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Distributed Egg Production Functions for *Meloidogyne arenaria* in Grape Varieties and Consideration of the Mechanistic Relationship between Plant and Parasite[1]

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Abstract: Nematode egg production rates, as mediated by environmental conditions and host status, are important determinants of population development. Rates of egg production by *Meloidogyne arenaria* varied from 0.48 to 1.0 egg per female per DD_{10} (degree days above 10 C) in different grape varieties. The length of the egg production period ranged from 550 to 855 DD_{10} where measurable, and was generally longer in those varieties where the production rate was slow. We hypothesize that if a successful infection site is established, a constant number of eggs is produced if favorable environmental conditions prevail. Mechanistic coupling structures between plant growth and nematode population models are formulated. The nematode population influences metabolite supply through its effect on physiological efficiency and also acts as a metabolic sink; the degree of plant physiological stress influences nematode population development by affecting the sex ratio and egg production rates.

Key words: modeling, population biology, fecundity, model coupling structures.

The development of explanatory and predictive simulation models for nematode population dynamics requires understanding of the interaction of the nematode with both its biotic and abiotic environment. As with other poikilothermic organisms, the major extrinsic rate-determining factor for development and fecundity is temperature. The linearity of response of metabolic processes to temperature (within a specified range) supports a physiological time scale (heat units or degree days) for nematode phenology. The physiological time scale allows prediction of population development through environmental monitoring.

Biotic and abiotic factors other than temperature in the environment of the nematode are considered metabolic rate modifiers. Suboptimal soil moisture, for example, may prevent egg hatch or juvenile movement and consequently delay progress from one stage to the next. Extreme conditions may trigger survival strategies such as cryptobiosis (the equivalent of a vertical cut-off (1) in degree day accumulation). Nature and quality of food are rate modifiers which may also limit development.

We have previously reported on the influence of host cultivar on the nematode infection process (6) and on the rate of post-infection development (5). This paper reports the influence of host cultivar on the rate of egg production, the length of the egg production period, and the total eggs produced per female in different grape varieties. Biological variability in the system, a function of genetic variation in the pest and host and feeding-site suitability, is examined, and a basis for a distributed fecundity population model is developed. The experiments were conducted to fill data gaps revealed during the development of simulation models of *Meloidogyne arenaria* on grape (2,3).

Materials and Methods

Single-bud hardwood cuttings of grape varieties were rooted in 2.5-cm-d tubes embedded in a heated sand bed until at least two leaves had expanded. Each tube was then inoculated with 50 freshly hatched second-stage juveniles of *Meloidogyne arenaria.* After 3 days the roots were washed and transplanted into nematode-free sand. Eighteen days later, each root system was washed from the soil and suspended in a light-proof cylinder with a funnel fused to the base (Fig. 1). Roots were sprayed with water at 2.38 liters/hour for 8 seconds every 10 minutes through a 90-degree solid cone nozzle. Water draining from the grape roots was collected in a 1-liter flask. Nematodes were retained in the flasks by

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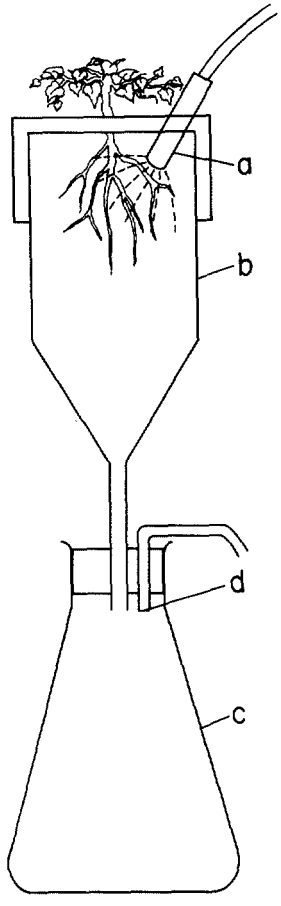

FIG. 1. Extraction apparatus for *Meloidogyne* juveniles hatching from egg masses on growing plants. a = nozzle delivering water at a rate of 2.38 liters/hour for 8 seconds every 10 minutes; b = light-proof chamber; c = collection flask; d = 45-μm-opening sieve on drainage port.

a 45-μm opening sieve covering the overflow aperture. The cylinders were placed in a growth chamber at 25 C, 27 C, and 30 C in separate experiments.

