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Growth and Energy Demand of *Meloidogyne incognita* on Susceptible and Resistant *Vitis vinifera* Cultivars

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Abstract: Food (energy) consumption rates of *Meloidogyne incognita* were calculated on *Vitis vinifera* cv. French Colombard (highly susceptible) and cv. Thompson Seedless (moderately resistant). One-month-old grape seedlings in styrofoam cups were inoculated with 2,000 or 8,000 *M. incognita* second-stage juveniles (J2) and maintained at 17.5 degree days (DD—base 10 C)/day until maximum adult female growth and (or) the end of oviposition. At 70 DD intervals, nematode fresh biomass was calculated on the basis of volumes of 15–20 nematodes per plant obtained with a digitizer and computer algorithm. Egg production was measured at 50–80 DD intervals by weighing 7–10 egg masses and counting the number of eggs. Nematode growth and food (energy) consumption rates were calculated up to 1,000 DD based on biomass increase, respiratory requirements, and an assumption of 60% assimilation efficiency. The growth rate of a single root-knot nematode, excluding egg production, was similar in both cultivars and had a logistic form. The maximum fresh weight of a mature female nematode was ca. 29–32 μg. The total biomass increase, including egg production, also had a logistic form. Maximum biomass (mature adult female and egg mass) was 211 μg on French Colombard and 127 μg on Thompson Seedless. The calculated total cost to the host for the development of a single J2 from root penetration to the end of oviposition for body growth and total biomass was 0.535 and 0.486 calories with a total energy demand of 1.176 and 0.834 calories in French Colombard and Thompson Seedless, respectively.

Key words: grape, *Meloidogyne incognita,* nematode energy demand, nematode growth, *Vitis vinifera.*

Plant-parasitic nematodes affect their hosts by a) removing cell contents (energy demand) and b) inducing pathogenic effects (2,8,17). Each effect varies with the nematode's feeding habit, pathogenicity (2,25), and population density (8). Depending on the nature of the host–parasite interaction, the combined effect of these effects influences host physiological processes such as photosynthesis and crop yield (17). To allow linkage of mathematical and simulation models of host plant and nematode growth, it is desirable that nematode energy demand and pathogenic effects on the host be quantified separately. The energy demand can be estimated from the growth rate of the nematode (6,8), and we hypothesize that the total demand is different in susceptible and resistant hosts.

Measurement of growth of sedentary parasites is technically difficult, however, and is an important obstacle to determination of energy demand and the effect of this demand on host physiological efficiency. The objectives of this study were to determine and compare the growth and energy demand of *Meloidogyne incognita* (Kofoid and White) Chitwood from the second-stage juvenile (J2) to the end of egg laying on a highly susceptible and a moderately resistant *Vitis vinifera* L. cultivar.

Materials and Methods

Nematode growth: The grape cultivars selected for this study, French Colombard and Thompson Seedless, exhibit susceptibility and moderate resistance, respectively, to *M. arenaria* (7,8). Thirty-two 1-month-old seedlings of each cultivar were inoculated with 2,000 or 8,000 24–48-hours-old *M. incognita* J2 in 414-ml styrofoam cups. To synchronize the nematode life cycle, all plants were exposed to nematode attack for 70 degree days (DD—base 10 C) (4 days), then they were repotted and maintained in noninfested soil in a growth chamber at 17.5 DD/day (25 C night and 30 C day) until 560 DD (32 days) had accumulated.

To determine volumes of J2 at inoculation, J2 were chilled to limit their move-

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ment and mounted in water under cover slips supported by fine glass rods, and their shapes were traced using a camera lucida. At 70 DD intervals, two plants from each cultivar and inoculation level were harvested, and the roots were stained with acid-fuschin lactic-acid (11). Nematodes were counted by developmental stage from 1 g of the stained root samples, and the stage composition relative to the total numbers was determined. Roots were teased apart to expose the nematodes, and 15–20 nematodes per plant in situ were mounted in glycerin for camera lucida drawings at a constant magnification. Volumes of 1,220 nematodes were calculated with a computer algorithm which determines the sum of the volumes of slices of the nematode taken along the longitudinal axis, based upon serial diameters along the axis (22). The volumes of developmental stages defined by Franklin (9), from first appearance up to 280 DD and thereafter females only, were traced. Nematode weights were calculated from the volumes assuming a uniform specific gravity of 1.084 for all the stages (1).

Egg production and total biomass increase: Egg production per female was determined by counting the number of eggs taken from 7–10 egg masses per treatment from plants treated in the same manner as in the nematode growth experiment. Eggs were counted at 50–80 DD intervals from 350–822 DD in French Colombard and from 400–912 DD in Thompson Seedless.

