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Life table for *Heterodera cajani* on pigeonpea *(Cajanus cajan)*

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Summary – *Heterodera cajani* is an important nematode pest of pigeonpea, *Cajanus cajan*. A life table for *H. cajani* was developed on pigeonpea at 25 °C. Mortality rates of *H. cajani* life stages were very high during egg and J2 stages prior to root penetration. Mortality of subsequent life stages was low and virtually constant. Egg laying began on the 23rd day and stopped on the 31st day after the start of the cohort. Mean generation time was 26.9 days and net reproductive rate 15.5 times per generation. The true intrinsic rate (r_m) was 0.102, and the first few days of egg laying contributed more to the value of r_m than did other age intervals. Assuming a finite rate of natural increase, *H. cajani* population would multiply 1.107 times a day, and double itself in about 7 days.

Résumé – ***Tables de survie concernant* Heterodera cajani, *parasite du pois d'Angole* (Cajanus cajan)** – *Heterodera cajani* est un important nématode parasite du pois d'Angole *(Cajanus cajan)*. Sa table de survie a été évaluée sur pois d'Angole, à 25 °C. Le taux de mortalité est très élevé pour les œufs et les J2 avant pénétration dans les racines. La mortalité des stades suivants, très faible, est pratiquement constante. La ponte commence le 23e jour et cesse le 31e après le début de la cohorte. La durée moyenne d'une génération est de 26,9 jours et le taux de reproduction net de 15,5 par génération. Le taux intrinsèque (r_m) est de 0,102 et les premiers jours de la ponte contribuent plus à ce taux que les autres intervalles d'âge. Supposant un taux fini d'accroissement naturel, la population de *H. cajani* s'accroît de 1,107 fois par génération et double en 7 jours environ.

Key-words : Cyst nematode, generation, gross reproductive rate, *Heterodera cajani*, life table, mortality rate, net reproductive rate, pigeonpea, population doubling time.

The cyst nematode, *Heterodera cajani* Koshy, is widely distributed in the major pigeonpea [*Cajanus cajan* (L.) Millsp.] producing states of India (Sharma *et al.*, 1992). Nematode infestation of more than three eggs and juveniles per cm^3 soil may cause a 30 % reduction in plant biomass and seed yield of pigeonpea (Saxena & Reddy, 1987; Sharma *et al.*, 1993). The nematode completes one generation in 16 days at 29 °C and has several generations in a year (Koshy & Swarup, 1971 *a*, *b*). Predictions of nematode population levels are important for making management decisions.

A life table is a systematic explication of survival and mortality of a population. It has a profound predictive function and is useful in relating population fluctuations with environmental factors and in identification of key factors responsible for changes in the population size (Harcourt, 1969; Atwal & Bains, 1974). A life table can be used to determine whether a population is growing, declining, or remaining stable. It can be used to simulate the outcome of management decisions. Development of a life table for an organism requires knowledge of the rate of development of the organism, age specific mortality, survival of the original population with time, and age-specific fecundity. These parameters are, nevertheless, difficult to determine in plant-parasitic nematodes primarily because of their obligate parasitism, microscopic size, and subterranean habitat (Ferris & Noling, 1987). It is not feasible to observe a single age cohort to determine the development stage, natality, and fecundity in plant-parasitic nematodes. Because of these constraints life tables have not been developed for plant-parasitic nematodes although some of the life table parameters were measured for *Meloidogyne arenaria* Chitwood on grape (Ferris & Hunt, 1979; Ferris *et al.*, 1978, 1982, 1984). Life tables for plant-parasitic nematodes, therefore, may have to be constructed by repeated sampling of a population in a habitat. The present study is an attempt to develop a life table for *H. cajani* on pigeonpea as a prelude to further research on host-nematode-environment interactions.

Materials and methods

A population of *H. cajani* was collected from a vertisol (typic pellusterts) field at the research farm of International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) and increased on pigeonpea cv. ICPL 87 in 20 cm diam plastic pots containing mixture of autoclaved sand and vertisol (3 : 1 w/w) in a greenhouse.

EGG HATCH

The egg sacs and white cysts were collected from a 30-day-old plant, inoculated with a single age cohort of juveniles, by processing roots and soil through 80 mesh sieve (180 µm pore size) (Cobb, 1918; Sharma & Nene, 1986). Twenty Petri dishes each containing one egg sac and twenty Petri dishes each containing one cyst were incubated at 25 °C for egg hatching. Juveniles emerged

from cysts and egg sacs were counted and removed every day for up to six days of incubation. The data on juvenile emergence from egg sacs and cysts were combined to determine the percentage of egg hatching.

