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# Stability and Characteristics of Spatial Description Parameters for Nematode Populations[1]

H. Ferris,[2] T. A. Mullens,[3] and K. E. Foord[4]

*Abstract:* The parameters of Taylor's Power Law ($s^2 = am^b$) relating variance ($s^2$) to mean population level ($m$) were acceptably stable in different fields with similar cropping systems. Values of both $a$ and $b$ parameters varied with nematode species. The value of $a$ was a function of sample size (number of cores) and was characterized for each species. The value of $b$ was stable across sample size and reflective of the life history strategy of the species. The relationship between the economic threshold and sampling intensity required to allow management decisions, with specified levels of risk, indicated the need for improved sampling technology.

*Key words:* economic threshold, management decision, precision, risk, Taylor's Power Law.

The spatial pattern of plant-parasitic nematode populations in an agricultural or natural ecosystem has both macro-distributional and micro-distributional components. Macro-distribution within the system is mediated by such factors as the length of time the population has been present in the system; variations in habitat suitability factors such as soil texture, soil moisture, and drainage patterns; and the selection pressures of differential host plant distributions or differential cropping history. The micro-distributional attributes of a nematode population are strongly linked to the population's life history and feeding strategies. Sedentary endoparasitic nematodes deposit all of their eggs in the same location, frequently in masses, resulting in a highly aggregated spatial pattern. Ectoparasitic nematodes invest a proportion of assimilated energy into movement and selection of feeding sites, presumably reducing the amount available for reproduction. Further, since eggs are deposited individually as ectoparasites move through the soil, a somewhat less aggregated pattern results. Nematode micro-distribution, however, is primarily mediated by the distribution of food sources; for plant-parasitic nematodes, spacing and morphology of the plant root system are primary determinants. The integral effect of biological and edaphic influences results in varying degrees of aggregation in the spatial pattern of nematode populations.

Aggregated population distributions usually can be described by the negative binomial model (2,8,15,18). The negative binomial model describes populations where the variance is greater than the mean. The mean and variance are estimated by the sample statistics $m$ and $s^2$, and the parameter $k$ by $k = m^2/(s^2 - m)$. In this model, $k$ may be defined as an index of dispersion; since it is a function of population mean and variance, it is a biologically descriptive parameter in that its magnitude is influenced by organism biology and ecology. As a function of the population mean, the magnitude of $k$ varies through time. This renders it difficult to use as a basis for determining required sampling intensity to

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[1] Field aspects of this research were completed while the first author was a member of the Department of Nematology, University of California, Riverside.

[2] Professor, Department of Nematology, University of California, Davis, CA 95616.

[3] Former Staff Research Associate, Department of Nematology, University of California, Riverside, CA 92521.

[4] Former Postdoctoral Fellow, Department of Nematology, University of California, Davis, CA 95616.

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measure a population with specified precision (10,11,23).

The relationship between variance and mean for an aggregated population also can be described by Taylor's Power Law ($s^2 = am^b$) (2,10,20,21). The parameters $a$ and $b$ are descriptive of the exponential relationship between variance and mean, such that $b$ is considered an aggregation parameter and $a$ is a scaling factor dependent on both sample size (8,20,22) and field size (19). In some organisms, values for both $a$ and $b$ have been reported to be influenced by biology, population stage-structure and age-structure, and sample size (1,25). Taylor's Power Law parameters have been estimated for several nematode species and, in some cases, their stability at different sites and in field plots of different sizes has been determined (3,6,17,19). If the parameters for a given species in a prescribed cropping system are stable over time, the model could provide a useful basis for sampling strategies for assessing nematode population densities. Experience in nematode advisory services has indicated that the field area represented by a single sample should be approximately 2–3 ha for annual crops in order to obtain acceptable precision levels for population assessment and economics (2). In addition to providing a basis for decisions on sample size and reliability, Taylor's Power Law also has been used to determine appropriate normalizing transformations for nematode count data prior to statistical analysis (6,17).

The relationship between variance and mean as a descriptor of population dispersion is important from an applied aspect. General formulae relating the number of samples required to measure a population with specified reliability, as a function of the mean and variance of that population, have been developed (16,24). The logic for using these relationships to project required sampling intensity, as a function of management costs and crop value, has been explored (10). Fundamental to such sampling decisions is definition of the relationship of variance to mean for a given nematode species. The objectives of this study were to determine, in one location, the $a$ and $b$ parameters of Taylor's Power Law for a range of plant-parasitic nematode species in a field area of the size recommended for advisory purposes; to examine the stability of these parameters through time; and to test their predictive capabilities for the same species in other locations.

## MATERIALS AND METHODS

*Model:* Taylor's Power Law reflects that the variance of a population is proportional to a fractional power of the mean $\sigma^2 = a\mu^b$ or, using the sample estimators, $s^2 = am^b$, where $a$ and $b$ are population parameters. Parameter $a$ is a scaling factor related to both sample and field size (8,19,20,22). Parameter $b$ is an index of aggregation, varying continuously from zero for a regular distribution (so that $s^2 = a$, with $a < 1$), through 1 for a random distribution (with $a = 1$ so that $s^2 = m$), to $\infty$ for a highly contagious distribution. The parameter $a$ is often fairly constant for a species (8). Since it is determined by linear regression, using the transformed relationship $\ln(s^2) = \ln(a) + b \ln(m)$, $b$ is a function of the natural log of the population mean, which has a stabilizing effect. As the variance predictor, $b$ is an exponent; thus, a predicted variance will be sensitive to small changes in $b$, and the apparent stability of this parameter may be deceptive. The value of $b$, however, is calculated with a definable confidence interval from population data. The width of the confidence interval associated with the estimate of $b$ may modify its apparent stability and the sensitivity of variance estimates to its magnitude.

