

Energetics of *Meloidogyne incognita* on Resistant and Susceptible Alyceclover Genotypes¹

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Abstract: To determine the energy cost of a population of *Meloidogyne incognita* on the roots of alyceclover, nematode biomass was estimated and equations in the literature were used to calculate energy budgets. Amounts of energy consumed, respired, or used in production of nematode biomass were calculated. Results suggested that severe infestations of root-knot nematodes can remove significant quantities of energy from their hosts. Over a 36-day period, a population of 2.6 females of *M. incognita* per root system removed less than 0.4 calories of energy from a resistant alyceclover plant but over 11 calories were removed by 28 females from a susceptible alyceclover. The calculations indicate that on the resistant alyceclover line, 53% of the energy assimilated by the root-knot population was allocated to respiration, with only 47% allocated to production, whereas on the susceptible line, 65% of the assimilated energy was allocated to production. Such energy demands by the parasite could result in significant reductions in yield quantity and quality at a field production level.

Key words: *Alysicarpus vaginalis*, assimilation, consumption, energy allocation, nematode, production, resistance, respiration, root-knot nematode.

Energy does not cycle within an ecosystem. It enters the system when bound photosynthetically as chemical energy in the form of organic compounds, and is gradually dissipated as it passes through the food chain (15). Generally, only about 10% of the energy in plant material consumed by parasites or other herbivores is converted to herbivore biomass (15).

Plant-parasitic nematodes can be considered as primary consumers in an ecosystem, feeding directly on the plant biomass (4,5,14,22). All herbivores affect the photosynthate partitioning within the plant, but when the primary consumer is a parasite, not only is there a loss of energy to the parasite (12), but the disruption of anatomy and physiology caused by the parasite (7,8) may further affect photosynthate partitioning and (or) availability. Thus, the energy demand required by the parasite to sustain its life processes may be very different from the energy impact on the plant. In either case, the net result may be

stunted growth or reduced reproductive success in the plant.

The high reproductive output of some sedentary endoparasitic nematodes may demand a high proportion of the photosynthate produced by their host. Initially, energy demand by root-knot nematodes may be minimal, and the animals begin substantial growth only after the final molt to the adult stage (17). Allocation of energy consumed by the nematode will also vary with the life stage, particularly when size and activity vary among stages (5,19). Energy is needed by the developing nematodes for metabolism and biosynthesis. Respiration is the sum total of the costs for all cell metabolic and respiratory functions, and is necessary for nematode survival. Production is the amount of energy used by the nematode for growth and reproduction (i.e., fixed in the biomass). The amount of energy assimilated by the nematodes, then, is the net energy utilized by the nematode, and is the sum total of the energy required for production and respiration. The amount of energy actually consumed by the nematode is equal to the amount of assimilated energy plus that dissipated to the system as waste.

Nematodes on a susceptible host should be able to receive all the energy demanded for their own growth and reproduction at

Received for publication 27 January 1992.

¹ Florida Agricultural Experiment Station Journal Series No. R-02136.

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The authors thank Barbara Taylor and Diane Mahoney of the Savannah River Ecology Laboratory for supplying Bioquant and instruction in its use.

the expense of the plant, provided that population sizes are not restricting. A nematode on a resistant plant, however, may suffer from an energy shortage if resistance mechanisms of the plant prevent the nematode from extracting all of the energy demanded for normal development (13).

The objectives of this study were to identify and compare adaptive processes and energy allocation patterns of adult *Meloidogyne incognita* (Kofoid & White) Chitwood on resistant and susceptible lines of alyceclover (*Alysicarpus vaginalis* (L.) DC. Ann.). This approach allows us to determine how a decrease in the amount of energy consumed by a nematode parasite (as on a resistant host) would affect the allocation patterns of consumed and assimilated energy over time.

MATERIALS AND METHODS

One hundred 7-day-old plants of each of two lines (FL-4 and FL-100) of alyceclover were transplanted into 80-cm³ disposable plastic cups containing pasteurized Arredondo fine sand (95.5% sand, 2.0% silt, 2.5% clay). The plants were grown in a temperature-controlled growth room at 26 C with a 14-hour photoperiod.