To separate gelatinous matrix production from egg production, 50 egg masses from both inoculum levels, at 560 DD in French Colombard and at 750 DD in Thompson Seedless, were grouped into batches of 10 on 1-cm-d plastic discs. They were observed under a microscope until all the water had evaporated from the surface of the egg masses and the plastic, then each group was weighed on an analytical balance. The total number of eggs were counted after squashing the egg masses on a gridded slide. The volumes of 53 J2 and 36 eggs (undetermined embryogenesis) were determined as already described. To determine the weight of an egg, we assumed a density of 1.084 (1). The weight of gelatinous matrix was estimated by subtracting the calculated egg weight from the egg mass weight.

Precision of volumetric measurements: At the end of the study, precision of the volumetric measurements was determined. Single specimens representing J2 before and after swelling, J3/4, and adult stages were randomly selected, and five volumetric measurements were made on each specimen. Also, weights of adult females determined gravimetrically were compared with weights determined volumetrically. One hundred adult females picked from stained roots were divided into four equal groups and weighed by the method used for the egg masses. For comparison, 58 of these females were placed in glycerin (the rest were damaged in the process) and their weight was determined volumetrically.

Respiratory metabolism: The biology and life history of *M. incognita* made measurement of every aspect of its respiratory metabolism difficult, and some assumptions were necessary. A mean fresh weight specific value for oxygen consumption of 1,000 ml $O_2 \cdot kg^{-1} \cdot h^{-1}$ at 16 C, suggested by Nielsen (19), has been widely accepted for nematode respiratory metabolism calculations (31). Yeates (31), however, found that individual nematode respiration calculations determined by this method were 83% of those calculated by Andrassy's (1) volumetric method, and he suggested an adjusted fresh weight specific value of 830 ml $O_2 \cdot kg^{-1} \cdot h^{-1}$. Since our nematode weight data are derived from volumetric measurements, we have adopted the values recommended by Yeates (31). The formula for calculating the respiratory rate is

$$Rx = R16 \times q16/qx$$

where Rx and R16 are O_2 consumption per unit nematode fresh weight per unit time at the experimental temperature and at 16 C, respectively, and qx and q16 are the respiration rate correction coefficients for the two temperatures. A qx value of 2.7

was calculated from the summary of Winberg's table for correcting respiratory rates (5). Calorific equivalents of 4.8 calories to 1 ml O_2 (30) and 2.152 calories per mg nematode fresh weight (31) were used. Total energy consumption and assimilation (calories) were calculated as

$$Ec = P + R + U$$
$$Ea = P + R$$

where Ec = energy consumed, P = energy incorporated into body, R = respiratory metabolism, U = energy unaccounted for, and Ea = energy assimilated. In order to determine U, we need to know the assimilation efficiency which is unknown for root-knot nematodes. Depending on the food source, assimilation efficiency of invertebrates ranges from 10 to 70% (10). Invertebrates that feed on lowest indigestible matter generally have the highest (66%) efficiency (28). Assimilation efficiencies of 59% for *Caenorhabditis briggsae,* a bacterial feeder (18), and 50% for *Tylenchorhynchus dubius,* a root ectoparasite (24), have been reported. These nematodes invest energy in movement, whereas root-knot nematodes, once established, do not. Also, *Meloidogyne* species feed exclusively on high quality cytoplasmic contents. Thus, we expect that they have a high assimilation efficiency, and we asume it to be around 60%.

Data analysis: Nonlinear regression techniques (23) were used to fit logistic curves to data for the growth (fresh weight) of the nematode body from penetration to maturity (about 500 DD) and for body growth plus egg production for an additional 500 DD (the average egg laying period per female) (8). The model used was

$$y = A/(1 + Ce^{BX})$$

where x = DD, A is the maximum (asymptotic) value of y, B determines the value of y when x = 0.0, and C determines the value of y at the inflection of the curve. Growth data for each inoculum level, separately and combined by cultivar, were subjected to the same curve fitting. Parameter values for curves were selected by minimizing the residual mean squares.

The logistic growth curves were used as a basis for calculating the rates of P (nematode growth and egg production), R, Ea, and net production efficiency (P/Ea × 100) per DD. The rates allowed determination of cumulative assimilation and consumption using numerical integration techniques to calculate and accumulate incremental amounts on a DD basis. Equations for each inoculum level are included in the results; however, graphs reported here on each cultivar are from the combination of both inoculum levels because there was little difference in growth rates between inoculum levels.

Results

Precision of volumetric measurements: Repeated measurements of nematode volumes were within a range of 2.2%. The mean fresh weight per female determined volumetrically was 36.5 ± 18.96 μg as opposed to 25 ± 3.83 μg when determined gravimetrically.

Nematode growth: J2 infection level was about 25 and 21% for French Colombard and 9 and 6% for Thompson Seedless, at the low and high inoculum levels, respectively. Males were rare, but the population age structure was similar for both inoculum levels and cultivars at a given time throughout the experiment; however, the numbers of the juveniles achieving the beginning of the adult stage (280 DD) was lower in Thompson Seedless than in French Colombard (Fig. 1).