In estimating parameters of the distribution and dispersion descriptors, initial approximations are determined from the mean and variance of the population. The relationship between variance and mean is strongly influenced by sample unit (field) size (8). If the size of the sample unit is smaller than the size of an aggregate of the population, the apparent dispersion may be random (variance = mean); if the sample unit size is approximately equal to aggregate size, the dispersion appears contagious (variance > mean); and if the sample unit size is very large, the dispersion appears regular (variance < mean) (8). Given the general recommendations that nematode samples for advisory purposes be representative of field units of 2–3 ha (2), the present study was restricted to that sample unit size.

*Data:* A field was selected in Pixley, California (Tulare County), in which cowpea (*Vigna unguiculata* (L.) Wolp. cv. California Blackeye 5) and cotton (*Gossypium hirsutum* L. cv. Acala SJ2), were grown in rotation. Preliminary assessment of plant-parasitic nematode species present included *Criconemella xenoplax* (Raski) Luc & Raski, *Helicotylenchus dihystera* (Cobb) Sher, *Meloidogyne incognita* (Kofoid & White) Chitwood, *M. javanica* (Treub) Chitwood, *Paratrichodorus minor* (Colbran) Siddiqi, *Pratylenchus* spp., and *Xiphinema americanum* Cobb. Cotton and cowpea differ in host status to these species, differentially affecting their population dynamics. As an extreme example, the *M. incognita*-resistant cowpea crop selected for *M. javanica,* whereas the *M. javanica*-resistant cotton crop selected for *M. incognita* (7).

A 25 × 25 grid pattern was superimposed on the field with grid intersection points 6.5 m apart. This placed each column of the grid over a row of the cowpea crop in the field at the first sampling date and distributed the intersection points along the cowpea rows. The site covered approximately 2.6 ha of the field. The corners of the grid pattern were surveyed so that the grid could be laid in exactly the same place at different periods in time. At any sampling period, an individual core of soil (2.5 cm d, 30 cm deep) was removed at each grid intersection. When the field was planted with cotton, and the rows did not correspond with those of the former cowpea crop, the grid intersections were placed in the nearest plant row. In each case, this involved a shift of no more than 30 cm. The field was sampled 11 times, at approximately monthly intervals from September 1982 until October 1983, such that repeated sampling sites were within a circle of 30-cm radius.

Although furrow irrigated, the field was slightly unlevel, resulting in variations in soil moisture. Also, the field was differentially weedy, with a preponderance of Bermuda grass (*Cynodon dactylon* (L.) Pers.) in the northwest sector. During the 1982 field season, the field was plowed, disked, and planted in a north–south direction for the cowpea crop. It was held fallow during the 1982–83 winter and then disked, bedded, and planted in the spring of 1983 in a northwest–southeast direction for the 1983 cotton crop.

Nematode species identification and population counts were made for nematodes extracted from the individual soil cores. The weight of soil in a core was determined to allow each sample to be standardized to a constant core weight. Nematodes were extracted from the individual cores using a semi-automatic elutriator and sugar flotation (4). Data for each nematode species on each sampling date were stored in a 25 × 25 matrix format (sets of 625 observations) in computer files.

*Analyses:* Computer software was developed to allow interactive interrogation and analysis of the field data sets. The software allows user input of the subset of the field to be examined (whole field, a specified stratum, a specified pattern of distribution of soil cores, etc.). The number of cores constituting a sample and the number of repeated samples to be drawn from the data set are also user determined. The program generates random numbers for selection of the soil cores that will constitute a specified sample. The same core cannot be selected twice for the same sample.

The impact of sample size (number of cores) on the *a* and *b* values of Taylor's power function was determined by calculating the mean and variance for two samples of the specified sample size, and repeating the procedure 100 times to produce a data set for determination of dispersion parameters. Means and variances were based upon two samples so that a maximum range of estimates of means was obtained in the 100 repetitions. When more samples are incorporated into each mean and variance calculation, the means tend to converge on the true mean of the finite data set, thus reducing their range. The computer program checked the range of the calculated means; if the range spanned less than three log units, the set was rejected and another set of observations selected. This provided greater resolution of the linear regression and greater confidence in the parameters of the regression model. The selection process also ensured that the regression slope was positive; if the range of mean values was small, the data points were clustered, and there was a possibility for the best-fit regression line to have a negative slope. Linear regression of the log-transformed variance and mean values allowed determination of ln *a* as the intercept, and *b* as the slope.

The core selection process was repeated with sample sizes increasing from 1 to 12 cores, and the procedure was conducted for *H. dihystera, Meloidogyne* spp., and *P. minor* for each of the 11 sampling dates. Population densities and frequency of occurrence for the other species in the field were considered too low on some dates to yield robust estimates of the power function parameters; however, they were determined where possible.

The effect of sample reporting size (the weight or volume of soil for which densities of nematodes are reported, e.g., per 100 g, 250 g, 1 kg, etc.) was also explored for its impact on determination of dispersion parameters. Standardized *a* and *b* values were determined for each species on each sampling date using 100 replications of two 100-g soil samples of 12-core size. This provided a basis for evaluation of change in *a* and *b* values with species and with time.