A population of *M. incognita* race 3 was maintained on tomato plants (*Lycopersicon esculentum* Mill. cv. Rutgers) in the greenhouse for 2 months before egg collection. Eggs were extracted from the roots (9) and placed on circles of Nitex (Tetko Inc., Briarcliff Manor, NY) polyamide nylon fiber fabric (20- μ m pores) in water. Nematode inoculum consisted of second-stage juveniles that hatched from these eggs and were collected within the same 24-hour period. Ten days after transplanting, each alyceclover plant was inoculated with approximately 100 infective juveniles. Five plants of each line were left uninoculated as controls.

After 6, 12, 24, and 72 hours, and every 3 days thereafter for a 36-day period, five plants of each line were removed from the soil. Excised root systems were washed,

stained (2), and stored in a glycerin-lactic acid solution (2.0 ml glycerol: 1.0 ml lactic acid: 2.0 ml water). All nematode life stages, except eggs and males, were dissected from each root system and counted under a dissecting microscope. The extracted nematodes were stored in glycerin acidified with lactic acid, and grouped according to host line, date, and replicate number.

The nematodes were measured on the BQ System IV (Bioquant; R&M Biometrics, Nashville, TN), a computerized image-analysis system. A phototube, connected to a dissecting scope, projected an image of the field of vision to a black and white video monitor. A mouse was used to trace the nematode dimensions on the video screen. Bioquant software on an IBM PC converted the measurements from screen to actual measured sizes. Length and width were measured for each age class of juveniles and adult females on each alyceclover line. Numbers removed from roots and measured on each sampling date varied. Over all sampling dates, a mean (\pm SE) of 11.8 ± 2.7 nematodes were removed on each sampling date from five plants of FL-4 and 139.4 ± 28.2 nematodes from the five plants of FL-100.

Biomass, respiration, and production are all related to average individual nematode weight or biomass. As in previous studies of nematode energetics (5,19,22), estimates of nematode weight were obtained from Andrassy's (1) formula:

$$W = \frac{(w^2)(L)}{(1.6)(10^6)}$$

where W is the weight of the nematode in μ g, w is the maximum width, and L is the total length of the nematode in μ m. To check the combined accuracy of the Bioquant measurement technique and Andrassy's formula, the equation was applied to the mean length (0.531 mm) and width (0.273 mm) of the adult females of *M. incognita* race 3 in the roots of a third alyceclover line, FL-5. The calculated weight, 24.7 μ g, agrees closely with the 25 μ g mea-

sured gravimetrically by Melakeberhan and Ferris (11).

Respiration for soil nematodes over time is generally determined by multiplying nematode fresh weight by estimated respiration rate over the time involved (5). Nematode respiration rate was estimated from the formula of Klekowski et al. (10):

$$R = 1.4G^{0.72}$$

where R is the nanoliters of O₂ consumed per individual per hour, and G is the fresh weight of the nematodes in micrograms. One milliliter of O₂ consumed is equivalent to 4.8 cal of respiration energy (22). The value of R obtained from the formula of Klekowski et al. (10) gives an estimate of respiration at 20 C. Nematode respiration varies with temperature according to Krogh's curve (3). The temperature correction factors for this curve given by Duncan and Klekowski (3) were used to calculate respiration at 26 C. This was accomplished by multiplying the value of R by q₂₀/q₂₆, where q₂₀ = 1.00 and q₂₆ = 0.609 (3).

Production is defined here as the amount of energy used by the nematode for growth and reproduction. The caloric equivalent of nematode biomass was estimated at 2.152 cal/mg fresh weight (22). The incremental contribution to nematode production over a 24-hour period was estimated by multiplying the incremental growth in biomass by this conversion factor.