Parameter determinations for the logistic curves as descriptors of nematode growth were selected with acceptably low residual mean squares (Table 1). The growth pattern was similar for both levels of inoculum and cultivars. Growth was minimal during the first 70 DD after inoculation on French Colombard and during the first 140 DD on Thompson Seedless (Fig. 2). Thereafter, body growth was logistic in form. The maximum body size achieved by a single adult female ranged

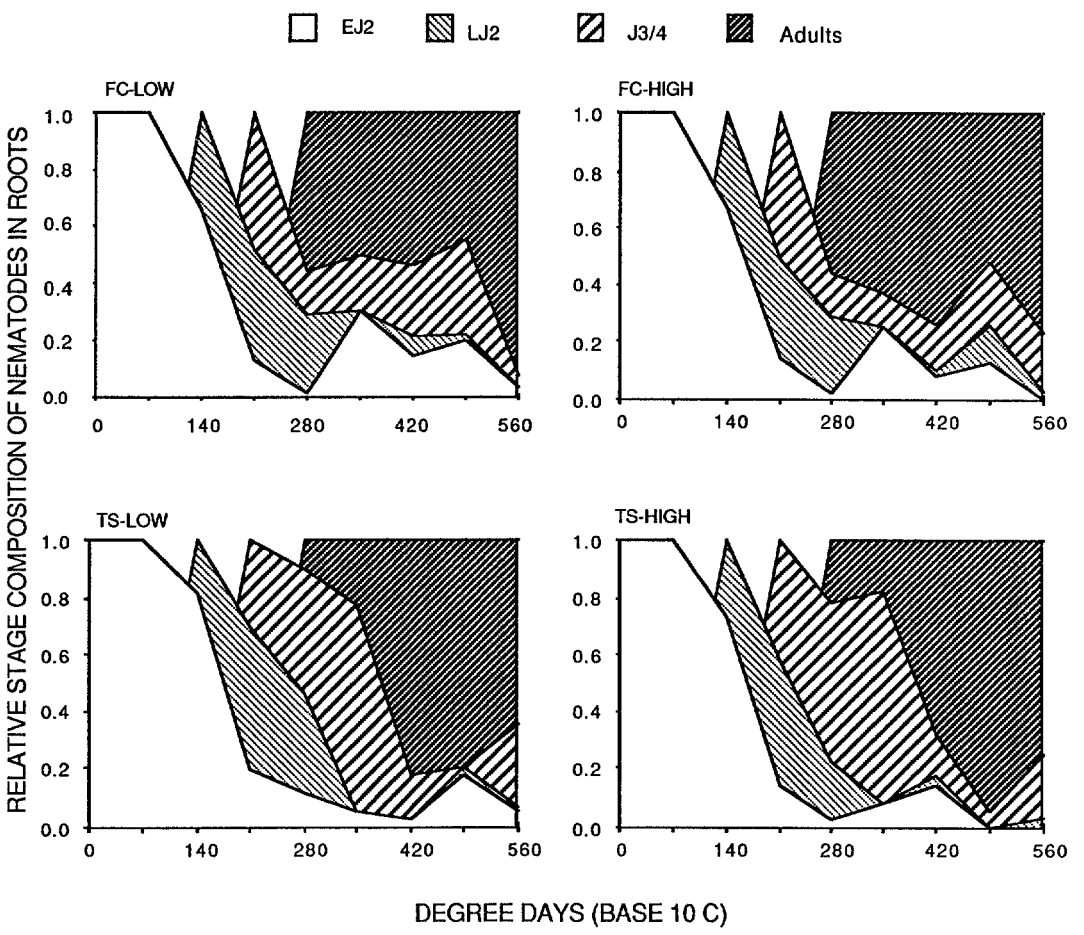

FIG. 1. Relative composition of early (EJ2) and late (LJ2) second-stage juveniles and third plus fourth-stage juveniles (J3/4), and adults from roots at two inoculum levels of *Meloidogyne incognita* on French Colombard (FC-) and Thompson Seedless (TS-) over 560 DD. Note: The sum of the stage proportions at any given time is 1.

TABLE 1. Equations for growth (increase in μg fresh weight) models of a single *Meloidogyne incognita* from J2 root invasion to mature female stage on French Colombard and Thompson Seedless. Each inoculum level (low = 2,000 J2 and high = 8,000 J2) was analyzed separately and combined.

