SPATIAL DISTRIBUTION OF THE NEMATODE COMMUNITY ON PERRINE MARL SOILS¹

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ABSTRACT

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Taylor's power law was used to investigate patterns in the spatial distribution of plant-parasitic and free-living nematodes in fallow Perrine marl soil used mainly for potato production in southern Florida. Highly significant (P=0.01) linear regression equations relating logarithms of means and variances were developed for populations of most nematode genera examined. Fits to regression lines were slightly better for genera having only one species represented in the study sites than for genera represented by several species. Estimates of the parameter b of Taylor's power law, an index of aggregation, ranged from 0.66 (dispersed) to 2.12 (aggregated) for the cases studied, with most estimates ranging from about 1.10 to 1.80. For each genus, there was relative consistency in the magnitude of b, regardless of plot size. Examples of strongly aggregated and weakly aggregated genera could be found among both plant-parasitic and free-living nematodes, with little relationship to feeding habits. The parameter a from Taylor's power law, a sampling coefficient, showed general increases as plot size was increased from 0.2 to 1.2 ha.

Additional key words: free-living nematodes, sampling, Taylor's power law, plot size, aggregation, nematode ecology.

RESUMEN

McSorley, R., W. H. Dankers, J. L. Parrado, y J. S. Reynolds. 1985. Distribución espacial de las comunidades de nematodos en los suelos Perrine marl. Nematropica 15:77-92.

La ley de fuerza de Taylor fué usada para investigar los modelos de distribución espacial de los nematodos parasiticos y de vida libre en suelos Perrine marl, en barbecho limpio, usados principalmente en cultivos de papa en el sur de la Florida. Se desarrollaron ecuaciones de regresión linear altamente significativas (P=0.01) relacionando los logaritmos de los promedios y las varianzas de las poblaciones de la mayoria de los géneros examinados. Los géneros con sola una especie representada en los lotes experimentales se ajustaron mejor a las ecuaciones de regresión que aquellos representados por varias especies. Los estimados del parámetro b de la ley de fuerza de Taylor, que representan un indice de agregación, variaron de 0.66 (dispersión) a 2.12 (agregación) para los casos estudiados, con la mayoria de los estimados variando desde 1.10 a 1.80. Para cada género hubo una estabilidad relativa en la magnitud de b independientemente del tamaño del lote. Ejemplos de géneros con agregaciones fuerte y debil pueden encontrarse tanto entre los nematodos parasiticos como entre los de vida libre siendo muy baja su relación con los

habitos de alimentación. El parámetro a de la ley de fuerza de Taylor, un coeficiente de muestreo, mostró un aumento general a medida que aumentó el tamaño del lote de 0.2 a 1.2 ha.

Palabras claves adicionales: nematodos de vuda libre, muestreo, ley de fuerza de Taylor, tamaño del lote, agregación, ecologia de los nematodos.

INTRODUCTION

Interest in the spatial distribution and sampling of plant-parasitic nematodes has increased in recent years. Several recent studies have found that the spatial distributions of many plant-parasitic species could be described by the negative binomial distribution (1,5,11,13,21). Knowledge of the spatial distribution can then be used to develop sampling plants for specific situations by using equations derived from negative binomial models (9,11) or by simulation from the data base even if the model is not negative binomial (6).

Little information exists, however, on the spatial distribution and sampling of free-living nematodes, which may form a substantial portion of the nematode community of most agroecosystems. The present study was designed to investigate the spatial distribution of free-living nematodes and to compare it with that of the more familiar pant-parasitic species. Perrine marl soils (4) were sampled for this study, since spatial distribution and sampling studies on this soil type are nonexistent. These soils are important in southeastern Florida for potato production, and with the recent loss of ethylene dibromide (EDB) as a soil fumigant, growers need information on nematode densities based on sound sampling procedures in order to make sound management decisions about the need for expensive alternatives to EDB.