Energy consumption and assimilation of *M. incognita* were calculated according to:

$$E_c = P + R + U$$

$$E_a = P + R$$

Where E_c is the energy consumed, E_a is the energy assimilated, P is the energy fixed as tissue in growth and reproduction, R is the energy required for respiration (cost of maintenance), and U is energy that is consumed but not assimilated by the nematode (11). This unassimilated energy value cannot be calculated from biomass measurements. We used an estimate of

60% for the assimilation efficiency of root-knot nematodes (11). Note that if E_a = 0.60 E_c, then U = 0.67 E_a.

Daily respiration, production, consumption, and assimilation values per nematode were all calculated in relation to biomass. Regression lines were fit to the relationships between each of these energy values and the time following inoculation. Differences across host lines were analyzed using a standard test for equality of slopes (6). Individual cumulative respiration and production costs and cumulative energy consumption and assimilation over time were calculated as the sums of the daily values. Population respiration and production costs and population consumption and assimilation were calculated as the cumulative energy costs per female over time, multiplied by the total number of females in the roots of the inoculated plants, obtained through the original counts.

RESULTS

The biomass of individual nematodes on both resistant (FL-4) and susceptible (FL-100) lines of alyceclover increased over time (Fig. 1). Over the length of the experiment, nematode growth rate on FL-100 was nearly four times more rapid (*P* ≤ 0.01) than the growth rate on FL-4 (Table 1). The growth of nematodes on FL-4 was most nearly approximated by a linear function, whereas that of nematodes on FL-100 more closely resembled a logarithmic function (Table 1).

The nematodes on both alyceclover lines

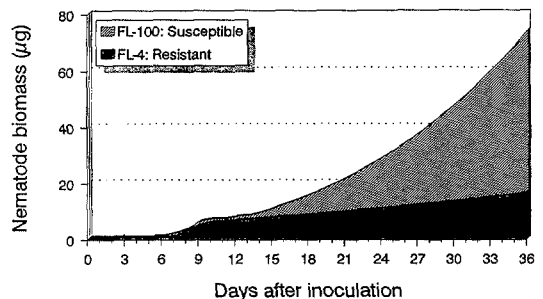


FIG. 1. Change in average biomass of individual *Meloidogyne incognita* after inoculation on susceptible and resistant alyceclover.

TABLE 1. Regression equations relating biomass and natural log of biomass of *Meloidogyne incognita* (y) on resistant (FL-4) and susceptible (FL-100) lines of alyceclover to time (x) in days from inoculation.

Alyceclover line	Time vs. biomass	Time vs. natural log of biomass
FL-4	$y = 0.477x - 0.36$ a $r = 0.983^{**}$	$\ln y = 0.077x + 0.55$ b $r = 0.881^{**}$
FL-100	$y = 2.022x - 13.89$ b $r = 0.956^{**}$	$\ln y = 0.125x - 0.26$ a $r = 0.968^{**}$

Slopes of regression lines with the same letter within the same column are not different ($P \leq 0.05$) according to the standard test for the equality of slopes (6). Asterisks (**) indicate significant correlation coefficients (r) at $P \leq 0.01$.

exhibited a relatively rapid growth rate between days 6 and 9, a slower rate between days 9 and 12, and increasingly rapid growth thereafter, particularly on FL-100 (Fig. 1). As a result, the daily production (incremental increase in biomass) shows a peak at day 9, followed by a drop, and then a gradual increase after day 12 (Fig. 2). Because increase in production showed a very different pattern before day 9 than after day 12, regression equations were calculated separately for each time period rather than over the entire data set. Before day 9, calculated rates for respiration and production showed no differences ($P \geq$

0.10) for nematodes on the two lines (Table 2). As nematodes matured, however, daily respiration costs on susceptible FL-100 increased from 0.0011 calories to 0.0059 calories over a 24-day period (Fig. 2A). There was only a small increase, from 0.0011 calories to 0.0020 calories in the same amount of time in individuals on resistant FL-4 (Fig. 2B). Slopes of the regression lines fit to \log_e -transformed respiration, and production data were significantly different at $P \leq 0.01$ (Table 2). The calculated cumulative respiration cost for one individual on FL-100 for the entire 36-day period was nearly twice that required by a nematode of the same age on FL-4 (Table 3).