Parameters	Low inoculum (± SE)	High inoculum (± SE)	Both (± SE)
		French Colombard	
A	31.0 (± 0.0)	32.1561 (± 0.2205)	31.9134 (± 0.2449)
B	−0.02441	−0.02046	−0.02010
C	4,958.1266	1,000.0	1,000.0
RESMSQ	2.0701	1.5703	3.2990
df	304	314	617
		Thompson Seedless	
A	30.4255 (± 0.1102)	28.6865 (± 0.5062)	28.9 (± 0.0)
B	−0.02779	−0.01893	−0.02703
C	10,000.0	1,000.0	10,000.0
RESMSQ	0.6469	4.5365	5.5698
df	299	299	599

Model used to fit the logistic curves was $y = A/(1 + Ce^{Bx})$. For details of equations, see Materials and Methods section of text. SE = standard error. RESMSQ = residual mean squares. df = degrees of freedom.

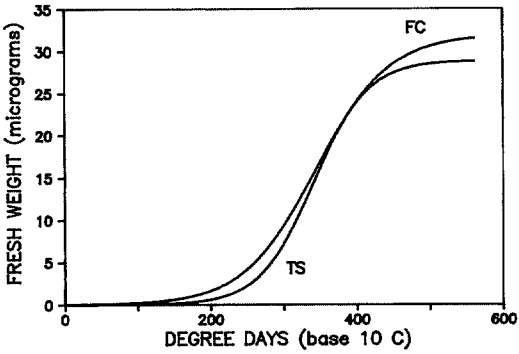

FIG. 2. Growth rate of a single *Meloidogyne incognita* from J2 root invasion to the mature adult stage on Thompson seedless (TS—lower line) and French Colombard (FC—top line) over 560 DD. Curves are combination of both inoculum levels for each cultivar. Equations are given in Table 1.

between 29 and 32 μg (Table 1). Inoculum level did not affect growth in French Colombard, whereas nematodes in the high inoculum level of Thompson Seedless were about 5% smaller than those in the low inoculum level (Table 1).

Based on our calculations, the growth per DD and respiration and assimilation rates (in calories) increased in the same general form as the fresh weight curves until the nematode reached its maximum body size. After this point, respiration and assimilation rates per DD leveled off (Fig. 3). Net production efficiency was calculated as 78–80% on both cultivars for the first 400 DD, and then it declined as growth rate slowed or ceased (Fig. 4).

Egg production and total biomass increase: By subtracting the juvenile volume from the total egg volume, the egg shell accounted for only 1.7% of the total egg volume (Table 2). When egg weight was separated from the total egg mass weight, the weight of the gelatinous matrix per egg was 3.9 and 3.1 times that of the eggs in French Colombard and Thompson Seedless, respectively (Table 2). Inoculum level did not affect the number of eggs per female in French Colombard, but the high inoculum level in Thompson Seedless produced about 6% fewer than the low level. The overall mean number of eggs produced per female in Thompson Seedless (195.87 ± 92.40) was 36.8% lower than that in French Colombard (309.76 ± 125.70). When total egg mass size was combined with nematode growth, it followed the same form as nematode growth alone (Fig. 5). The overall average maximum weight (adult female body with egg mass) of the combined inoculum

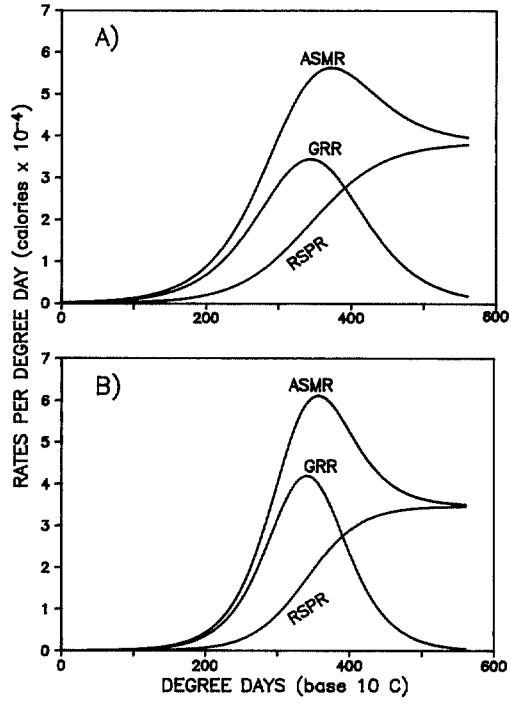

FIG. 3. Respiration (RSPR), growth (GRR), and assimilation (ASMR) rates per DD of a single *Meloidogyne incognita* from J2 root invasion to the adult stage. A) French Colombard. B) Thompson Seedless.