The study was designed to facilitate use of Taylor's power law (18), which relates the mean (\bar{x}) and variance (s^2) of a series of samples:

$$s^2 = a\bar{x}^b$$
 or $\log s^2 = \log a + b \log \bar{x}$,

where a and b are constants. The power law is similar in form to Smith's (15) formula for plot heterogeneity. The parameter b is an index of dispersion characteristic of the species and a is a parameter related to sample size (2,17). Although useful in determining transformations (13,14), Taylor's power law can also be used to develop sampling plans (3). In sampling studies, there are several advantages to using Taylor's power law rather than approaches based on the negative binomial distribution (3). In the first place, Taylor's power law does not require a mathematical fit to a specific statistical distribution, a major consideration here since erratic spatial patterns, which may not fit standard statistical models, were anticipated for some free-living nematode genera,

such as *Rhabditis*. Secondly, the parameter b of Taylor's power law is also a convenient index of aggregation (17,20) which can facilitate comparisons among species.

MATERIALS AND METHODS

Three fallow fields, all located on Perrine marl soils (4) east of Homestead, Florida, were sampled during Oct.-Nov. 1984 for this study. During the previous summer, two had been planted to field corn (Zea mays L.) and one to malanga (Xanthosoma caracu Koch et Bouche). A 2.4-ha portion of each field was selected for sampling and subdivided into six 0.4-ha plots, from which 12 cores of soil were removed in a systematic pattern. The individual cores were collected to a depth of 15.2 cm with a cylindrical sampling tube 2.0 cm in diameter (12). Thus, an individual core had a volume of 48 cm³. Cores were extracted and counted individually. Nematodes were extracted by a modified sieving and centrifugation technique (7,10). The extracted nematodes were counted at 100X on a dissecting microscope with capacity to increase magnification to 140X when necessary. Specimens difficult to identify at that magnification were transferred to a compound microscope at 400X. The equivalent of 1/5 of each core was counted, corresponding to 9.6 cm³; all data analysis was performed on the actual, untransformed counts.

For each nematode, means $(\bar{\mathbf{x}})$ and variances (\mathbf{s}^2) were computed over the 12 cores from each of the six 0.4-ha plots in each of the three fields (18 plots total). The relationship between the base 10 logarithms of both the means and the variances for the 18 points was determined by linear regression for comparison with Taylor's power law (2,17), and the parameters a and b determined from the equation $\mathbf{s}^2 = a\bar{\mathbf{x}}^b$. In this approach, data can be pooled over several fields (17), insuring a wide range in the counts of most nematode species sampled.

Because of the systematic sampling pattern used, the data base could be viewed not only as 18 0.4-ha plots of 12 cores each, but also as 36 0.2-ha plots of 6 cores each, or as 9 0.8-ha plots of 24 cores each, or as 6 1.2-ha plots of 36 cores each. Data were reanalyzed for each of these scenarios to determine fits to Taylor's power law for different sampling schemes and field sizes.

RESULTS AND DISCUSSION

The most common nematodes found in the study and their percentages of the total nematode community were: *Rhabditis* spp. (29.2%), *Criconemella onoensis* (Luc) Luc & Raski (16.7%), *Quinisulcius acutus* (Allen) Siddiqi (11.5%), *Aphelenchoides* spp. (10.3%), *Helicotylenchus dihyst-*

era (Cobb) Sher (8.9%), Acrobeloides spp. (6.2%). Tylenchus spp. (5.7%), Aphelenchus spp. (3.4%), Psilenchus hilarulus deMan (2.0%), Panagrolaimus sp. (1.2%), Cephalobus spp. (0.7%), Rotylenchulus reniformis Linford & Oliveira (0.7%), Meloidogyne incognita (Kofoid & White) Chitwood (0.6%), Eucephalobus spp. (0.5%), Diphtherophora sp. (0.5%), and Alaimus spp. (0.4%). Also present were several other genera, accounting for only 1.4% of all nematodes found; but none of these genera individually accounted for more than 0.3% of the total nematode community. Data analysis was not attempted for these rare genera. Microarthropods were also extracted regularly, including Collembola, Protura, and various mites. Only oribatid mites were found frequently enough to attempt reasonable data analysis.