Daily production per individual female in FL-100 increased from 0.0016 calories to 0.0104 over the same 24-day period (Fig. 2A), whereas the increase in production by an individual female on FL-4 (0.0006 to 0.0011 calories) was significantly ($P \leq 0.01$) less (Table 2, Fig. 2B). Cumulative production per individual nematode on FL-100 was more than four times the cost for a nematode on FL-4 after the 24-day period (Table 3).

Daily assimilation and consumption rates, then, increased in proportion to the increases in respiration and production. By day 36, nematodes on susceptible FL-100 were assimilating and consuming approximately five times more energy than nematodes on FL-4 (Fig. 2). Cumulative amounts of energy assimilated and consumed by nematodes on FL-100 were over three times as great as those assimilated and consumed by nematodes of the same age on FL-4 (Table 3).

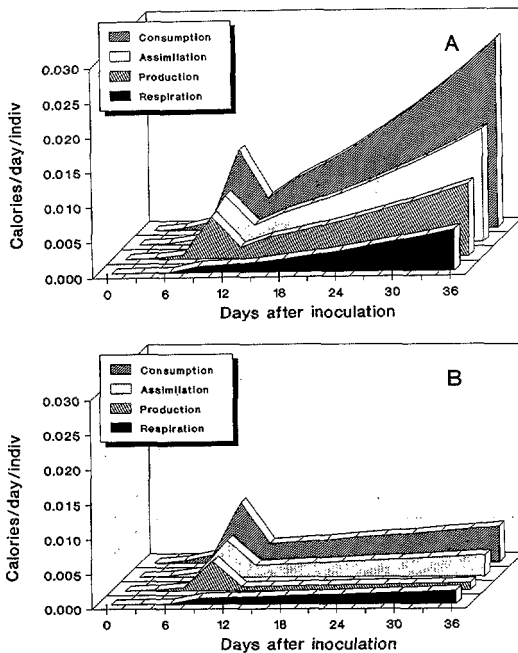


FIG. 2. Changes in daily respiration, production, assimilation, and consumption of individual *Meloidogyne incognita* after inoculation on alyceclover. A. FL-100: susceptible. B. FL-4: resistant.

TABLE 2. Regression equations relating natural logarithms of respiration, production, assimilation, or consumption of *Meloidogyne incognita* (y) on resistant (FL-4) and susceptible (FL-100) lines of alyceclover to time (x) in days from inoculation. Separate regression equations calculated for days 1-9 and 12-36.

Alyceclover line	Respiration	Production	Assimilation	Consumption
FL-4	$\ln y = 0.512x - 11.60$ a $r = 0.996^{**}$	Days 1-9		$\ln y = 0.621x - 10.77$ a $r = 0.979^{**}$
		$\ln y = 0.660x - 11.29$ a $r = 0.969^{**}$	$\ln y = 0.621x - 10.77$ a $r = 0.979^{**}$	
FL-100	$\ln y = 0.521x - 11.62$ a $r = 0.996^{**}$	Days 1-9		$\ln y = 0.647x - 10.81$ a $r = 0.980^{**}$
		$\ln y = 0.690x - 11.34$ a $r = 0.970^{**}$	$\ln y = 0.647x - 10.81$ a $r = 0.980^{**}$	
FL-4	$\ln y = 0.026x - 7.14$ a $r = 0.999^{**}$	Days 12-36		$\ln y = 0.025x - 6.67$ a $r = 0.999^{**}$
		$\ln y = 0.023x - 7.64$ a $r = 0.997^{**}$	$\ln y = 0.025x - 6.67$ a $r = 0.999^{**}$	
FL-100	$\ln y = 0.069x - 7.53$ b $r = 0.994^{**}$	Days 12-36		$\ln y = 0.071x - 6.03$ b $r = 0.957^{**}$
		$\ln y = 0.074x - 7.07$ b $r = 0.898^{**}$	$\ln y = 0.071x - 6.03$ b $r = 0.957^{**}$	

Slopes of regression lines with the same letter within the same column and for the same days are not ($P \leq 0.05$) different according to a standard test for equality of slopes. Asterisks (***) indicate significant correlation coefficients (r) at $P \leq 0.01$.

