Chapter 2

ECONOMIC IMPORTANCE AND CROP LOSSES

2.1 NEMATODE—THE MICROSCOPIC ENEMY

Although tiny, parasitic plant nematodes are mighty. It is estimated that nematodes cause $85 billion dollars of crop losses worldwide each year. Since parasitic nematodes are microscopic and below the soil surface, above-ground symptoms can often be misdiagnosed.

In general, root symptoms vary widely but can include galling, lesions, cysts, stunting, and decay. Roots infected by parasitic nematodes are often darker than healthy roots. In addition, infected roots are more susceptible to secondary infection by opportunistic bacteria and fungi. Above-ground symptoms include wilting, yellowing, and loss of foliage. Often, new growth is stunted and infected plants are smaller than their healthy counterparts.

On most crops, threshold ranges from 100 to 5000 nematodes per kg of soil depending on the nematode genera. However, there are some crops that can sustain higher levels of damage. For example, newer processing tomato varieties with vigorous growth can sustain a threshold of 2000 root-lesion nematodes per kg of soil, while fresh market tomato varieties have a threshold of 1000 nematodes per kg of soil. Conversely, some crops like carrot cannot sustain any nematode damage.

There are numerous estimates of the economic importance of nematodes in crop production on a worldwide and individual country basis, but precise values cannot be determined. For many countries, few or no studies have been made to determine the prevalence and extent of damage caused by parasitic nematodes. Extensive research in developed countries and more than 70 developing countries leaves little doubt concerning the destructive nature of plant-parasitic nematodes and the importance of their management for successful crop production.

Nematodes continue to threaten agricultural crops throughout the world, particularly in tropical and sub-tropical regions. For centuries, man's essential crop plants have been plagued by these microscopic organisms, which feed on the roots buds, stems, crowns, leaves, and developing seed. The degree of damage to a particular crop is influenced by the crop and cultivar nematode species, level of soil infestation, and environment. Severe damage may result if high infestations levels occur in soil where susceptible crops are planted. These

Tylenchulus (citrus nematode): Immature females are in soil and are vermiform. The anterior part of mature female is embedded in root tissues; the slender posterior part protrudes from roots and is swollen. Males and juveniles are vermiform and slender.

The major species is *T. semipenetrans*, which is found everywhere in citrus growing areas.

Helicotylenchus (spiral nematode): Small to medium-sized nematodes (0.4-1.2mm), usually spiral in shape. Ectoparasitic, semi-endoparasitc or endoparasitic nematodes of roots. The most damaging species is *H. multicinctus.*

Major species: *H. multicinctus, H. mucronatus, H. dihystera,* and *H. pseudorobustus*

Xiphinema, Longidorus, Trichodorus*, and *Paratrichodorus (dagger, needle and stubby root nematodes): Slender, virus transmitting nematodes, 0.8-5mm long. Ectoparasites on roots of perennial and woody plants, Worldwide distribution.

Major species: *X. americanum, X. elongatum, L. africanus,* and *P. minor.*

In addition to the above worldwide spread plant-parasitic nematodes in India, several other major nematodes also attack crop plants. They are as follows:

Anguina (seed gall nematode): Typical gall forming endoparasites of seeds, stems, and leaves of cereals, grasses, and other plants. Adult stages are found only in plant galls; juveniles are found in galls, plant tissues, or soil. As the galls mature and die, the infective juveniles can survive many years in a quiescent state.

Major species: *A. tritici, A. agrostis,* and *A. wevelli.*

Hirschmanniella (root nematode): Medium size to long, slender migratory endoparasites, many on roots (1-4mm). *H. oryzae* is a major pest of rice in several countries.

Major species: *H. oryzae, H. mucronata,* and *H. spinicauda.*

Hoplolaimus (lance nematodes): These are an important group of migratory ectoparasites, which feed on roots of many kinds of fruits and other economic plants worldwide. Medium length (1-2mm).

Major species: *H. columbus, H. seinhorsti,* and *H. indicus.*

Criconemella (ring nematode): Migratory ectoparasites. Females are 0.2-1mm long, stout with prominent retrorse annules. Males are slender and short; juveniles are like females with annules.