The rationale of the experimental design is that egg development and hatch rate of *M. arenaria* will be constant under constant temperature (4). The rate of recovery of juveniles in the collection flasks indicates the rate of egg production by female nematodes. Juveniles were collected from the flasks and counted daily. When egg production diminished, or plants deteriorated, experiments were terminated (20 to 60 days in separate experiments). Roots were stained in acid fuchsin lactophenol and the

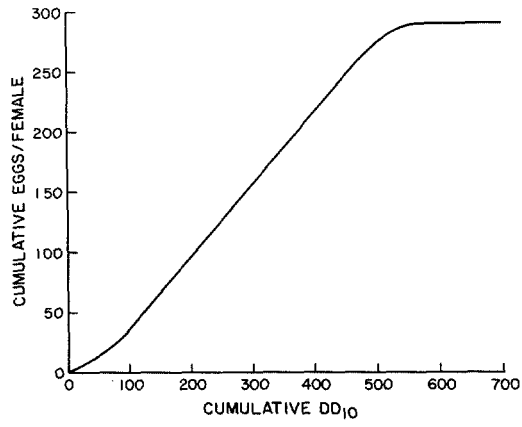

FIG. 2. General form of the relationship between cumulative eggs produced per female and elapsed DD_{10} from first egg production.

egg-laying females were counted. A few immature nematodes in the root probably resulted from reinvasion by hatched juveniles. Only mature females with egg masses were counted.

Four replications of three varieties of grapes were used in each experiment. If a plant died, suffered injury, was not growing as vigorously as other plants of the same variety, or did not appear to be infected, those data were omitted from the subsequent analysis. Plants were suspended in 40% Hoagland's nutrient solution for 10 minutes each week. Juveniles collected from the Hoagland's solution were included in the daily count for that plant.

The lower temperature threshold for this population of *M. arenaria* is 10 C (4). Consequently, the egg production per day was divided by the number of egg-laying females and cumulative egg production per female was plotted against cumulative DD_{10} (1) from the onset of egg production. The typical form of the relationship (Fig. 2) for any grape variety was an initial period of apparently increasing rate of egg production per female followed by a period of constant rate and then a period of declining rate of production. Since juveniles vary in the rate at which they penetrate roots (6), and subsequently develop to maturity at different rates (5), the initial increasing rate of egg production is probably an artifact. As increasing numbers of females became productive, the deflation of production rate disappeared. Later, as females

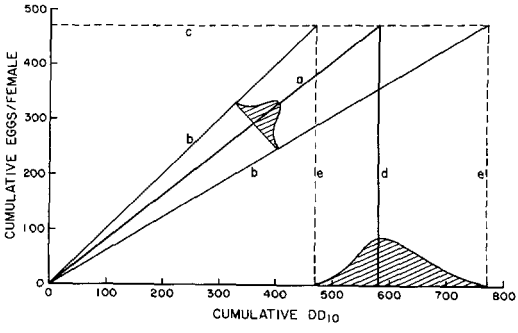

FIG. 3. Standardized relationship between egg production per female and elapsed DD_{10} indicating variability. Mean rate of egg production is indicated by the slope of line a, with a probability distribution indicated by lines b; maximum egg production per female indicated by line c; mean length of productive period indicated by line d, and the limits of its probability distribution by lines e.

progressively became nonproductive, the effect of dividing by the maximum number of productive females was again to deflate the apparent rate of egg production.

The linear portion of the relationship is considered the true rate of egg production per female, consistent with the relationship between metabolic rates and temperature. Consequently, the slope of the linear portion of the graph measures the egg production per female per DD_{10}. The standard deviation of the slope about the regression line reflects variation in production in individual replicates (Fig. 3).

The physiological time at which the upper plateau of the production graph is reached indicates the end of the egg productive period. The height of the plateau represents the total productivity of the female. The length of the productive period is measured from the mid-point of the rate increase period to the mid-point of the rate decrease period, to avoid inflation by variability in female maturity. Variability in the productive period is approximated by the extremes of slope of the regression line intercepting with the maximum productivity line (Fig. 3). These measurements could only be made in those experiments of sufficient length for females to complete their productive cycles.