*Validation:* For assessment of the stability of the dispersion and variance-predicting parameters for various species at the Pixley site, four population data sets were collected from cotton fields in California's San Joaquin Valley. These fields are designated Demaster, Corcoran, Lombardi, and Superior. Because it has been shown that parameter values of Taylor's power function change with size of the area sampled (19,22), the Pixley data set was sampled repeatedly in a systematic pattern, using the computer sampling program, to determine the smallest subset of cores for which the distribution parameters were the same as those of the entire data set. This smallest common subset consisted of every second core across the entire 2.6-ha field area. Thus, the smallest subset was 144 cores (12 × 12 matrix with 13 m between cores). A 144-core subset on a closer spacing did not provide the same parameter values, consistent with the expected impact of sample unit size (8,19,20,22). Data sets from the four new fields were used to test the stability of the descriptions of distribution derived from the Pixley data set. Data from all five fields were used to develop parameters of distribution more generally descriptive for all sites. The validity of the Taylor's Power Law model, with these parameter values, and the degree to which the *a* and *b* values were stable over time and across fields were tested.

For each species in each field, on one date during the winter (January) and one date during the summer (August) growing season, 30 separate determinations of *a* and *b* were made. These were based on 100 means and variances derived from two samples of 1-core sample size. The average of these 30 *a* and *b* determinations became the field estimator for each date. For every field in which a species occurred, the field estimators were averaged to form a global estimator. To test the field and global estimators, a new set of 100 means and variances was created for each field and each date, as before, using 1-core sample size. Least squares linear regression provided determinations of best-fit *a* and *b* values for that field. Least squares regression was used to explore the degree to which the field and global *a* and *b* values were descriptive of mean to variance relationships for any field.

A lack-of-fit (model appropriateness) test (5) was used to determine whether the Taylor Power Law model with global and field parameter values was adequately descriptive of variance to mean relationships for a particular field and date. In summary, this standard test involves partitioning the sum of squares (SS) residual (SS total − SS regression) into that portion which represents the random fluctuation of points and that portion which represents the lack of fit of the model. This can be accomplished by having multiple ordinate (variance) values for a single abscissa (mean) level or, as was done with these data sets, by dividing the abscissa into segments and calculating an average abscissa value for each segment. The sums of squares of deviations of the individual ordinate values from the average ordinate value in each segment are pooled. This pooled SS estimates a SS "pure error" which can be subtracted from the SS residual to give a SS lack-of-fit. The SS lack-of-fit and SS pure error estimates are divided by the respective degrees of freedom to give a mean squares lack-of-fit (MSL) and a mean squares pure error (MSE), allowing an $F$-test for model appropriateness (MSL/MSE). A significant $F$ value indicates that the model with the current parameter values is inadequate because the lack of fit is greater than that expected by random variation. If the $F$ value is not significant, there is no statistical reason to reject the model.

For each regression, the sum of squares error (squared deviation between observed variance and variance predicted by the regression equation) was calculated and two ratios determined, (field SSE)/(best SSE), (F/B), and (global SSE)/(field SSE),(G/F). Thirty random samples were taken from the respective data sets and an average of the ratios determined. The F/B ratio is an indicator of the reliability of the field $a$ and $b$ values as descriptors of the variance to mean relationships for that field. The G/F ratio is an indicator of the degree to which the global $a$ and $b$ parameters, established across fields, are good estimators of population mean and variance relationships in any particular field. The F/B ratio also was used to test the stability of the $a$ and $b$ parameters over time in one location; i.e., the August values against other dates in the cropping season and the January values against other dates in the overwinter season at the Pixley field. The G/F ratio was used to test the predictive capabilities of the parameters across different fields by testing the global values against samples from all locations (Pixley, Demaster, Lombardi, Superior, and Corcoran).

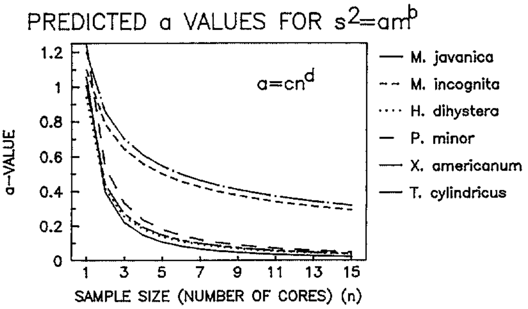

FIG. 1. Relationship between the $a$ value of Taylor's Power Law ($s^2 = am^b$) and sample size ($n$), as defined by the model $a = cn^d$, for *Meloidogyne javanica, M. incognita, Helicotylenchus dihystera, Paratrichodorus minor, Xiphinema americanum,* and *Tylenchorhynchus cylindricus.*

## RESULTS

*Sample size:* The study of the impact of number of cores on $a$ and $b$ parameters of Taylor's power function was confounded by computational problems as larger numbers of cores were used for each sample. As the number of cores increased, the range of population levels exhibited in the data set decreased. This resulted from samples of larger size being more representative of the mean population in the field and, therefore, being more consistent. Since the parameters are determined by linear regression and extrapolation to determine the ordinate intercept (ln $a$), the precision of the intercept estimate will decrease as the range of abscissa values (ln $m$) decreases. Precision of determination was greatest at low sample size when there was a wide range of values along the abscissa.