Major species: *C. xenoplax, C. axestis,* and *C. spharocephalum.*

Aphelenchoides (bud and leaf and pine wood nematodes): They have a worldwide distribution. *A. fragariae* and *A. besseyi* feed on and damage strawberry plants; the later species also damages rice. *A. ritzemabosi* causes necrosis on leaves of chrysanthemums and other ornamentals. Pine wood nematode (*Bursaphelenchus xylophilus*) has been implicated in a serious disease of pine trees (pine wilt), which has devastated pine forests in Japan and occurs in North America on various pines. More recently, in 1997, white pine trees in

Maryland were devastated due to the heavy infestation of this nematode. This is a serious quarantine pest, and all pine wood chips or wood products for import and export purposes need to be checked for this nematode.

2.2 CROP LOSSES

Nematodes are non-segmented roundworms, which are not related to earthworms and are generally considered as a distinct phylum. Although more than 15,000 species have been described, but more than 500,000 different species are suspected to exist. Nematodes range in length from 3/1000 of an inch (found in ocean mud) to 27 feet (parasite in the placenta of whales). Species found in soil or plant materials average about 1mm (4/100 in) in length. Parasites of mint range in size from 1/2mm to 5mm.

Nematodes are one of the most ecologically diverse animal groups on earth, and can be found in habitats ranging from the tops of mountains to the deep ocean sediments and from hot deserts to Antarctica. Different species of nematodes may eat algae, bacteria, fungi, yeasts, diatoms, or several kinds of small animals in soil or sediments. There are even large nematodes that eat smaller nematodes. Nematodes may be parasites of invertebrates such as insects, or of vertebrates, including man. Many serious tropical diseases of man and many diseases of domestic animals are caused by nematodes. While most nematodes in soil are actually beneficial, farmers are concerned only with the nematodes that are pathogens of roots, stems, leaves, or seeds of plants. Only about 10% of all nematode species are plant-parasites, however, most are free-living species that feed on other organisms in marine sediments (50%) or nematodes in freshwater sediments or soil (25%). The remaining 15% are the parasites of animals or man.

Annual estimated crop losses due to nematodes in India have been worked out to be about Rs. 242.1 billion. Plant pathogenic nematodes are responsible for an annual loss of over $100 billion worldwide. Additional losses to grower revenues also occur from:

1) sampling costs to determine if the treatment is necessary;
2) yield losses in crops, which are not treated due to the decisions of growers or the lack of a registered nematicide, or where treatment does not fully compensate for nematode damage; and
3) loss in revenue when land must be rotated out of a high cash value crop to a less profitable crop to reduce nematode populations and/or avoid nematode damage.

While substantial yield increases have been realized with the discovery and use of nematicides, considerable work remains to be done in many aspects of nematode biology and management. On the average, only 0.2% of the value of crop loss due to nematode damage is being invested into nematode research.

Furthermore, Nematology is a relatively young science (the first textbook in the India was not published until 1971), and although many crops suffer several qualifications of this statement. The relationship is usually curvilinear, increasing the numbers of nematodes having proportionally diminishing effects. There is some evidence that at low densities the host plant can repair the damage and growth may even be slightly stimulated. Seinhorst (1965) termed the population density (Pi) at which damage first became apparent as the tolerance limit (T).

Equally, at very high values of Pi, increasing numbers of nematodes may not further reduce the dry matter productivity. Seinhorst termed this as the minimum yield (m). There are various reasons why minimum yield may occur. There may be some growth before attack starts or after it finishes, and a significant biomass may be planted (e.g., potato tubers). However, m applies to total dry matter, and because of the effects on partitioning, the harvest value of m may be greater or less than that the total dry matter.

The third parameter in the Seinhorst equation is z—a constant slightly less than one. The equation is:

$$y = m + (1-m)z^{(Pi-T)}$$

$$\text{for } Pi>T$$

$$y = 1 \text{ where } Pi>T$$

Where y is the yield.

An important qualification is that y is expressed as a proportion of the nematode-free yield. Hence, greater the yield potential, greater the loss in tonnes per hectare for any value of Pi.