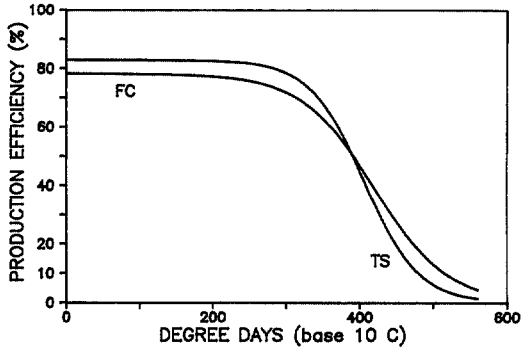

FIG. 4. Net production efficiency of a single *Meloidogyne incognita* from J2 root invasion to the adult female stage on French Colombard (FC) and Thompson Seedless (TS) over 560 DD.

TABLE 2. Mean volumes (μl) and weights (μg) of 53 J2, 36 eggs, and 50 egg masses used for separating the weight of the unhatched juvenile from that of the total egg and the weight of eggs from that of gelatinous matrix of *Meloidogyne incognita* on French Colombard and Thompson Seedless. Numbers in parentheses are standard deviations.

Egg		J2		Egg shell volume as % egg vol.	Egg mass (μg)	Number of eggs/ egg mass	Total egg (μg)	Gelatinous matrix (μg)	Gelatinous matrix size/egg
(μl)	(μg)	(μl)	(μg)						
				French Colombard					
0.1073 (0.0437)	0.1164 (0.0473)	0.1055 (0.0354)	0.1144 (0.0383)	1.66	116.0000 (23.0217)	202.6 (26.9)	23.5826 (3.0788)	92.8226 (23.0015)	3.9180 (1.272)
				Thompson Seedless					
					64.0000 (11.4000)	147.5 (55.86)	17.1690 (6.5019)	46.830 (13.5229)	3.1244 (1.1466)

levels reached about 211 μg in French Colombard and 127 μg in Thompson Seedless (Table 3). It was achieved 160 DD later in Thompson Seedless than in French Colombard (Fig. 5). Daily growth, respiration, and assimilation rates (Fig. 6) were similar to those for nematode growth alone. Net production efficiency continued to increase as body growth and egg production overlapped on French Colombard, whereas it declined because of delayed peak egg production period on Thompson Seedless (Fig. 7).

Energy demand: From our calculations (Fig. 8), a single J2 assimilated 0.147 and 0.135 calories to reach the mature adult female stage (as shown in Fig. 2) and consumed 0.245 and 0.225 calories, respectively, on French Colombard and Thompson Seedless. The feeding cost thereafter is 0.0006385 and 0.0005793 calories/DD. To reach maximum biomass size (Fig. 5, top two lines), a single J2 assimilated 0.545 and 0.402 calories with a total consumption of 0.909 and 0.671 on French Colombard (600 DD) and Thompson Seedless (750 DD), respectively. The demand on the plant for nematode body growth alone over 1,000 DD (Fig. 5, bottom two lines) was 0.535 calories on French Colombard and 0.486 calories on Thompson Seedless. At the end of the reproductive period (1,000 DD), the total demand on the host was 1.176 calories on French Colombard and

TABLE 3. Equations for models for the nematode growth and egg mass size (increase in μg fresh weight) of a single *Meloidogyne incognita* from J2 root invasion to the end of egg production on French Colombard and Thompson Seedless. Each inoculum level (low = 2,000 J2 and high = 8,000 J2) was analyzed separately and combined.

Parameters	Low inoculum (± SE)	High inoculum (± SE)	Both (± SE)
		French Colombard	
A	212.3329 (± 1.1814)	208.8301 (± 1.0474)	210.7387 (± 0.7935)
B	−0.02220	−0.02245	−0.02232
C	10,000.0	10,000.0	10,000.0
RESMSQ	57.581	47.5162	52.6236
df	289	295	584
		Thompson Seedless	
A	138.4066 (± 3.0867)	119.2 (± 1.3273)	126.5 (± 0.1981)
B	−0.00993	−0.01510	−0.01206
C	176.5322	1,165.0414	379.445
RESMSQ	91.9304	62.2558	59.82
df	298	295	591

Model used to fit the logistic curves was $y = A/(1 + Ce^{Bx})$. For details of equations, see Materials and Methods section of text. SE = standard error. RESMSQ = residual mean squares. df = degrees of freedom.

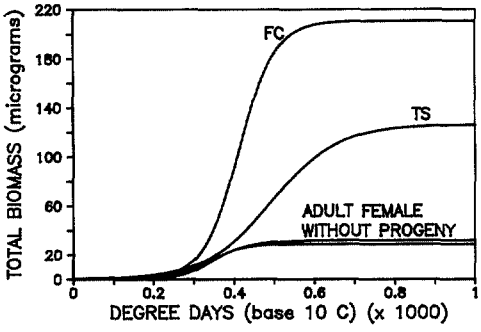

FIG. 5. Total biomass, including egg production, increase of a single *Meloidogyne incognita* from J2 root invasion to the end of oviposition by adult female on French Colombard (FC—top line) and Thompson Seedless (TS—middle line) and mature female size (bottom two lines) up to 1,000 DD. Equations are given in Table 3.