As sample size increased, the value of $a$ decreased in a manner described by the equation $a = cn^d$, where $n$ is the number of cores, $c$ is the intercept, and $d$ is a negative

TABLE 1. Sample and field $c$ and $d$ values for $a = cn^d$, relating the $a$ value of Taylor's power function to sample size ($n$; number of cores).

| | *H. dihystera* | | *P. minor* | | *M. javanica* | | *M. incognita* | |
|---|---|---|---|---|---|---|---|---|
| Sample month | $c$ | $d$ | $c$ | $d$ | $c$ | $d$ | $c$ | $d$ |
| Sep | 0.90 | −1.09 | 1.1 | −0.75 | 1.16 | −2.10 | | |
| Oct | 0.90 | −1.08 | 1.25 | −1.19 | 0.94 | −1.18 | | |
| Nov | 1.38 | −1.24 | 1.66 | −2.44 | 1.07 | −1.56 | | |
| Jan | 1.23 | −1.94 | 0.48 | −0.74 | 1.12 | −1.41 | | |
| Feb | 0.87 | −1.51 | 1.08 | −1.41 | 1.14 | −1.33 | | |
| Mar | 0.74 | −1.22 | 1.18 | −0.52 | 0.94 | −0.99 | | |
| Apr | 0.83 | −1.75 | 2.64 | −2.60 | | | | |
| Jun | 0.96 | −1.34 | 0.66 | −0.56 | | | | |
| Jul | 0.79 | −0.54 | 1.05 | −0.56 | | | | |
| Aug | 0.96 | −0.85 | | | | | | |
| Oct | 0.75 | −0.49 | | | | | 1.10 | −0.49 |
| Field mean | 0.94 | −1.19 | 1.24 | −1.20 | 1.06 | −1.43 | 1.10 | −0.49 |
| SE† | 0.19 | 0.43 | 0.59 | 0.76 | 0.09 | 0.35 | 0.00 | 0.00 |

Only data for dates where significant $r^2$ values were obtained in the regressions are presented.
† SE = standard error.

value. The parameters of this predictive equation for $a$ were determined for each species on each date (Table 1, Fig. 1). The regressions of variance against mean, for determination of $a$ values, became inconsistent at sample sizes greater than six cores. This tendency was greatest for species with a less aggregated distribution, thus confounding parameter determination. Repeated determinations of $a$ values for higher core numbers, however, revealed an average result consistent with that determined by extrapolation of the curve through the $a$ values for sample sizes of 1–6 cores (Fig. 1). Consequently, the coefficients of the negative exponential model relating $a$ values to sample size were determined for sample sizes of 1–6 cores. For larger sample sizes, $a$ values were calculated by extrapolation using these coefficients. Where the $r^2$ value indicated significant deviation of points from the log-transformed linear regression model, parameter values are not reported (Table 1). The $c$ and $d$ parameters were defined for each species to allow determination of the $a$ values for any sample size across sampling dates (Table 2, Fig. 1).

For *Meloidogyne* spp., the $a$ values separated into defined groups at different times of the year (Fig. 1); one group represents the $a$ values for sampling dates between crops, and the other group represents the $a$ values for sampling dates within the cot-

TABLE 2. Global values of $c$, $d$, and $b$ and degree of confidence in the estimates for $s^2 = (cn^d)(m^b)$, relating variance ($s^2$) to mean ($m$) and sample size ($n$) for plant-parasitic nematodes in cowpea and cotton.

| | $c$ | $d$ | $b$ | SE ($b$)† | ($c12^d$) ($1{,}000^b$)‡ | Conf.§ |
|---|---|---|---|---|---|---|
| *Meloidogyne javanica* | 1.06 | −1.43 | 2.19 | 0.12 | 113,443 | 10 |
| *Meloidogyne incognita* | 1.10 | −0.49 | 2.07 | 0.04 | 537,148 | 8 |
| *Helicotylenchus dihystera* | 0.94 | −1.19 | 1.94 | 0.04 | 32,122 | 10 |
| *Paratrichodorus minor* | 1.24 | −1.20 | 1.81 | 0.39 | 16,920 | 4 |
| *Xiphinema americanum* | 1.20 | −0.49 | 2.01 | 0.04 | 389,836 | 6 |
| *Tylenchorhynchus cylindricus* | 1.01 | −1.20 | 2.08 | 0.08 | 88,982 | 5 |

Only data for dates and locations where significant $r^2$ values were obtained in the regressions were included in the global estimators.
† SE ($b$) = standard error of b value.
‡ Calculated variance associated with a population mean of 1,000 obtained with 12-core samples.
§ Author's subjective confidence rating of the robustness of the $c$, $d$, and $b$ values.