RESULTS

Fecundity periods of *M. arenaria* females (where measurable) ranged from 550 ± 60 to 855 ± 109 DD_{10} in different grape varieties (Table 1). The variety-specific rate of egg production per female per DD_{10} ranged from 0.48 ± 0.02 to 1.0 ± 0.03. Multiplying the rate of production by the production period reveals an average total egg output per female ranging from 292 to 845 in different grape varieties. The variability in the rate of egg production per female on different replicates of the same variety is reflected by the standard deviation of the slope for the regression line.

DISCUSSION

The synthesis of information from reductionist experimentation to simulate the behavior of populations, requires quantification of the variability of biological processes. The variability associated with the mean time for development to maturity (5) and in the infection period of a single age cohort of J2 (6) were measured previously.

TABLE 1. Fecundity data for *Meloidogyne arenaria* on grape varieties. Varieties are grouped into two classes of host status revealed in penetration and development studies.

Variety	Fecundity		
	Production (eggs/DD_{10})	Period (DD_{10})	Total eggs
Carignane	0.98 ± 0.018	660 ± 60	647 ± 71
French Colombard	0.81 ± 0.066	580 ± 70	470 ± 95
Ruby Cabernet	0.76 ± 0.052		
$\bar{x}$	0.85 ± 0.048	620 ± 66	
Perlette	1.0 ± 0.026	845 ± 160	845 ± 182
Rubired	0.48 ± 0.020	855 ± 109	410 ± 70
Thompson Seedless	0.53 ± 0.028	550 ± 60	292 ± 47
$\bar{x}$	0.67 ± 0.027	738 ± 111	

Since the distribution associated with these variances may differ, the behavior of the population may not be reflected adequately by that of the median individual. These results show a normal distribution of egg production rates about the mean and promote the development of a distributed fecundity function for *M. arenaria* females. Because a frequency distribution of expected production rates about the mean can be established (Fig. 3), the proportion of females in a population producing eggs at various rates is calculable, and the total production per DD_{10} is the sum of the population-productivity products. The calculations can be patterned after the distributed-delay functions of Manetsch (8).

Egg production rate by *M. arenaria* differs among grape varieties (Table 1), but, when the length of the productive period is considered, the total number of eggs produced does not separate varieties into groups as clearly as in previous studies on susceptibility to infection (6) and developmental period (5). Slower rates of egg production, however, do result in a slower mean generation time and a slower rate of population increase. The productive period was shorter in varieties supporting higher rates of egg production, consistent with a hypothesis that individual females have the capacity to produce a fixed number of eggs. Once an infection site is established and the female achieves maturity, eggs are produced rapidly over a short period of time on good hosts and slowly over a longer time period on less suitable hosts. We recognize that weaknesses occur in the analyses, since the finite length of the egg productive period is difficult to determine and those measurements are the least reliable in the current data set.

The life cycle of the root-knot nematode has parasitic and nonparasitic phases. All phases are affected by density-independent environmental conditions, with temperature a primary variable. Parasitic stages are also subjected to density-dependent and host-mediated pressures. Linkages between pest and plant submodels for a population simulator are conveniently quantified by considering the energetics of the system (7,10). Net energy supply into the producer (plant) system (S) is a function of current leaf area (L), photosynthetically active radiation (PAR), temperature (t), photosynthetic efficiency of the current leaf age structure (θ), and the metabolic costs of the photosynthetic process (m) (Fig. 4). Therefore:

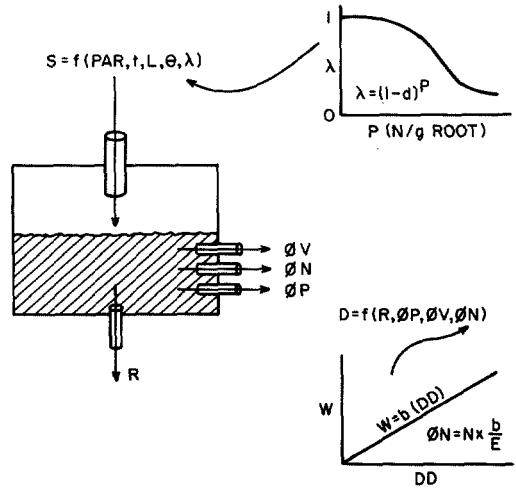

FIG. 4. Coupling structures between plant and nematode based on metabolic pool concept of plant growth. Supply is a function of PAR, temperature, leaf area, photosynthetic efficiency of current leaf age structure, and physiological efficiency as influenced by current nematode population density. Plant demand is a function of maintenance respiration and the cost of new tissue formation (vegetative or propagative) including growth respiration, and nematode demand is a function of nematode growth rate (adapted from Wang et al. [10]).