Graphical relationships between mean and variance are depicted for 6 selected nematodes in 0.4-ha plots in Figs. 1-3. Each example data set shows a highly significant (P = 0.01) fit to the regression line defining Taylor's power law. Coefficients of determination (r²) appeared to be greater when data represented only one species within a genus (Figs. 1-2) than when the counts likely included more than one species (Fig. 3). The free-living nematode *Psilenchus hilarulus* fits Taylor's power law about as well as the plant-parasitic species. Coefficients of determination and power law coefficients are summarized for various plot sizes (Tables 1-2). Both plant-parasitic and free-living nematodes showed excellent fits to this relationship. As expected, lack of fit occurred most in the 1.2-ha plots since degrees of freedom were low in this case (only 6 plots).

The ranges in means and variances are also given for each case, since any conclusions from Taylor's power law must be restricted to the range of densities over which it is developed. Rare species, besides being restricted to limited ranges, may have the additional problem of showing deviation from true contagion and revealing pseudorandom behavior at low densities (20). Such tendencies are suggested by the data for the relatively rare Eucephalobus spp. (Fig. 4). The low intercept and slope value near 1.0 suggest random distribution and a close approximation to the y = x line.

Most species show slopes (represented by b of Taylor's power law) above 1.0, suggesting contagious distribution (2). The parameter b is considered to be an index of aggregation (or dispersion) characteristic of the species (2,17). The present data show that estimates of b did not vary much with field size, but encompassed a relatively narrow range for most genera sampled (Table 3). The genera in Table 3 are listed roughly in order of their degree of aggregation, with values of b near 1.0 suggesting randomness, while nematodes such as b0. b1. b2. b3. b4. b4. b5. b5. b6. b8. b8. b9. b

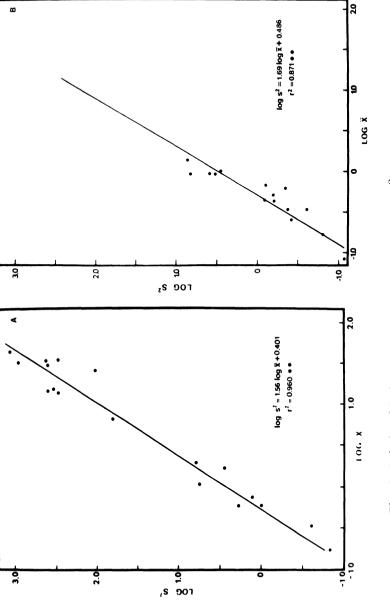
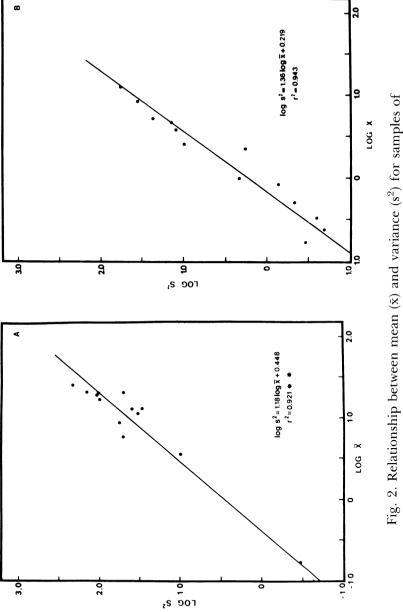


Fig. 1. Relationship between mean (x̄) and variance (s²) for samples of 12 cores each, collected in 0.4-ha plots. A. Criconemella onoensis. B. Meloidogyne incognita.



12 cores each, collected from 0.4-ha plots. A. Quinisulcius acutus. B. Psilenchus hilarulus.

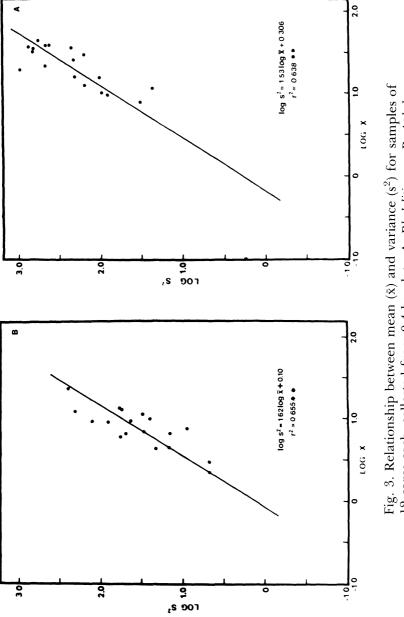


Fig. 3. Relationship between mean $(\bar{\mathbf{x}})$ and variance (s^2) for samples of 12 cores each, collected from 0.4-ha plots. A. Rhabditis spp. B. Aphelenchoides spp.