The Seinhorst equation is usually plotted with Pi on a logarithmic scale, producing a sigmoidal curve (Fig. 2). In practice, T is usually small, and the Pi

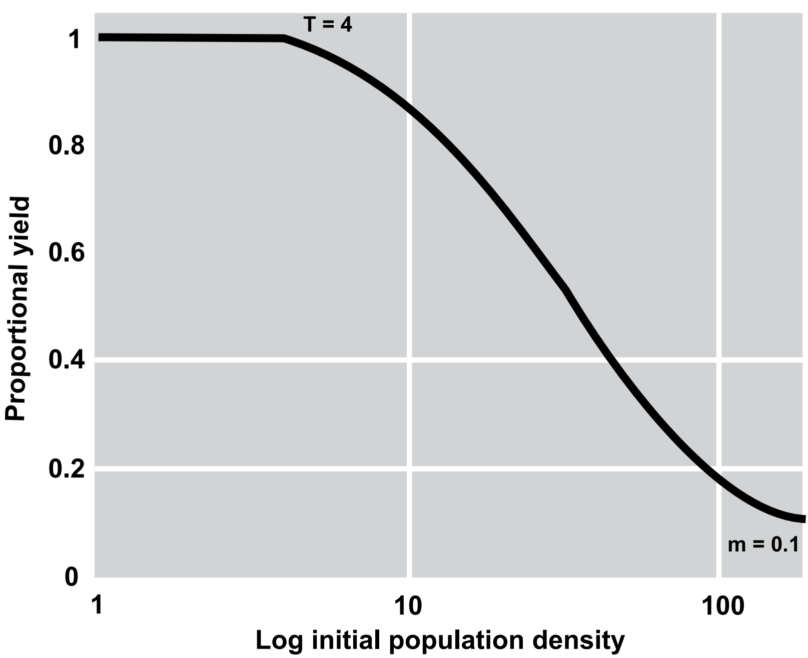

***Figure 2**: The relationship between proportional yield loss and initial population density*

value at which m is reached is so large that it is only the central part of the curve that is of practical use. Oostenbrink (1966) suggested that this approximated to a straight line. The equation for such a line is:

$$y = y\ (\text{max}) - \text{slope constant} \times \log Pi$$

Even the simplified Oostenbrink relationship is not very helpful. Yield is still expressed in proportional rather than real (tonnes per hectare) terms. Also, there is no way of applying the relationship without considerable experimentation to determine the slope of the regression.

The slope of the regression varies due to several reasons. These include differences in pathogenicity (capacity to cause damage) between species, e.g., *Meloidogyne* spp. may be inherently more damaging than *Tylenchus*, but we have no measure of their relative pathogenicities. Different plant species and varieties within species differ in their tolerance (capacity to withstand nematode damage). Also, there are large environmental influences on the damage suffered, and particularly how that damage is translated into effects on final yield.

An important consideration, often overlooked, is the basis of measuring Pi. Usually it is given as numbers per gram of soil. A more appropriate measure is per unit volume of soil, as this allows for bulk density differences. Numbers per gram of root is probably the most appropriate, but is difficult to measure because it is always changing. This latter aspect becomes important while trying to relate results from experiments where root densities are very different, e.g., pot and field trials.

A further problem is encountered while considering damage by nematodes that have two or more generations in the lifetime of a crop. Usually, the Pi is measured at planting, but on a good host population of, for example, *Meloidogyne* spp., it can increase from below the value of T to a level in mid-season where it causes significant damage. Even so, it is a race between increasing Pi and increasing plant size that brings with it increasing tolerance (in Seinhorst terms, increasing m). In such situations, suitability as a host (susceptibility) and tolerance can have a marked effect on the degree of damage.

In summary, both the Seinhorst and Oostenbrink equations are, without the addition of a substantial amount of additional information, purely descriptive and cannot be successfully used to predict actual yield losses.

2.3.2 Mechanisms and Environmental Effects of Damage

Damage is proportional to the intensity of attack. This is often proportionally greater in sandy soils where nematodes can move more freely, than in heavier soils where their movement is impeded. Adequate soil moisture is essential for free movement, so attack is often limited as soils dry out later in the season. Temperature also influences the rate of nematode movement, but plant growth is usually equally affected.

Primary damage to the attacked roots can be attributed to mechanical damage associated with feeding or invasion, withdrawal of nutrients, and/or to more on the tuber yields of different cultivars classified on their degree of tolerance and sites classified by their soil type. However, the losses are still predicted as a proportion of the nematode-free yield. The prediction of the actual loss in tonnes per hectare requires an estimate of the yield potential of the cultivar and site, which requires yet further modeling (Fig. 3).