$$S = f(PAR,t,L,\theta,m).$$

The demand (D) for energy is prioritized to satisfy respiratory demands (R) of the existing biomass (vegetative [V] and propagative [P]), followed by the growth and growth costs of the appropriate tissues for the current state of plant phenology (ϕV and ϕP):

$$D = f(R,\phi V,\phi P).$$

The ratio F= S/D (modified by stored reserves) provides an indication of plant physiological stress, such that growth processes will proceed at a maximum if F = 1, and be constrained if F < 1 (in effect the maximum value of F is assigned as 1) (Fig. 5).

The F ratio can be modified to include the nematode impact on plant growth and used to mediate density-dependent processes in nematode population dynamics.

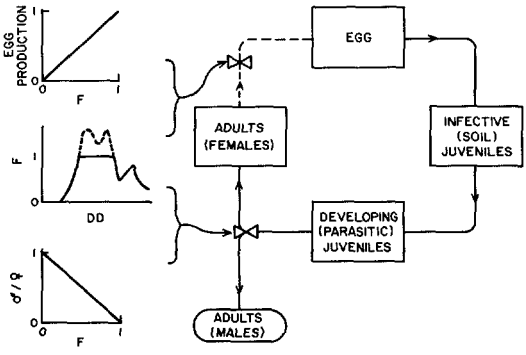

FIG. 5. Coupling structures between plant and nematode. Effect of plant physiological stress (F) as influenced by phenology, metabolite demand priorities, and physiological stress on nematode population development (sex ratio and egg production rate).

Root-knot nematodes affect both supply and demand of the producer. Supply is influenced as the physiological efficiency of the plant is reduced by disruption of vascular tissues. The proportional influence depends on the amount of feeder root tissue and the current parasitic population size, related by a damage function (9). Then physiological efficiency (λ) is a function of population size (N) and damage per nematode per gram of root (d). Therefore:

$$\lambda = (1 - d)^{N/G}$$

where G is the current feeder root mass (Fig. 4). The supply function considering nematode influence becomes $S = f(PAR,t,L,m,\theta,\lambda)$.

Demand is also influenced by the parasitic nematode population. If a nematode at a syncytial feeding site increases in weight by Q g in X DD, assuming a constant feeding rate, the growth rate b = Q/X g/DD. Since assimilation is partitioned into production and respiration, the food demand by the nematode is b/E g/DD where E is the productive efficiency (perhaps 0.2 in these sedentary systems). The demand per day attributable to the nematode population: $\phi N = N(b/E)H$ where H is the number of soil temperature DD this day and N is the population size. Then, for the plant system (Fig. 4): $D = f(R,\phi V,\phi P,\phi N)$. Again, the ratio F = S/D moderates the growth rate of the plant and the development and fecundity of the nematode.

Assuming that the ancestral sex ratio for *Meloidogyne* spp. is 1:1 (♀:♂), and that the system has evolved such that the sex ratio under favorable conditions approaches 1:0, we hypothesize that under the stress of resource limitation the ratio progressively reverts to 1:1 (Fig. 5). As F tends to zero, survival of developing juveniles tends to 0.5 in the sense that half of the population becomes non-egg-producing males. Similarly, density and host-dependent influences on fecundity are mediated by F. The experiments reported in this paper were conducted at minimal resource limitation, so that fecundity rates are maximum values. Subsystem linkages (plant and nematode) may be expressed by multiplying the maximum fecundity value by the current F value (Fig. 5).

In summary, we have addressed the biological potential for fecundity as influenced by host variety in this paper. Further, we have considered the biological impact of host- and density-dependent factors on fecundity and formalized our understanding in a quantitative hypothesis. The hypothesis recognizes the dynamic nature of the interaction of plant and pest subsystems, as influenced by phenology, environmental conditions, and population densities.

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