Table 1. Taylor's power law regression equations for data from 0.2 and 0.4 ha plots.

			0.2-ha plots²	plots²					0.4-ha plots ^z	plots²		
			Power law coefficients	r law zients	Effecti	Effective range			Power law coefficients	r law cients	Effectiv	effective range
Soil organism	п	\mathbf{r}^2	a	q	×	S ₂	u	Γ^2	a	q	×	S ₂
Acrobeloides spp.	36	0.475**	0.71	1.75	1.8-11		18	0.739**	1.25	1.59	1.8-8.9	2.4-51
Alaimus spp.	24	0.675**	1.68	1.24	0-1.5		12	0.748**	1.90	1.47	0 - 1.2	0-5.2
Aphelenchoides spp	36	0.672**	0.62	1.83	1.7-24	0.7-427	18	0.655**	1.26	1.62	2.2-23	4.7-245
Aphelenchus spp.	36	0.394**	2.33	99.0	0.2-8.8	_	18	0.676**	1.67	1.26	0.5 - 6.3	0.6 - 123
Cephalobus spp.	33	0.753**	1.24	1.13	0-1.7	_	18	0.852**	1.32	1.06	0.1 - 1.4	0.1-2.3
Criconemella onoensis	36	0.932**	2.12	1.51	0.2-60		18	**096.0	2.52	1.56	0.2-44	0.2 - 1148
Diphtherophora sp.	15	0.830**	1.78	1.42	0-2.5	_	6	0.880**	2.14	1.51	0.1 - 1.9	0.1-7.7
Eucephalobus spp.	27	0.555**	1.00	0.94	0-1.5		15	0.774**	1.12	1.06	0-1.4	0-1.9
Helicotylenchus dihystera	25	0.837**	1.66	1.43	0-25		13	0.879	2.54	1.33	0-50	0-174
Meloidogyne incognita	31	0.867**	2.37	1.66	0-2.5	_	18	0.871**	3.06	1.69	0.1 - 1.3	0.1 - 7.3
Oribatid mites	30	0.819**	1.49	1.46	0-3.7	_	16	0.865**	2.00	1.47	0-2.3	0-26
Panagrolaimus spp.	31	**962.0	1.13	1.13	0.4.0	_	17	0.838**	1.31	1.17	0-3.2	0-3.5
Psilenchus hilarulus	25	0.912**	1.42	1.42	0-8.7		14	0.943**	1.66	1.36	0-8.5	0-36
Quinisulcius acutus	25	0.805**	2.21	1.21	0-30	_	13	0.921**	2.80	1.18	0-56	0-214
Rhabditis spp.	36	0.640**	1.02	1.69	5.8-50		18	0.638**	2.02	1.53	8.0-45	23-955
Rotylenchulus reniformis	19	0.964**	2.08	1.52	0-4.8		11	0.961**	2.48	1.56	0-4.4	0-31
Tylenchus spp.	36	0.777**	1.18	1.40	0.2 - 16	0.2 - 174	18	0.819**	1.25	1.50	0.6-11	86-9.0

²n = number of nonzero points; only nonzero points used in determining regression equations. r² = coefficient of determination for fit to equation $\log s^2 = \log a + b \log x$ where $\bar{x} = \text{mean}$, $s^2 = \text{variance}$. Effective range = range of \bar{x} and s^2 data. Asterisks (*, **) indicate significance at P = 0.05 and P = 0.01, respectively.

Table 2. Taylor's power law regression equations for data from 0.8 and 1.2 ha plots.