JUVENILE PENETRATION AND DEVELOPMENT

Seeds of pigeonpea cv. ICPL 87 were sown in cavity trays with 54 cells (5 cm diam) containing a mixture of autoclaved sand and vertisol (3 : 1, w/w). The trays were kept at 25 °C in a growth chamber with 12 h photoperiod and 65-70 % relative humidity. After one week, the seedlings were thinned to one plant per cell. Second-stage juveniles were obtained by incubating cysts and egg sacs at 25 °C in 6 cm diam. plastic Petri dishes containing distilled water. Four hundred freshly-hatched juveniles were inoculated into each plant. The inoculated plants were removed after 48 h and roots were washed with tap water. They were transplanted in trays containing sterilized sand and vertisol mixture (3 : 1, w/w). All juveniles that had entered the roots within the same 48 h constituted an inoculum cohort of the same age. To study the nematode development and age specific survival, eight seedlings were carefully removed from the trays at 48 h intervals, and the roots were stained with 0.1 % cotton blue lactophenol solution and stored in clear lactophenol. The roots were compressed between two glass plates (15 × 10 cm) and the number of juveniles in different stages were counted under a stereoscopic binocular microscope. For identification of different growth stages, roots with nematodes were separated, mounted in lactophenol and observed with a high resolution microscope (100 ×). Peak occurrence of each life stage was used to calculate survival of the development stage. This procedure was continued for 16 days or until adult females were developed. The soil was also processed through 400 mesh (38 µm pore size) sieve after 9 days using Cobb's decanting and sieving technique followed by modified Baermann funnel method to collect males and juveniles (Cobb 1918; Schindler, 1961; Sharma & Swarup, 1984). Sex ratio was determined at J4 stage.

AGE SPECIFIC SURVIVAL AND FECUNDITY OF FEMALE

After 17 days, the plant roots and soil from eight cavity trays were processed daily and examined for number of males, females, eggs and juveniles formed in each root system. The numbers of eggs in twenty females, and twenty egg sacs were counted daily from day 16 until day 34 to estimate number of eggs laid/female/day. The females were assumed dead as soon as egg laying was stopped.

CONSTRUCTION OF LIFE TABLE

Since it was not possible to observe a single age cohort for determining development, survival, and fecundity, the data from egg hatch and juvenile development and reproduction in pigeonpea roots was combined to construct a life table for *H. cajani*. All data were corrected and adjusted in such a way that the life table commenced with a cohort of 500 eggs.

Two types of life tables were constructed as suggested by Deevey (1947).

Age specific survival/mortality life table

Freshly hatched juveniles inoculated to the pigeonpea seedlings and juveniles penetrated within 48 h were taken as single age cohorts of juveniles for penetration and development, respectively. Similarly, white cysts and egg sacs functioned as single age cohorts of eggs. The age specific survival/mortality life table was constructed with the following columns as described by Deevey (1947) :

x = age of cohort.
l_x = number surviving at the beginning of age x.
d_x = number dying in the age interval x.
$100\ q_x$ = mortality rate/100 alive at beginning of age interval.
L_x = number alive between age x and $x + 1$: $\frac{l_x + (l_{x+1})}{2}$
T_x = total number alive beyond the age x (summing all the L_x values from the bottom of the table upwards).
e_x = expectation of life at age x : T_x/l_x.

Life table (for females) and age specific fecundity

A fertility table was prepared by using the formulae suggested by Birch (1948) :

x = age of individuals in days (pivotal age).

l_x = the proportion of individuals still alive at age x (age specific survival). l_x value for females was calculated from l_x for immature, and for adult stages.

m_x = mean number of female offspring produced per female in the age interval (x). The sex ratio (male : female) calculated at J4 stage was 1 : 1.95. The daily increase in egg number per female was taken as age specific fecundity. The following fertility parameters were calculated :

i) Gross reproductive rate *(GRR)* = Total number of female eggs laid per female. Calculated as summation m_x.

ii) Net reproductive rate (R_0) = Number of females produced in each generation : $R_0 : \Sigma l_x m_x$.

iii) Approximate cohort generation time (T_c). Is the mean generation time (birth to weighted mean reproductive age of the adult) :
$$T_c = \Sigma x\ l_x m_x / R_0$$

iv) Innate capacity for natural increase (r_c) = Capacity of a species to increase in number (the reproductive rate) :
$$r_c = log_e R_0 / T_c$$

v) True intrinsic rate of increase (r_m) = Calculated from $\Sigma e^{-r_m x} l_x m_x = 1$. In the present study, both sides of the equation were multiplied by a factor e^7 for

convenience and r_m was calculated iteratively from the expression $\Sigma e^{7-r_m x} l_x m_x = 1097$ (Birch, 1948).