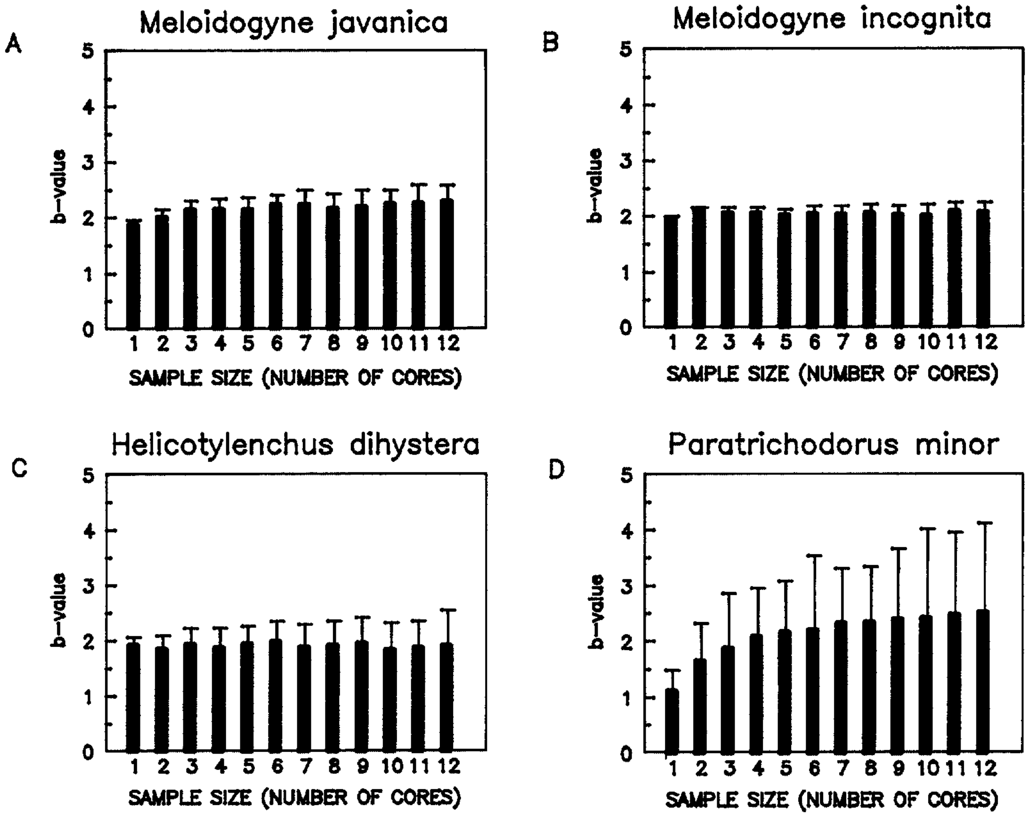

FIG. 2. The relationship between the *b* value of Taylor's Power Law ($s^2 = am^b$) and sample size ($n$), with regressions forced through calculated *a* values. A) *Meloidogyne javanica.* B) *M. incognita.* C) *Helicotylenchus dihystera.* D) *Paratrichodorus minor.*

ton crop. When the cowpea–cotton cropping sequence is considered, the difference in the relationship of *a* to sample size probably reflects differential host status to the two *Meloidogyne* species present, rather than seasonal difference, thus allowing definition of *a* values for each species separately.

Regression of variances and means were recomputed with the regression line forced through the average predicted *a* value intercept for a given number of cores. This allowed determination of *b* values for stabilized regression lines for each species, across all sampling dates relative to number of cores (Table 2, Fig. 2A–D). The *b* parameter appeared stable for a given species at different sample sizes, except in the case of *Paratrichodorus minor* where it was variable but tending to increase as sample size increased. The large standard errors associated with *b* value estimates for *P. minor*, however, indicates lower sensitivity of variance to change in *b* than in other species.

*Sample reporting size:* The effect of increasing the reporting size of the population density (for example, per 100–1,000 g soil) shifts the data set along the abscissa, which results in further extrapolation to the ordinate to determine the ln *a* intercept during the linear regression. Repeated trials with different nematode species and different dates indicated no effect of sample reporting size on *a* and *b* parameters but, rather, resulted in a decrease in their consistency of estimation. Sample reporting size, of course, impacts both mean and variance by a constant and should not affect the parameter values, assuming that there is no uncorrected change in efficiency of extraction with any change in sample size removed from the field.

TABLE 3. Stability of Taylor's Power Law parameters for *Helicotylenchus dihystera* at the Pixley location, measured as ratios of SSE values.

| Sample month | F/B‡ | m.a.‡ | $r^2$§ |
|---|---|---|---|
| Sep | 1.017 | n.s. | 0.84 |
| Oct | 1.019 | n.s. | 0.85 |
| Nov | 1.042 | * | 0.88 |
| Jan | 1.015 | n.s. | 0.83 |
| Feb | 1.028 | n.s. | 0.82 |
| Mar | 1.013 | n.s. | 0.84 |
| Apr | 1.025 | n.s. | 0.76 |
| Jun | 1.013 | n.s. | 0.84 |
| Jul | 1.028 | n.s. | 0.86 |
| Aug | 1.025 | n.s. | 0.80 |
| Oct | 1.020 | n.s. | 0.81 |
| *m* | 1.022 | | |
| SE‖ | 0.008 | | |

† F/B = ratio of SSE for predictions based on August Field values to Best estimates on each date.

‡ m.a. = lack-of-fit (model appropriateness) test.

§ $r^2$ values are for regression to determine Best estimates using data for each date.

‖ SE = standard error.

*Validation:* The degree to which the field and global estimators of Taylor's power function parameters were stable over time and across fields (Tables 3–5) varied with the nematode species. *Helicotylenchus dihystera* was monitored at the Pixley location but was not found at appreciable densities at other sampling sites. For this nematode species, average field values were established and tested for predictive ability over time at the Pixley site. There was a low, stable incidence of zero counts over the sampling dates. The August field value was a very good predictor of the mean–variance relationship in this species throughout the 11 sampling dates, with an average deviation from the August field value of 2.2%. The greatest departure from this value was 4.2% (Table 3). The Taylor Power Law model, with the measured parameter values, was an appropriate and stable descriptor of the mean–variance relationship for *H. dihystera* at Pixley, with some indication of weakness at the November sampling.