			0.8-ha	0.8-ha plots²					1.2-h	1.2-ha plots ^{z}		
			Powe	Power law coefficients	Effectiv	Effective range			Powe	Power law coefficients	Effectiv	Effective range
Soil organism	и	\mathbf{r}^2	a	9	×	s ²	п	\mathbf{r}^2	a	9	×	s ₂
Acrobeloides spp.	6	0.410n.s.			3.1-8.1	8.7-36	9	0.510n.s.			3.2-7.8	7.8-30
Alaimus spp.	7	*289.0	2.25	1.36	8.0-0	0-2.7	ಸರ	0.588n.s.	١		8.0-0	0-1.8
Aphelenchoides spp.	6	0.869**	1.07	1.75	2.6-17	4.4-170	9	0.442n.s.			4.9-15	28-141
Aphelenchus spp.	6	0.825**	1.77	1.14	0.6 - 6.1	1.3-36	9	0.855**	1.69	1.22	0.7-5.6	1.1-26
Cephalobus spp.	6	**098.0	1.28	0.99	0.2-1.0	0.3 - 1.6	9	0.841**	1.27	0.93	0.2 - 1.1	0.3 - 1.3
Criconemella onoensis	6	0.978**	2.62	1.60	0.2-35	0.2-692	9	0.956**	4.45	1.48	0.4-35	0.8-589
Dıphtherophora sp.	70	**026.0	2.84	1.40	0-4.1	0-1.4	4	0.984**	2.68	1.34	0-1.2	0-4.9
Eucephalobus spp.	œ	0.918**	1.26	1.10	0-1.1	0-1.4	5	0.845**	1.37	1.21	6.0-0	0-1.32
Helicotylenchus dihystera	7	0.982**	3.04	1.34	0-18	0-114	5	0.973**	4.09	1.32	0-17	0-109
Meloidogyne incognita	6	0.912**	4.05	1.94	0.2 - 1.1	0.3-2.2	9	**668.0	4.77	2.12	0.2 - 0.8	0.3-4.7
Oribatid mites	6	0.952**	2.40	1.37	0.0-2.1	0.0 - 1.4	9	0.951**	2.54	1.45	0.1-2.0	0.1-10
Panagrolaimus spp.	6	0.917**	1.45	1.15	0.2-5.4	0.2-5.9	9	0.326n.s.	,	•	0.2 - 1.9	0.3-4.7
Psilenchus hilarulus	œ	0.962**	2.00	1.27	9.9-0	0-28	5	**096.0	2.10	1.33	0-5.2	0-25
Quinisulcius acutus	7	**4296.0	3.34	1.18	0-50	0-170	32	0.992**	3.47	1.18	0-50	0-129
Rhabditis spp.	6	0.673**	2.98	1.42	9.0-42	56-640	9	0.628n.s.	1	1	10-40	50-497
Rotylenchulus reniformis	9	0.819**	1.74	1.29	0-3.1	0-21	κ	0.971**	3.38	1.38	0-2.1	0-16
Tylenchus spp.	6	**908.0	1.85	1.45	1.0-7.6	18-60	9	0.891**	2.90	1.26	1.5-7.2	5.1-43

²n = number of nonzero points; only nonzero points used in determining regression equations. r² = coefficient of deterrmination for fit to equation $\log s^2 = a + b \log \bar{x}$, where $\bar{x} = mean$, $s^2 = variance$. Effective range = range of \bar{x} and s^2 data. Asterisks (*, **) indicate significance at P = 0.05 and P = 0.01, respectively; n.s. = no significant regression.

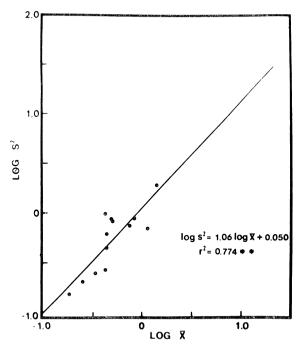


Fig. 4. Relationship between mean (\bar{x}) and variance (s^2) of *Eucephalobus* spp. for samples of 12 cores each, collected from 0.4-ha plots.

trophic preference of the nematode, since parasites of higher plants, fungal feeders, and bacterial feeders are represented among those genera having both high and low degrees of aggregation (Table 3). Thus the spatial distribution of free-living nematodes appears to be similar to that of plant-parasites, suggesting that they can be sampled in similar ways.

The parameter a does not show consistency with species, but may vary widely depending on sampling method (19). Thus when the same data base is examined using plots of differing size, differences in a are anticipated. A general trend of increase in the magnitude of a is observed as plot size increases from 0.2 to 1.2 ha for several of the general examined here (Fig. 5).