vi) True generation time $(T) = \log_e R_0 / r_m$

vii) Finite capacity for increase (λ) = Number of times the population increases per unit time :
$\lambda = antilog_e r_m$

viii) Doubling time (DT) = Time taken by species to double its population :
$DT = \log_e 2 / r_m$

Results

Survival and life expectancy of different *H. cajani* life stages on pigeonpea

Mortality rates were very high between 0 and 6 day age intervals with life expectancy of 2.68 to 3.04 days (Table 1; Fig. 1). Mortality was low between 8 and 14 days and then again increased at age intervals between 14 and 18 days. The survivorship (l_x) decreased nearly at a constant rate with slight increase in d_x value between 22 and 24 days age interval, and fell to zero after 34 days with the death of all females. The life expectancy (e_x) increased between age interval of 8 and 10 days, then decreased steadily until the 34th day (Table 1).

Table 1. *Survival and life expectancy* (e_x) *of* Heterodera cajani *on pigeonpea.*

x^*	l_x	d_x	$100\,q_x$	L_x	T_x	e_x
0	500	100	20.0	450.0	1520.0	3.04
6	400	298	74.5	251.0	1070.0	2.68
8	102	6	5.9	99.0	819.0	8.03
10	96	5	5.2	93.5	720.0	7.50
12	91	4	4.4	89.0	626.5	6.88
14	87	9	10.3	82.5	537.5	6.18
16	78	16	20.5	70.0	455.0	5.83
18	62	5	8.1	59.5	385.0	6.21
20	57	2	3.5	56.0	325.5	5.71
22	55	9	16.4	50.5	269.5	4.90
24	46	3	6.5	44.5	219.0	4.76
26	43	3	7.0	41.5	174.5	4.06
28	40	3	7.5	39.5	133.0	3.33
30	39	1	2.6	38.5	93.5	2.40
32	38	1	2.6	37.0	55.0	1.45
34	36	36**	100.0	18.0	18.0	2.00

* x = Age of cohort; l_x = Number surviving at the beginning of x; d_x = Number dying in the age interval x; 100 q_x = Mortality rate/100 alive at beginning of age interval; L_x = Number alive between age x and $x + 1$; T_x = Total number alive beyond the age x; e_x = Life expectancy at age $x = T_x / l_x$.

** All the females were assumed to be dead after 33 days of start of cohort.

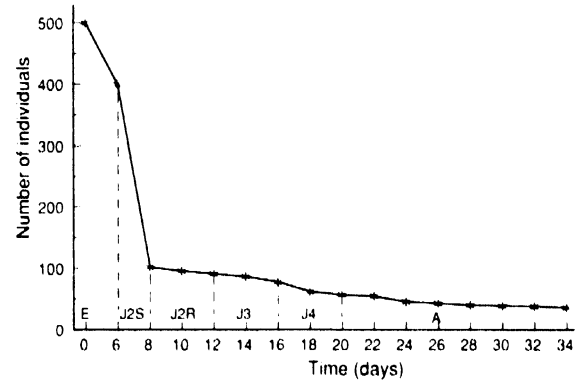

Fig. 1. *Survival curve for* Heterodera cajani *(E = eggs, J2S = J2 in soil, J2R = J2 in roots, J3; J4; A = adults).*

Life table (for females) and age specific fecundity

Survival fraction (l_x), and age specific fecundity of females are given in Table 2. Females started laying eggs after 23 days and ceased after 33 days ($l_x = 0.11$ and 0.09, respectively). l_x remained constant from 25 days onward due to low adult mortality. The fecundity rate (m_x) and reproductive rate $(l_x m_x)$ of each group did not show any set pattern.

Life table parameters for *H. cajani* on pigeonpea are given in Tables 3 and 4. The mean generation time was 26.9 days and net reproductive rate was 15.5. The true intrinsic rate (infinitesimal rate of increase) r_m was 0.102. The first few days of egg laying (23-25 age interval) contributed more to the value of r_m than other age intervals (Table 5). The finite rate of natural increase indicated that *H. cajani* population would multiply 1.107 times a day and it would take about 7 days (DT) to double the population.

Table 2. *Life table for females and age specific fecundity of* Heterodera cajani *on pigeonpea.*

Pivotal age in day (x)	l_x*	m_x	$l_x m_x$	$x l_x m_x$
0-21 immature stages				
	0.11			
23.0	0.11	25.3	2.78	63.94
25.0	0.10	33.9	3.39	84.75
27.0	0.10	21.7	2.17	58.59
29.0	0.10	26.7	2.67	77.43
31.0	0.10	44.1	4.41	136.71
33.0	0.09	0.7	0.06	1.98

* l_x = Proportion of females alive at age x; m_x = Number of female offspring produced per female in the age interval (x); $l_x m_x$ = Number of female births in each age interval.