TABLE 4. Stability of Taylor's Power Law parameters for *Meloidogyne javanica* at the Pixley location, measured as ratios of SSE values.

| Month | F/B† | m.a.‡ | $r^2$§ |
|---|---|---|---|
| Sep | 1.073 | n.s. | 0.70 |
| Oct | 1.023 | n.s. | 0.86 |
| Nov | 1.020 | n.s. | 0.86 |
| Jan | 1.019 | n.s. | 0.88 |
| Feb | 1.015 | n.s. | 0.87 |
| Mar | 1.022 | n.s. | 0.87 |
| *m* | 1.029 | | |
| SE‖ | 0.020 | | |

† F/B = ratio of SSE for predictions based on January Field values to Best estimates on each date.

‡ m.a. = lack-of-fit (model appropriateness) test.

§ $r^2$ values are for regression to determine Best estimates using data for each date.

‖ SE = standard error.

TABLE 5. Stability of Field and Global Taylor Power Law parameters for *Meloidogyne incognita*, measured as ratios of SSE values.

| Location | Month | F/B† | G/F‡ | m.a.§ | $r^2$‖ |
|---|---|---|---|---|---|
| Pixley | Oct | 1.000 | 1.000 | n.s. | 0.88 |
| Lombardi | Jan | 1.018 | 1.112 | n.s. | 0.63 |
| | Aug | 1.080 | 0.964 | n.s. | 0.80 |
| Superior | Jan | 1.018 | 1.079 | n.s. | 0.96 |
| | Aug | 1.026 | 1.130 | n.s. | 0.97 |
| *m* | | 1.028 | 1.057 | | |
| SE¶ | | 0.027 | 0.064 | | |

† F/B = ratio of SSE for predictions based on Field values to Best estimates on each date.

‡ G/F = ratio of SSE for predictions based on Global values to Field values on dates indicated.

§ m.a. = lack-of-fit (model appropriateness) test.

‖ $r^2$ values are for regression to determine Best estimates using data for each location and date.

¶ SE = standard error.

The two *Meloidogyne* species at Pixley were not separated quantitatively at each sampling date. Qualitative impacts of cropping sequence on the populations were detected. Incidence of detection of this genus was high in the Pixley field throughout the overwinter period (September to March), and because this period followed the *M. incognita*-resistant cowpea crop, the population is assumed to be predominantly *M. javanica.* Population densities were lower during the early part of the crop season, presumably as the *M. javanica*-resistant cotton selected for *M. incognita,* and only reached appreciable densities by October. The population density of *M. incognita* was high at the Lombardi and Superior fields in January and August but too low for consideration at Corcoran and Demaster.

The field parameters were good predictors of the mean–variance relationships of *M. javanica* at the Pixley site during the period of abundance of that species (Table 4). Since *M. javanica* was only detected at the Pixley site, the field estimators are also the best available global values. The mean deviation resulting from use of global parameters was 3% and only as high as 7% on one occasion. The power law model, with the measured parameter values, was appropriate in describing the mean–variance relationships, except on one sampling date when it was questionable.

At the Pixley site, population densities of *M. incognita* juveniles were sufficiently frequent for model parameter estimation only in October. Thus, the October assessment at Pixley constituted the field values for that field (Table 5). The field values for the Lombardi and Superior fields adequately described the variance to mean relationship in those fields. Global *a* and *b* values were acceptable predictors of the variance to mean relationship for *M. incognita* in all fields. The average deviation was 6% and the largest was 13%. With these parameters, the model was an appropriate descriptor of the mean–variance relationship for *M. incognita* in all cases (Table 5).

The population distribution of *P. minor,* in the Pixley field, was less aggregated than that of the other species, and the frequency of zero observations in cores was very low. Repeated samples from the data set tended to produce a cluster of mean–variance points and to reduce precision in fitting the model to the data set (Table 6). The problem was accentuated during the growing season as population densities increased across the field (Table 6). The Demaster, Lombardi, and Corcoran sites had a higher frequency of zero counts and a wider range of estimates of the mean, thus resulting in higher $r^2$ values for the Taylor model and more stable parameters. The Superior field was heavily populated with *P. minor* with a low frequency of zero counts, and reduced precision in fitting the model was again experienced (Table 6). At all locations and across all sampling dates, however, Taylor's power function, with the measured parameter values, was an appropriate descriptor of the mean–variance relationship for *P. minor.*

TABLE 6. Stability of Field and Global Taylor Power Law parameters for *Paratrichodorus minor,* measured as ratios of SSE values.

| Location | Month | F/B† | G/F‡ | m.a.§ | $r^2$‖ |
|---|---|---|---|---|---|
| Pixley | Sep | 1.015 | 1.009 | n.s. | 0.54 |
| | Oct | 1.022 | 1.010 | n.s. | 0.47 |
| | Nov | 1.055 | 1.028 | n.s. | 0.32 |
| | Jan | 1.039 | 1.025 | n.s. | 0.37 |
| | Feb | 1.053 | 1.029 | n.s. | 0.29 |
| | Mar | 1.026 | 1.017 | n.s. | 0.38 |
| | Apr | 1.095 | 1.224 | n.s. | 0.29 |
| | Jun | 1.018 | 1.128 | n.s. | 0.43 |
| | Jul | 1.025 | 1.074 | n.s. | 0.41 |
| | Aug | 1.053 | 1.196 | n.s. | 0.23 |
| | Oct | 1.266 | 1.296 | n.s. | 0.11 |
| Demaster | Jan | 1.015 | 1.025 | n.s. | 0.69 |
| | Aug | 1.016 | 1.016 | n.s. | 0.80 |
| Lombardi | Jan | 1.016 | 1.013 | n.s. | 0.67 |
| | Aug | 1.009 | 1.056 | n.s. | 0.82 |
| Superior | Jan | 1.020 | 1.029 | n.s. | 0.41 |
| | Aug | 1.051 | 1.097 | n.s. | 0.37 |
| Corcoran | Aug | 1.014 | 1.017 | n.s. | 0.77 |
| *m* | | 1.045 | 1.072 | | |
| SE¶ | | 0.058 | 0.083 | | |

† F/B = ratio of SSE for predictions based on Field values to Best estimates on each date.

