes 1 through 4) categories are considered.

A summary of the prescribed run conditions and of the most relevant model predictions is contained in Table 4. Cases 1 through 3 are the dust devil simulations, 4 through 6 the regional scale wind erosion cases, and 7 through 16 the tillage sources. For winds greater than 11 mps it is irrelevant whether natural or anthropogenic activity is the cause of lofting. Three particle types are used as defined by their terminal velocities. The source strength is 10^6 particles per second for the point sources and 10^6 particles per meter per second for the line sources.

DISCUSSION

The results of the model calculations are apparent from examination of Table 4. We reemphasize that these calculations are approximate and based on highly idealized conditions. Therefore, the predicted concentrations should be interpreted as the relative probability (per million particles lifted) that nematodes would reach the ground at that point. The greater this probability, the more nematodes are likely to be deposited there. The plume centerline ground impaction point (X_g) should be conservatively interpreted as the maximum distance at which there is a finite probability of any particles reaching the ground. Noting these criteria, the model predictions are summarized as follows:

In general, the ground level concentrations at a point X downwind decrease with decreasing stability, increasing wind speed, and increasing release height. The max-

Table 4. Summary of gaussian plume model conditions and predictions. ($Q_o = q_o = 10^6$)

#	ū	H_o	Stab. class	$W_s = 0.1$				$W_s = 0.3$				$W_s = 0.6$			
				X_{MX}	C_{MX}	$C_{2/4}$	X_g	X_{MX}	C_{MX}	$C_{2/4}$	X_g	X_{MX}	C_{MX}	$C_{2/4}$	X_g
1	2	300	1	700	2.2	0.2	6.0	640	3.2	2.1	2.0	560	5.5	(0.2)	1.0
2	3	600	1	1000	0.5	0.1	18.0	960	0.6	0.1	6.0	900	0.8	0.1	3.0
3	4	1000	1	1300	0.2	0.1	40.0	1260	0.2	0.1	13.3	1220	0.2	0.1	6.7
4a	10	10	3	120	5500	(378)	1.0	120	6930	(333)	.33	100	9240	(209)	.17
4b	10	10	4	220	6020	(971)	—	160	8570	(373)	—	120	12690	(11)	—
5a	15	30	3	440	1190	254	4.5	400	1420	(248)	1.5	340	381	(190)	0.75
5b	15	30	4	900	1320	678	—	700	1800	(565)	—	520	640	(507)	—
6a	20	100	3	1680	264	178	20.0	1540	309	188	6.7	1360	28240	(64)	3.3
6b	20	100	4	3980	301	301	—	3860	456	456	—	2560	40820	(50)	—
7a	2	5	1	80	22900	(66)	0.1	60	27700	(66)	0.03	40	19900	(64)	0.02
7b	2	5	2	40	76900	(748)	—	20	120000	(393)	—	20	189000	(44)	—
8a	2	10	1	80	27100	(66)	0.2	80	29700	(65)	0.07	60	24400	(64)	0.03
8b	2	10	2	80	38100	(750)	—	60	67900	(400)	—	40	91500	(45)	—
9a	2	30	1	180	11440	66	6.0	140	19810	(65)	0.2	100	28240	(64)	0.1
9b	2	30	2	240	12600	762	—	160	23540	(418)	—	100	40820	(50)	—
10a	4	5	2	40	30200	(397)	0.2	40	45800	(338)	0.07	20	59900	(200)	0.04
10b	4	5	3	60	32500	(862)	—	40	52400	(355)	—	40	61400	(17)	—
11a	4	10	2	100	15200	(397)	0.4	80	22500	(340)	0.13	60	34000	(200)	0.07
11b	4	10	3	120	16500	(871)	—	80	26500	(370)	—	60	42400	(18)	—
12a	4	30	2	260	5110	(400)	1.2	200	7570	(348)	0.4	160	11770	(209)	0.2
12b	4	30	3	380	5670	(904)	—	260	9330	(418)	—	160	15050	(24)	—
13a	7	10	3	120	8310	(532)	0.7	100	11400	(406)	0.2	80	16500	(155)	0.1
13b	7	10	4	200	9370	(1239)	—	140	14700	(162)	—	100	23300	(0)	—
14a	7	30	3	420	2820	(541)	2.1	320	3960	(435)	0.7	240	5800	(180)	0.4
14b	7	30	4	780	3416	(1410)	—	500	5620	(272)	—	300	8830	353	—
15a	11	10	3	120	4940	(344)	1.1	120	6130	311	0.4	100	8060	(212)	0.2
15b	11	10	4	220	5370	(898)	—	180	7450	412	—	120	10800	(23)	—
16a	11	30	3	420	1680	(347)	3.3	380	2120	(324)	1.1	300	2830	(233)	0.6
16b	11	30	4	860	1920	(950)	—	620	2820	(560)	—	420	4140	(46)	—