Taylor's power law can be readily applied to the development of sampling plans (3). Before sampling plans can be optimized, the reliability must be assessed through some measure of relative error. The definition of relative error or reliability is arbitrary (8), and both the standard error to mean ratio (E) and the ratio of the half-width of the confi-

Table 3. Ranges in the magnitude of the parameter b from Taylor's power law for selected nematodes.

		,	Value of p	arameter b ^z	
		Plot si	ze (ha)		
Nematode	0.2	0.4	0.8	1.2	Range
Aphelenchus spp.	0.66	1.26	1.14	1.22	0.66-1.26
Cephalobus spp.	1.13	1.06	0.99	0.93	0.93-1.13
Eucephalobus spp.	0.94	1.06	1.10	1.21	0.94-1.21
Panagrolaimus spp.	1.13	1.17	1.15	_	1.13-1.17
Quinisulcius acutus	1.21	1.18	1.18	1.18	1.18-1.21
Alaimus spp.	1.24	1.47	1.36		1.24-1.47
Tylenchus spp.	1.40	1.50	1.45	1.26	1.26-1.50
Psilenchus hilarulus	1.42	1.36	1.27	1.33	1.27 - 1.42
Rotylenchulus reniformis	1.52	1.56	1.29	1.38	1.29 - 1.56
Helicotylenchus dihystera	1.43	1.33	1.34	1.32	1.32-1.43
Diphtherophora sp.	1.42	1.51	1.40	1.34	1.34-1.51
Rhabditis spp.	1.69	1.53	1.42	_	1.42-1.69
Criconemella onoensis	1.51	1.56	1.60	1.48	1.48-1.60
Acrobeloides spp.	1.75	1.59	-	_	1.59-1.75
Aphelenchoides spp.	1.83	1.62	1.75	_	1.62-1.83
Meloidogyne incognita	1.66	1.69	1.94	2.12	1.66-2.12

²Values from fitted regression equations; nonsignificant regressions indicated by dashes.

dence interval to the mean (D) have been used in nematology (3,11). The notation is that of Southwood (17), but the interpretation of these indices has caused considerable confusion in the literature (8), and so a practical comparison is offered (Table 4). The two indices are interrelated, with D = tE, where t depends on the number of samples (16), but usually approximates to 2 for 95% confidence intervals and more than 10 samples (17).

In the context of this paper, where a "sample" is represented by a single core, the number of cores needed to achieve a given level of reliability are given by:

$$n = \left(\frac{s}{E\bar{x}}\right)^2 \text{ or } \hat{n} = \left(\frac{ts}{D\bar{x}}\right)^2$$

where n and ń are the number of cores required, depending on the index used to define reliability (17). Since by Taylor's power law, $s^2 = a\bar{x}^b$, the variance term can be substituted into either of the above formulae, yielding in the case of the second formula (3):

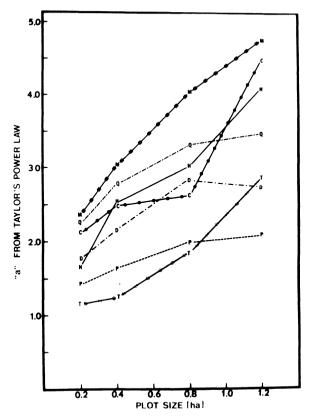


Fig. 5. Relationship between parameter a of Taylor's power law and plot size for selected nematodes. C = Criconemella onoensis; D = Diphtherophora sp.; H = Helicotylenchus dihystera; M = Meloidogyne incognita; P = Psilenchus hilarulus; Q = Quinisulcius acutus; P = Tylenchus spp.

$$\acute{n} = \left(\frac{t}{D}\right)^2 a \ddot{x}^{(b\text{-}2)}$$

Thus the number of cores needed to achieve a given level of reliability can be readily calculated once the parameters of Taylor's power law are known. Example results for several species of nematodes exhibiting a range in the parameters a and b are shown (Table 5). For example, 45 cores per 0.4 ha plot would be required to sample a Q. acutus density of $10/100 \text{cm}^3$ soil with a standard error to mean ratio of 25%. Note that there is a fourfold difference (assuming $t\approx 2$) in the number of cores required, depending on the index of reliability chosen. This is expected,

		d error to mean $E(E) = 25\%$		th of confidence al (D) = 25%
Nematode	Standard	95% confidence	Standard	95% confidence
count	error	interval	error	interval
10	2.5	5-15	1.25	7.5-12.5
100	25	50-150	12.5	75-125
1000	250	500-1500	125	750-1250