‡ G/F = ratio of SSE for predictions based on Global values to Field values on dates indicated.

§ m.a. = lack-of-fit (model appropriateness) test.

‖ $r^2$ values are for regression to determine Best estimates using data for each location and date.

¶ SE = standard error.

Significant population densities of *X. americanum* occurred in the Pixley (on some dates) and Corcoran data sets. The global *a* and *b* values (Table 2) were very similar to the field values and were sufficient predictors of mean–variance relationships occurring throughout the year. The genus *Pratylenchus* occurred in low population densities in four fields. There was a high incidence of zero counts, and the individual field and global *a* and *b* values obtained from these data sets were considered not sufficiently robust for reporting. Populations of *Tylenchorhynchus cylindricus* Cobb occurred at the Demaster and Superior fields. Field *a* and *b* values were very similar, and the global values (Table 2) were descriptive of variance to mean relationships for both fields on both sampling dates.

## DISCUSSION

Taylor's Power Law parameters, measured in a particular field, can be used to estimate mean–variance relationships for nematode species in that field at various times. Pooled global values for a nematode species across several fields are acceptably descriptive of variance in individual fields, confirming the results of Mathias (17). Pooled values provide useful information for the design of sampling strategies and determination of sampling intensity. Obtaining parameter values for the model requires large data sets distributed over areas similar in size (2–3 ha) to the strata from which samples will be removed in population assessment. Parameter values are readily calculated from data sets for most nematode species, but they are more difficult to obtain when populations exhibit less aggregation or when fields contain very low population densities resulting in a high frequency of zero observations. In the former case, the mean–variance data sets used to obtain parameter values are too tightly grouped for reliable linear regression analysis. In the latter case, the parameter values of the model are functionally based on very few observations, resulting in low $r^2$ values and unacceptable $F$ values for model appropriateness. In both cases, the problem is an analytical one, rather than a lack of model descriptiveness, and can be overcome by repeating the calculation many times to obtain stable, average values.

Characterization of the relationship between $a$ and sample size allows generalization of the Taylor Power Law model,

$$s^2 = (cn^d)(m^b),$$

where $n$ is the number of cores, and $c$ and $d$ are the parameters which relate $a$ to $n$. The data in Table 2 provide parameter values for this generalized form of the model. The $b$ parameter is undoubtedly influenced by organism biology and age-structure, as demonstrated by Banerjee (1) and Wilson and Room (25) for other organisms. The value of $b$ was substantially influenced by sample size only at very low numbers of cores or when the distribution was less aggregated (few zero counts, high population densities, generally dispersed) as with *P. minor*.

The comparative variances expected for 1,000 individuals of six nematode species (Table 2) indicate differences compatible with species feeding habits and life history strategies. The migratory ectoparasites tend to show lower variance than the second-stage juveniles of sedentary endoparasites. The variance associated with *X. americanum* is high, but this species is prevalent only in the northwest quadrant of the Pixley field; consequently, samples removed from the whole field had considerable variability.

The difference in distribution of the two *Meloidogyne* species may reflect differences in distribution of root systems of the host crop plants. The cowpeas supporting *M. javanica* were more densely planted than the cotton supporting *M. incognita*. Speculatively, then, the higher variance of *M. incognita* on cotton than *M. javanica* on (and following) cowpea may result from the food distribution of the nematode rather than any fundamental differences in organism biology.

When parameter values for the Taylor's Power Law model are determined for species of plant-parasitic nematodes, at least in one large geographic region in Central California and in a similar cropping sequence, pooled values appear sufficiently robust to describe mean–variance relationships for the same species in various locations. These parameter values provide a basis for assessing the required sampling intensity to measure a nematode population at various densities. Duncan et al. (6) observed a similar robustness in Power Law parameters for *Tylenchulus semipenetrans* Cobb in Florida citrus orchards, based on samples taken at different time periods and in different geographic locations. We have addressed elsewhere (9,10) the logic of calculating sampling intensity as a basis for management decisions based upon determination of the population density if it is at the economic threshold. Those discussions did not address the fact that the species composition of the nematode community in the field may not be known in advance of the sampling. If a species of known virulence to a crop is suspected to be present, however, sampling intensity can be determined for that species. On the other hand, because root-knot nematodes are frequently the most virulent nematode pathogens expected in a cropping sequence, and because their biology and reproductive potential tend to make them the most aggregated of plant-parasitic species, often it will be appropriate to use distribution parameters for the most highly aggregated species as a general basis for determining sampling intensity.