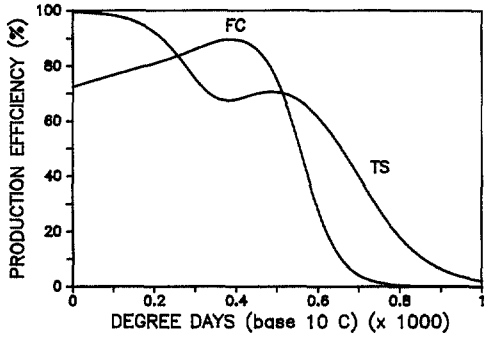

FIG. 7. Net production efficiency of *Meloidogyne incognita* from J2 root invasion to the end of oviposition by adult female on French Colombard (FC) and Thompson Seedless (TS).

0.834 calories on Thompson Seedless (Fig. 8). In our study, the swollen J2, J3/4, and the beginning of the adult stages first appeared at 140, 210, and 280 DD, respectively. The total costs to the host for each of these stages, respectively, were 0.00228, 0.00934, and 0.03283 calories on French Colombard and 0.00054, 0.00359, and 0.02083 calories on Thompson Seedless.

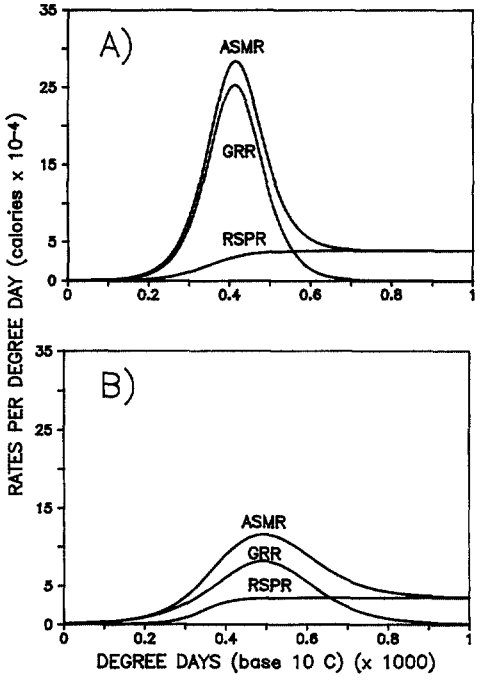

FIG. 6. Respiration (RSPR), growth (GRR), and assimilation (ASMR) rates per DD of a single *Meloidogyne incognita* from J2 root invasion to the end of oviposition by adult female. A) French Colombard. B) Thompson Seedless.

DISCUSSION

Nematode growth outside the root has been measured by area (3), gravimetric (1), volumetric (1,15,22), and oxygen consumption (13,21) methods. For technical reasons, we chose a volumetric method, which is accurately reproducible, and compared it with a gravimetric method. Although our results are of comparable magnitude, the two methods are probably closer than the difference shown. The difference between the two methods probably reflects that we were unable to test both methods with the same nematodes. The difference

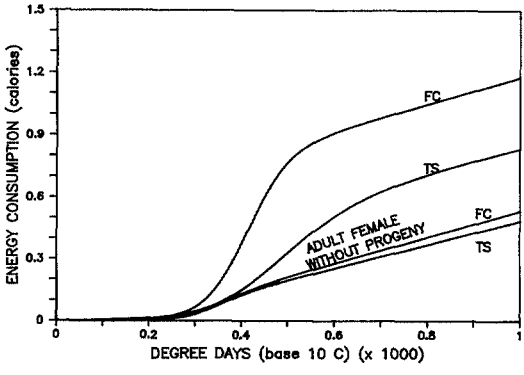

FIG. 8. Cumulative energy consumption of an individual *Meloidogyne incognita* from J2 root invasion to mature adult female without progeny (bottom combined lines), including oviposition on Thompson Seedless (TS—middle line) and on French Colombard (FC—top line) over 1,000 DD.

also reflects that the nematodes may have lost water when being weighed, whereas in the subsequent volumetric measurements, the natural shapes were restored, providing more accurate results than the gravimetric method. Nematode weight is the basis of all our calculations, and our growth data are similar to other reports for *Meloidogyne* species (3) and *Heterodera sacchari* (21).

The lower proportion of nematodes infecting the roots and the slower development of *M. incognita* in Thompson Seedless than in French Colombard, reflect differences in susceptibility of the cultivars. These differences are similar to those reported for *M. arenaria* (7,8). Once established, however, the *M. incognita* females grew to a similar size in both inoculum levels and cultivars. The mature female was about 265 times larger than the J2. When egg and gelatinous matrix production are included, the total biomass achieved was ca. 1,840 and 1,140 times that of the J2 in French Colombard and Thompson Seedless, respectively. The size of the egg mass was about six times that of the female in French Colombard, and about 3.5 times in Thompson Seedless. Approximately 75–80% of the egg mass was gelatinous matrix. Thus, the large difference in total size (female plus egg mass) between the two cultivars is due to the rate of egg and gelatinous matrix production, which was about 37% less in Thompson Seedless, consistent with other studies on egg production (7). The lack of significant difference in either the growth of the female or the rate of egg production between the two levels of inoculum on either cultivar suggests that the high inoculum level may not have been high enough to cause plant damage.