Table 4. Comparison of indices of reliability for three example nematode counts².

due to the more rigorous definition of D compared to E. In general, more cores are required to sample larger plots, based on the increase of parameter a observed with field size. A value of the parameter b above 2.0 represents a particularly difficult and aberrant case (Table 5), but fortunately most values observed for this parameter for nematodes seem to be in the range 1.0 to 2.0 (3,13, Table 3). Of the examples given, moderate densities (50-100/100cm³ soil) of less aggregated species could be sampled with a relatively convenient number of cores, but in sampling more aggregated species such as M. incognita or Aphelenchoides spp., multiple samples, each of multiple cores, should be considered (6,9).

Taylor's power law provides a convenient alternative to development of sampling plans based on the negative binomial distribution (11) or simulation studies (6,9). Both of the latter approaches require specific computer programs (if an iterative procedure is used for finding the negative binomial k), but only a linear regression program and computational programs for means and variances are required to apply the power law, and the latter are usually more widely available. Taylor's power law is independent of any spatial distribution and so fit to a negative binomial distribution is not a prerequisite for its use. Several studies pointing out that nematode spatial distribution often fits a negative binomial model (5,11,21) also acknowledge that in some cases the model failed to apply or that a different statistical distribution applied. Taylor's power law can deal with even these "non-fit" situations as well

²Assuming t \approx 2 for 95% confidence interval; thus, half-width \approx 2 standard errors, or D \approx 2E. Note that for similar levels of reliability (25%), definition of reliability in terms of D implies a 0.05 chance of missing the true mean by more than 25%, while definition in terms of E implies a 0.32 chance of missing the true mean by more than 25%.

Table 5. Number of cores needed to achieve a 25% level of reliability as defined in terms of standard error to mean ratio (E) or confidence interval half-width to mean ratio (D)

		Co		number of vel of reliability	λ
Mean count	Mean count	0.4-ha	plots	1.2-ha	plots
per sample ^y	per 100cm ³	D	E	D	E
 Quinisulcius acı	ıtus				
0.1	1.0	1184	296	1468	367
1.0	10	180	45	222	56
5.0	52	48	12	60	15
10.0	104	28	7	34	9
Taylor's powei Psilenchus hilar	· law parameters: ulus	a = 2.80,	b = 1.18	a = 3.47,	b = 1.18
0.1	1.0	464	116	629	158
1.0	10	107	27	135	34
5.0	52	38	10	46	12
10.0	104	25	7	29	8
Taylor's power	· law parameters:	a = 1.66, t	$\rho = 1.36$	a = 2.10,	b = 1.33
Criconemella on	oensis				
0.1	1.0	445	111	944	236
1.0	10	162	41	285	72
5.0	52	80	20	124	31
10.0	104	59	15	86	22
Taylor's power	law parameters:	a = 2.52,	b = 1.56	a = 4.45,	b = 1.48
Meloidogyne ınd	ognita				
0.1	1.0	400	100	232	58
1.0	10	196	49	306	77
5.0	52	119	30	371	93
10.0	104	96	24	402	101
Taylor's power	r law parameters:	a = 3.06.	b = 1.69	a = 4.77.	b = 2.12

^zAssume $t \approx 2$ for 95% confidence interval.

as cases in which the spatial distribution of the species changes with density (20). The power law applies across all densities, while this is not necessarily true with conclusions based on the negative binomial, since k may change with density, and often does (20). Only when k does not change with density, can a common k value be found (2), allowing an extension of specific sampling formulae to more general cases (11). Ferris (3) has pointed out the difficulties with the rather specific data required to implement the negative-binomial-based approach to developing sampling plans. Use of Taylor's power law requires knowledge of

^yBased on a sample size of 9.6cm³.

^{*}All fractional values rounded up to nearest integer.

only two parameters, one related to the species (b) and the other related to the methodology (a). If fairly consistent values of b can be found, then perhaps a detailed knowledge of the variation in the parameter a with sampling pattern, location, etc. can lead to the development of more generalized sampling plans.

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