An applied use of the distribution parameters allows understanding of the risk associated with the management decisions for a given level of sampling intensity. Conversely, the sampling intensity must be great enough to measure the populations so that the management decision can be made at an acceptable level of risk (10). For preplant management decisions regarding plant-parasitic nematodes in annual crops, the economic threshold is defined as that population density of nematodes causing damage equal to the cost of the control considered (9). Thus, the expected crop value corresponding to the economic threshold population is considered to be the decision threshold (10). The economic threshold varies with the magnitude of the control cost. If the control cost is considered at different proportional levels of the gross crop value, the number of samples of specified sample size (number of cores) needed to measure the population so that a management decision is made with a defined level of risk (Fig. 3) can be calculated. Damage function parameters for cotton and tomato (*Lycopersicon esculentum* L. cv. UC82) (13) were used, and the population densities were calculated for economic thresholds corresponding to control costs representing varying proportions of the crop value,

$$P = (\ln((y' - m)/(1 - m))/\ln Z) + T,$$

where P is the economic threshold population, y′ is the relative crop value at the decision threshold such that $1 - y'$ is the cost of control as a proportion of crop value, m is the crop value at minimum yield, Z is a rate-determining parameter, and T is the nematode tolerance level (10). The acceptable risk level for the management decision is established as a range about the decision threshold; for example, 10% as a conservative level and 20% representing a higher risk level, corresponding to 90% and 80% precision in the crop value prediction, respectively.

The population levels ($P_1$ and $P_2$) corresponding to the extremes of the decision range are calculated as for the threshold, which allows calculation of the half-width of the confidence range (R) within which the population should be measured ($R = 0.5(P_2 - P_1)/P$). The number of samples (N) necessary from a uniform stratum of 2–3 ha or less is then defined by the generalized relationship,

$$N = (t/R)^2(cn^d)(P^{(-2)}),$$

derived from both the sampling intensity equation of Karandinos (16) and Taylor's Power Law (20), modified for sample size (n). Parameter values used were for *M. incognita* (Table 2) from this study. An iterative process for selecting a Student's *t*-value, appropriate for the calculated number of samples, was used in the calculations.

The number of samples required to predict damage, with a specified level of precision (or risk), is a complex function of the shape of the damage function, sample size, rate of increase of population variance relative to population size, and the magnitude of the nematode management investment contemplated (Fig. 3). For any precision level (e.g., 90%, that is crop value prediction within a 10% range, as in Fig. 3A), the required number of samples increases as the management cost increases. As the management cost increases, however, the economic threshold at which the decision is made also increases, and the associated variance increases, thus increasing the

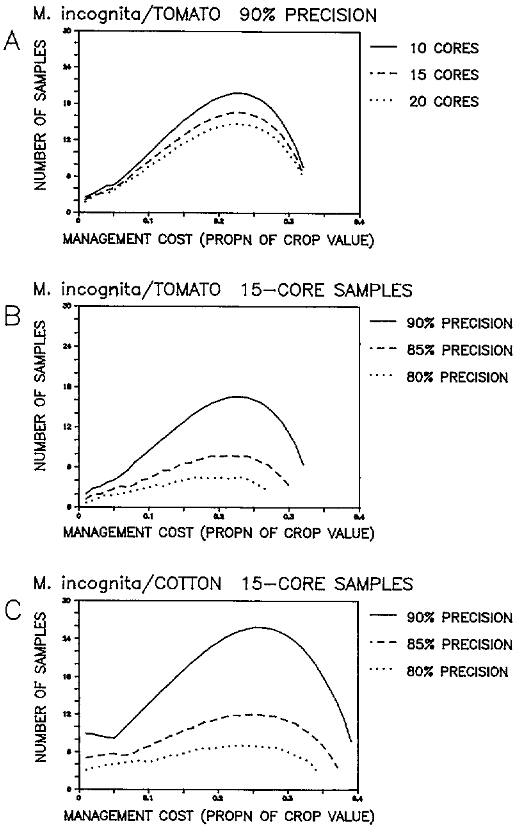

FIG. 3. Relationship between sampling intensity and proportional nematode management costs based on distribution parameters for *Meloidogyne incognita* and the damage functions for this nematode on tomato and cotton. A) Number of 10-core, 15-core, and 20-core samples required to measure the population with 90% precision in the damage estimate for tomato, at different management costs. B, C) Number of 15-core samples required to measure the population with 90, 85, or 80% precision in the damage estimate at different management costs for tomato (B) and cotton (C).

range within which the population must be measured and decreasing the required number of samples. The required number of samples can also be decreased by increasing the sample size (Fig. 3A); this increases the physical effort per sample in the field but reduces the total diagnostic effort in the laboratory.

The number of samples required decreases dramatically as the precision (risk) level for the management decision is relaxed (Fig. 3B, C). For 15-core samples, the sampling intensity for a management decision costing 10% of the expected crop value drops from 9 to 3 samples on tomato (Fig. 3B), and from 14 to 4 on cotton (Fig. 3C), as the precision requirement is relaxed from 90% to 80%.

A precision level of 85% may be reasonable and attainable as a basis for nematode management decisions. Depending on the cost of the management alternative, the required number of 15-core samples ranges from 1 to 7 for tomato (Fig. 3B) and from 5 to 12 for cotton (Fig. 3C). This level of sampling intensity, however, is severalfold higher than that of current recommendations (14) and would involve additional costs not factored into the calculations. Although extraction and processing technology have improved (4,12), soil sampling methodology for nematode population detection and assessment has changed little in the last century. Equipment for obtaining representative soil samples of greater size is necessary. A single 100-core sample would substantially increase the precision of the damage estimate. An automated device capable of economically obtaining such a sample would revolutionize the management decision process in nematology.

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