Total energy budgets for nematodes on resistant and susceptible hosts differ in energy allocation as the nematodes age from 12 to 36 days after inoculation (Fig. 2). Nematodes on FL-100 consistently allocated higher amounts of assimilated energy to production (Fig. 2A) than did nematodes on FL-4 (Fig. 2B). Respiration costs increased gradually for nematodes on both lines as the nematode size increased (Fig. 2). However, animals on FL-100 allocated 65% of their available energy into production and 35% into respiration, whereas those on FL-4 allocated approximately 50% of their available energy into each (Table 4).

Total cumulative energetic costs to the susceptible and resistant plants, based on the numbers of nematodes in the root systems 36 days after inoculation, indicated a substantial difference in the potential impact on the host plant. After 36 days, the nematode population on FL-100, consisting of an average of 28 adult females, had drained more than 11 calories of energy from their host, whereas the population on FL-4, consisting of an average of only 2.6 females, had drained only 0.3 calories from their host (Fig. 3).

DISCUSSION

The size of root-knot nematodes on susceptible and resistant alyceclover plants differs, particularly during the adult stage (17). Biomass measurements of nematodes on both the susceptible (FL-100) and resistant (FL-4) lines were similar in the early stages of growth but diverged ($P \leq 0.05$) with time (Fig. 1). By 36 days after inoculation, adults on the susceptible FL-100 were nearly five times the size of those on FL-4. There are two periods of rapid growth during nematode development, from 6-9 days after inoculation and beyond 15 days.

Greater differences in size occur between the vermiform J2 and swollen J2 stages than between the swollen J2 and other juvenile stages (17). The timing of these events varies with *Meloidogyne* species

TABLE 3. Cumulative energetic demands (cal) of individual adult females of *Meloidogyne incognita* on resistant (FL-4) and susceptible (FL-100) lines of alyceclover.

Line	Respiration	Production	Assimilation	Consumption
FL-4	0.042	0.035	0.077	0.129
FL-100	0.083	0.159	0.242	0.403

and race and with the host cultivar (18). Triantaphyllou and Hirschmann (21) placed rapid development of J2 of *M. incognita* on tomato at 9–11 days, and the first adult females at 13–15 days after penetration. On FL-100 alyceclover, some swollen juveniles were evident by 6 days after inoculation, and over 30% of the nematodes in the roots were adults by 18 days after inoculation (18). Therefore, it is likely that the first period of rapid increase corresponds to the swelling of the J2, whereas the second period corresponds to adult growth.

Peaks in nematode production, assimilation, and consumption at 9 days after inoculation (Fig. 2) result from the fact that the incremental change in growth up to day 9 is greater than the incremental change in growth from days 9 to 12 (Fig. 1). Overall energy uptake was greater on the susceptible line than on the resistant line. These observations agree with previous work (11) in which *M. incognita* consumed more energy on the susceptible grape rootstock 'French Colombard' than on the moderately resistant 'Thompson Seedless'.

Differences in energy allocation within nematodes on resistant and susceptible hosts were also evident. Nematodes on the resistant FL-4 consistently allocated half of their assimilated energy (nearly one-third

of their consumed energy) to respiration, whereas nematodes on the susceptible FL-100 were able to allocate significantly more ($P \leq 0.05$) assimilated and consumed energy to production. A higher allocation toward production would likely indicate a higher reproductive output, leading to elevated nematode populations in the field following planting with a susceptible variety. This is supported by the observation (16) of an average of only 113 eggs per female of *M. incognita* race 3 on the resistant FL-4, compared to 1,093 eggs per female on the susceptible FL-100.