In general, little is known about the net production efficiency of plant-parasitic nematodes. As in other invertebrates (10), it probably varies with their diet. Soyza (26) showed that the net production efficiency of *Aphelenchus avenae* feeding on *Botrytis cinerea* was 52–80%, whereas the efficiency on *Alternaria tenuis* was 6–20% (27). In the present study, there was little nematode body growth in the first 70–140 DD, probably because of time lag in establishing a feeding site. Once the feeding site is established, body growth along with respiration and assimilation rates per DD, increased. At the point of zero increase in body growth, respiration equaled assimilation and leveled off until the end of the life cycle. Net production efficiency of about 80% has been reported in freshwater nematodes (29). Our data show similar values at the active growth or peak egg production period with sharp declines thereafter.

In his preliminary model of energetic interaction between a plant root system and cyst nematodes, Atkinson (2) suggested that nematode energy demand contributes to the impact on the host. Whether it is the energy demand or pathogenicity that is more important depends on the plant-nematode interaction, the rate at which the nematode feeds and grows, and what host physiological processes are affected. For example, if the nematode induces destructive changes at the feeding site (4), the effect may be due to pathogenicity more than to energy demand, as has been reported for *Ditylenchus dipsaci* on field bean (25). Elsewhere (16), we showed that energy consumed by nematodes accounts for a significant portion of the difference in dry weight between nematode-infected and uninfected grape plants, indicating that energy demand is a significant factor in this host–nematode interaction. Ingham and Detling's (12) data indicate that *T. dubius* feeds proportionally to its body size. Since the body size of *T. dubius* is 1% that of an *M. incognita* female (13), it would require a large number of *T. dubius* to have an equivalent effect on the host by energy demand alone. Obligate root parasites, such as *M. incognita,* have large body size and high egg production that are highly proteinaceous in nature (14) and require large amounts of energy for synthesis. Thus, in addition to the pathogenic effects on the host, root-knot and probably cyst nematodes may have higher energy demands than most plant-parasitic nematodes and

hence exert considerable extra drain on the host.

The total calculated energy cost to the host for a single juvenile to complete the life cycle was about 29% more on French Colombard than on Thompson Seedless. The resistant cultivar experienced fewer nematodes and lower energy demand per female. If we assume, however, that the nematode grows to a similar size and reproductive capacity and consumes ca. 1 calorie, as shown here, there may be a significant impact on host productivity. By conversion, the total consumption per nematode is ca. 0.213 mg of tissue dry weight of grapes and contains a carbon fraction equivalent to 0.4 mg CO_2 (20). The same amount of energy consumed from a susceptible or a young plant might be more damaging than it would be to a tolerant or a mature plant. In the case of obligate sedentary parasites, however, the expense to the host is not only the energy that goes into the somatic growth and reproduction of the nematode, but also the formation and maintenance of specialized feeding sites. Our ability to estimate the energy cost involved in this process depends on how well we can characterize the biochemical changes that take place at the feeding sites.

Finally, we wish to re-emphasize that certain of the quantitative conclusions in the paper are based on assumptions of uniform specific gravity across developmental stages and assimilation efficiency derived from estimates in the literature. Nonetheless, our findings contribute to separating the nematode energy demand from the effect on host physiological processes.

Literature Cited

1. Andrássy, I. 1956. Die Rauminhalts- und Gewichtsbestmmung der Fadenwurmer (Nematoden). Acta Zoologica Academiae Scientiarum Hungaricae 2:1–15.

2. Atkinson, H. J. 1985. The energetics of plant parasitic nematodes—a review. Nematologica 31:62–71.

3. Bird, A. F. 1959. Development of the root-knot nematodes *Meloidogyne javanica* (Trueb) and *Meloidogyne hapla* Chitwood in tomato. Nematologica 4: 31–42.

4. Dropkin, V. H. 1980. Introduction to plant nematology. New York: John Wiley and Sons.

5. Duncan, A., and R. Z. Klekowski. 1975. Parameters of an energy budget. Pp. 97–147 *in* W. Grodziniski, R. Z. Klekowski, and A. Duncan, eds. Methods for ecological bioenergetics. IBP Handbook No. 24. Oxford: Blackwell Scientific Publications.

6. Ferris, H. 1981. Mathematical approaches to the assessment of crop damage. Pp. 405–420 *in* B. M. Zuckerman and R. A. Rohde, eds. Plant parasitic nematodes, vol. 3. New York: Academic Press.