Table 3. *Calculation of* r_m *for* H. cajani *by the trial and error method.*

		$r_m = 0.09^*$		$r_m = 0.10$		$r_m = 0.11$	
x	$l_x m_x$	$e^{7-r_m x}$	$e^{7-r_m x} l_x m_x$	$e^{7-r_m x}$	$e^{7-r_m x} l_x m_x$	$e^{7-r_m x}$	$e^{7-r_m x} l_x m_x$
23.0	2.78	138.38	384.70	109.95	305.66	87.36	242.86
25.0	3.39	115.58	391.82	90.02	305.17	70.11	237.67
27.0	2.17	96.54	209.49	73.70	159.93	56.26	122.08
29.0	2.67	80.64	215.31	60.34	161.11	45.15	120.55
31.0	4.41	67.36	297.06	49.40	217.85	35.16	155.06
33.0	0.06	56.26	3.38	40.45	2.43	29.08	1.74
$\sum_{23.0}^{33.0} e^{7-r_m x} l_x m_x$		1501.76		1152.15		879.96	

* Innate capacity for natural increase (r_c) = 0.10.
Trial and error substitution in the expression $e^{7-r_m x} l_x m_x = 1097$.

Table 4. *Population growth parameters of* Heterodera cajani *on pigeonpea.*

Parameter	Value
Gross reproduction rate *(GRR)*	152.4 eggs/female
Net reproductive rate *(R_0)*	15.5
Approximate generation time *(T_c)*	27.4 days
Innate capacity for natural increase *(r_c)*	0.10
True intrinsic rate of increase *(r_m)*	0.102
True generation time *(T)*	26.9 days
Finite rate of natural increase *(λ)*	1.107
Doubling time *(DT)*	6.8 days

Table 5. *Contribution of each age group to the value of* r_m (r_m = 0.102).

Pivotage age group *(x)*	$l_x m_x e^{7-r_m x}$	Percentage contribution of each age group
23.0	291.91	26.71
25.0	290.27	26.56
27.0	151.52	13.87
29.0	152.03	13.91
31.0	204.77	18.74
33.0	2.27	0.21

Discussion

Age specific survival and mortality data revealed two age intervals during which survivorship *(l_x)* of *H. cajani* was low; *i*) during the egg stage (age 0 to 6 days), and *ii*) during the second-stage juvenile phase prior to root penetration (age 6 to 8 days). The survivorship curve for *H. cajani* resembled that of type IV of Slobodkin (1962), or type III of Deevey (1947) in which mortality of young stages was greatest. Egg mortality, inability of second-stage juveniles to penetrate the pigeonpea roots, and (or) juvenile mortality in soil before penetration were presumable factors responsible for low survivorship *(l_x)* and e_x values. Mortality of pre-parasitic stages in soil was probably higher than that of the subsequent parasitic stages. Many factors such as soil moisture and temperature greatly affect the migration of juveniles in soil and root penetration (Singh & Sharma, 1994). Availability of food and suitable environment for nematode development inside the plant roots, and shelter from lesser favorable soil environment might be responsible for lower mortality after root penetration.

The intrinsic rate of natural increase *(r_m)* is a useful parameter for comparing reproductive capacities among different species and under different environmental conditions. Initial egg laying (23-25 age interval) contributed greatly to the value of r_m for *H. cajani* on pigeonpea; this was true in the case of insects also (Atwal & Bains, 1974). Plant host is an important factor which influences the reproduction of plant-parasitic nematodes and it may affect the r_m value, which is likely to change with nematode species, and plant hosts. The r_m value would be an useful parameter for comparing reproductive potential of a nematode species on different plant hosts, and (or) between different nematode species.

Temperature is another important factor which influences the development and reproduction of plant-parasitic nematodes. The influence of extrinsic temperature on physiological rates results in variable fecundity, development period, and survival rates (Singh & Sharma, 1994). The r_m value will also change from one temperature condition to another and will possibly help in predicting nematode population densities under different temperature conditions. Other factors influencing the r_m value include change in sex ratio with host environment, and relation of nematode density with development and fecundity. With increase in nematode density, the damage to host increases, and nematode fecundity and survival decreases. The r_m value will then become a complex function of environmental conditions, nematode population density, and host damage.

This study contributes to the understanding of population biology of *H. cajani*. It will be useful in developing life tables for field populations of plant-parasitic nematodes, and eventually it will help in development of nematode pest management models.

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