Legend :

W_g = terminal velocity.
= model run number.
$\bar{u}$ = mean wind speed for model run (mps).
H_o = prescribed release height (meters) at source location ($x = 0$).
Class = atmospheric stability class (1 = most unstable, 4 = neutral).
X_{MX} = distance from source (meters) at which the maximum ground level concentration occurs.
C_{MX} = value of maximum ground level concentration (at X max) [particles/m^3].
$C_{2/4}$ = ground level concentration at 2 km down wind for point sources (1 to 3) or at 4 km down wind for line sources (4 to 16)—values in parenteses are unlikely as $X_g < 2$ or 4 km.

X_g = distance from source (km) at which the plume centerline reaches the ground ($X_g = \frac{\bar{u}H_o}{W_g}$).

imum transport distance (X_g) increases with increasing wind speed, and release height and decreasing sedimentation velocity. Note that throughout this discussion we only examine single events, not multiple deposition and re-erosion that is especially likely in the regional erosion cases.

More specifically, considering the larval stages only ($0.1 \leq W_s \leq 0.3$), the effect of dust devil events would be to redeposit a significant number of individuals within 0.5–1.5 km from a given vortex. There is also a finite probability that individuals could be deposited at 13–40 km downwind, depending on ambient conditions. The single-event regional scale-erosion cases are less effective in accomplishing a large-scale spread of forms, since most fall out within 0.2 km of the source for the 10 mps (22 MPH) cases. The relatively rare events of $\bar{u} \geq 15$ mps (33 MPH) would be more effective in depositing a large fraction of the lofted particles within 2–4 km of the source, with deposition up to 20 km possible.

The egg stages ($W_s = 0.6$) are generally less transportable because of their higher W_s. This means that most eggs would not likely travel more than 1 km in the convective vortex case or 0.2 km in the area erosion case. Maximum transports are probably less than 7 km for the former conditions and less than 3 km for the latter.

Similar results can be seen for the anthropogenic simulations, except that a wide range of effects is seen due to the greater range of prescribed conditions. These results indicate that larval forms lofted by tillage operations could be transported up to 3 km for the smallest forms and to 1 km for the larger ones. Eggs are not likely to travel more than 0.6 km per event.

In conclusion, this investigation indicates that if dry larvae or eggs are present at a surface of bare soil, lofting of these forms into the air is very likely as the result of a number of natural events and anthropogenic activities. Once injected into the air, a large fraction of these will be deposited on the surface within 4 km of the source. On rare occasions a few individuals could be transported up to 40 km away. In the event of regional scale natural erosion, the same conditions will prevail over many hundreds of square kilometers for periods of several hours to a day. Therefore, multiple lofting, transport, and redeposition is probable, implying that individual travel distances can be multiples of the single event transport distances considered explicitly here.

While these results depend on a highly simplified model, it is clear that if nematode forms are present at, or brought to, the surface, they can be carried on the wind to points up to tens of kilometers away. The necessary conditions to effect this range may be rare, but there is a finite occurrence probability for most locations. Since only one occurrence of erosion and deposition of a viable number of individuals may be necessary to establish a new colony, the frequency of such events is not the crucial concern. The fact that such events are possible at all can account for the spread of specific forms among locations when viewed over time scales of seasons or years. These findings are consistant with observations of generally low background ambient airborne nematode concentrations during light wind conditions (11), while also supporting the hypothesis for wind dissemination of *Heterodera avenae* in Australia (6) and of *H. rostochiensis* in New York (2).

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