7. Ferris, H., and W. A. Hunt. 1979. Quantitative aspects of the development of *Meloidogyne arenaria* larvae in grapevine varieties and root stocks. Journal of Nematology 11:168–174.

8. Ferris, H., S. M. Schneider, and M. A. Semenoff. 1984. Distributed egg production functions for *Meloidogyne arenaria* in grape varieties and consideration of the mechanistic relationship between plant and parasite. Journal of Nematology 16:178–183.

9. Franklin, M. T. 1978. *Meloidogyne*. Pp. 98–124 *in* J. F. Southey, ed. Plant nematology. MAFF Technical Bulletin No. 7. London: Her Majesty's Stationery Office.

10. Grodzinski, W., R. Z. Klekowski, and A. Duncan, editors. 1975. Methods for ecological bioenergetics. IBP Handbook No. 24. Oxford: Blackwell Scientific Publications.

11. Hussey, R. 1985. Staining nematodes in plant tissue. Pp. 197–199 *in* B. M. Zuckerman, W. F. Mai, and M. B. Harrison, eds. Plant nematology laboratory manual. Agricultural Experiment Station Publication, University of Massachusetts, Amherst.

12. Ingham, R. E., and Detling, J. K. 1986. Effect of defoliation and nematode consumption on growth and leaf gas exchange in *Bouteloua curtipendula*. Oikos 46:23–28.

13. Klekowski, R. Z., L. Wasilewska, and E. Papliniska. 1972. Oxygen consumption by soil inhabiting nematodes. Nematologica 18:391–403.

14. Lee, D. L., and H. J. Atkinson. 1977. Physiology of nematodes. New York: Colombia University Press.

15. Luc, M., and G. Merny. 1963. *Heterodera sacchari* n. sp. (Nematoda: Tylenchoidea) parasite de la canne a sucre au Congo-Brazzaville. Nematologica 9: 31–37.

16. Melakeberhan, H., and H. Ferris. 1988. Impact of *Meloidogyne incognita* on physiological efficiency of *Vitis vinifera*. Journal of Nematology, in press.

17. Melakeberhan, H., J. M. Webster, and R. C. Brooke. 1985. Response of *Phaseolus vulgaris* to a single generation of *Meloidogyne incognita*. Nematologica 31:190–202.

18. Nicholas, W. L., A. Grassia, and S. Viswanathan. 1974. The efficiency with which *Caenorhabditis briggsae* (Rhabditidae) feeds on the bacterium, *Escherichia coli*. Nematologica 19:411–420.

19. Nielsen, C. O. 1949. Studies on the soil microfauna. II: The soil-inhabiting nematodes. Natura Jutlandica 2:1–31.

20. Penning de Vries, F. W. T. 1974. Use of assimilates in higher plants. Pp. 459–479 *in* J. P. Coo-

per, ed. Photosynthesis and productivity in different environments. London: Cambridge University Press.

21. Reversat, G. 1987. Increase in chemical oxygen demand during the growth in *Heterodera sacchari*. Revue de Nematologie 10:115–117.

22. Robinson, A. F. 1984. Comparison of five methods for measuring nematode volumes. Journal of Nematology 16:343–347.

23. SAS Institute. 1985. SAS user's guide: Statistics. Cary, NC: The SAS Institute Inc.

24. Scot, J. A. 1979. An ecosystem-level trophic group arthropod and nematode bioenergetic model. Pp. 107–116 *in* N. R. French, ed. Perspectives in grassland ecology: Results and application of the US/IBP grassland biome study. New York: Springer Verlag.

25. Seymour, M. K. 1983. The feeding pump of *Ditylenchus dipsaci* (Nematoda:Tylenchida). Nematologica 29:171–189.

26. Soyza, K. 1973. Energetics of *Aphelenchus avenae* in monoxenic culture. Proceedings of the Helminthological Society of Washington 40:1–10.

27. Wasilewska, L., H. Jakubczyk, and E. Paplinska. 1975. Production of *Aphelenchus avenae* Bastian (Nematoda) and reduction of mycelium of saprophytic fungi by them. Polish Ecological Studies 1:61–73.

28. Wiegert, R. G. 1964. Population energetics of meadow spittlebugs (*Philaenus spurmarius* L.) as affected by migration and habitat. Ecological Monograph 34:225–245.

29. Woombs, M., and J. Laybourn-Parry. 1985. Energy partitioning in three species of nematodes from polysaprobic environments. Oecologia 65:289–295.

30. Yeates, G. W. 1979. Soil nematodes in terrestrial ecosystems. Journal of Nematology 11:213–229.

31. Yeates, G. W. 1972. Nematodes of a Danish beech forest I: Methods and general analysis. Oikos 23:178–189.