There are several problems with determining energetics in nematode systems, most of which are related to the obligatory nature of the host-parasite relationship (5,19). Respiration levels, difficult to measure on such small animals, are made even more difficult to determine by virtue of the position of the nematode within the root. Removal of a live nematode from the root will likely give an erroneous respiratory measurement due to its sudden environmental stress. Attempts to measure respiration of the animal within the host tissue will result in a measurement of animal and plant respiration combined.

Production values are also difficult to determine. Although a destructive sampling procedure may be used to pull nematodes of different age classes from the

TABLE 4. Average percentage expenditure of daily assimilated and consumed energy for respiration and production of *Meloidogyne incognita* adult females on resistant (FL-4) and susceptible (FL-100) lines of alyceclover.

Alyceclover line	Percentage of assimilated energy		Percentage of consumed energy	
	Respiration	Production	Respiration	Production
FL-4	0.53 a	0.47 b	0.32 a	0.28 b
FL-100	0.35 b	0.65 a	0.21 b	0.39 a

Means with the same letter within the same column are not significantly different ($P \leq 0.05$).

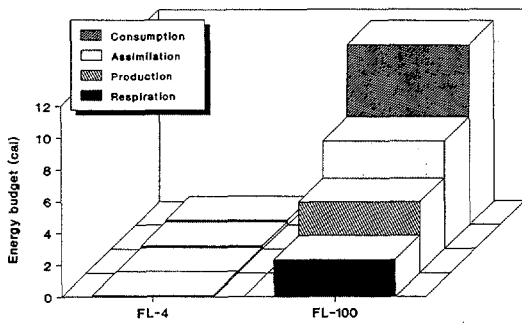


FIG. 3. Total cumulative energy budget over 36 days for all *Meloidogyne incognita* in roots of a susceptible (FL-100, mean of 28 females/root system) and a resistant (FL-4, mean of 2.6 females/root system) alyceclover line.

roots and obtain changes in dry weights over time, environmental differences make it difficult for valid comparisons to be made.

Energy consumption values depend on the amount of waste generated by the nematodes. Because the nematode is encased in root tissue, and because removing it from its environment will likely alter its life processes, this value is equally elusive. Similarly, the efficiency with which nematodes assimilate consumed energy requires more study. Although we used an estimate of 60% assimilation efficiency for root-knot nematodes (11), values as low as 20% have been used for other plant parasites (20).

Because of these problems in measuring nematode energetics directly, literature formulae are used in most studies involving energetics (5,19,22). Formulae based on values for free-living nematodes are applied to plant parasites, due to lack of data on the latter. Although the size of the organisms will be similar, the lifestyles are so different that calculated values will not likely be precise. Nevertheless, comparisons between the same nematode species on various hosts should be more valid because the same formulae are used for those on both resistant and susceptible hosts, and because the basic life cycle will not usually be changed by the suitability of the host. However some resistance factors, such as plant toxins, could have an effect on respiration.

The energy demand of the *M. incognita* population on the alyceclover host after 36 days was over 11 calories from the susceptible FL-100, but only about 0.3 calories from the resistant FL-4. Energy demands of a plant-parasitic nematode population on a host have been measured only infrequently. On small grape plants, 3.4 kcal of energy were demanded by an *M. incognita* population over a 59-day period (12). This amount was equivalent to 15% of the energy assimilated by the plant. Alyceclover is a much smaller plant, and our experimental period was shorter (36 vs. 59 days), so it is not known if the 11 cal utilized on FL-100 represents a similar proportion of the net primary productivity available on this host. It is not surprising that such energy demands by the parasite would result in growth reduction and (or) yield loss in the host.

In the grapevine study, the 15% energy demand by the nematodes resulted in a decline in the dry weight of most plant parts (12). The relationship between plant yields and energy budgets could provide a novel and productive approach toward understanding mechanisms by which nematode parasites influence yield, but requires much additional study. It is encouraging to note, however, that estimates of the energy demand on the host by a nematode population are large enough to be measured, and therefore make future studies much more feasible, because energy measurement in the nematode population itself remains a serious limitation.

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