Only with this information can yield losses be accurately quantified in financial terms and the tolerance limit identified. The alternative is to extrapolate from the available trial data and make allowances on the basis of experience

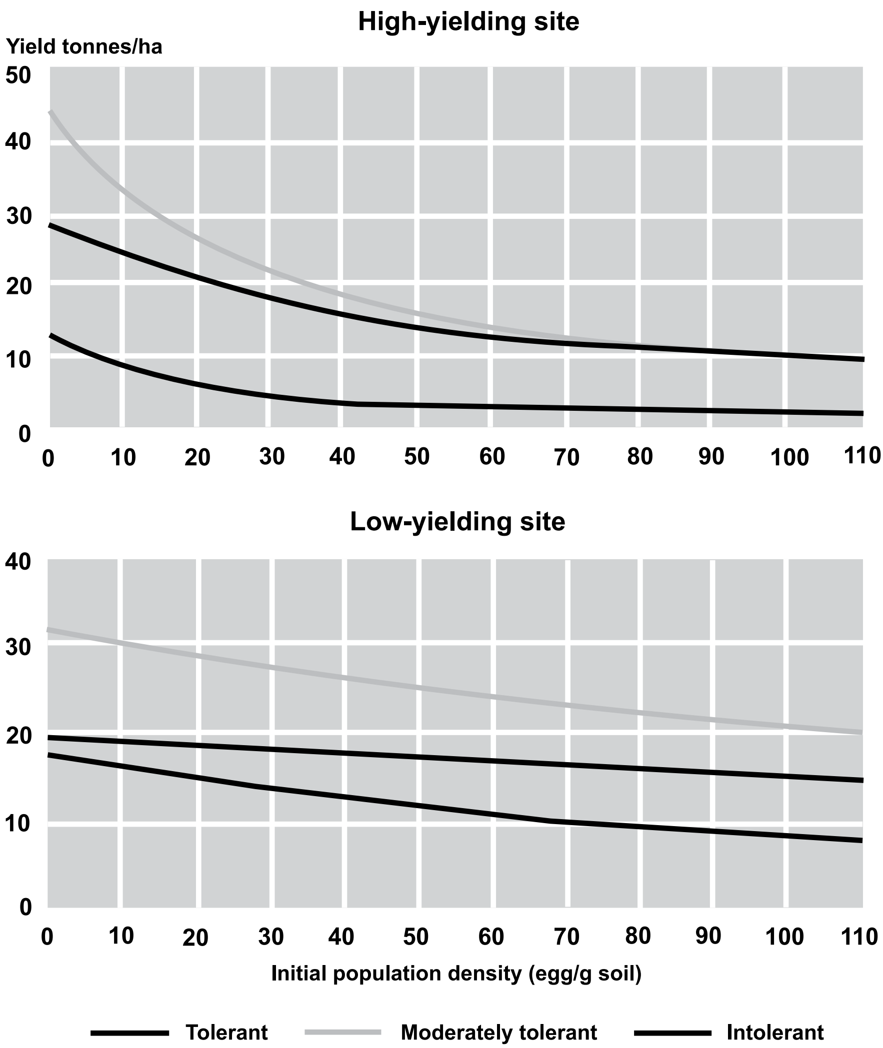

Figure 3 : *The relationship between initial population density of Globodera pallida and tuber yield for tolerant, moderately tolerant, and intolerant genotypes at two sites with contrasting yield potential*

for the obvious possible environmental influences. The Methods of estimating yield loss are therefore of central importance and are considered below.

2.3.5 Methods of Estimating Yield Losses

Pot studies can be used to determine some of the basic information on yield-loss relationships, but because of environmental differences and interactions, field studies are also needed. There are two approaches—one is to use nematicides at relatively uniformly infested sites; the other is to work at sites with a range of population densities, but which are uniform in other respects. A combination of both approaches is often a happy compromise. The former gives a practical information on the effectiveness and potential value of a particular treatment, but tells little about the nature of the relationship. It also suffers from the criticism that nematicides have a range of side effects. The latter has the benefit of producing information on the relationship between Pi and yield, but it requires experimental errors to be minimized. Because Pi estimates have large errors, accuracy is improved by reducing plot size and by taking and processing multiple samples from each plot. However, plot size must be large enough to obtain a realistic yield, and adequate guard plants are essential.

Another option is to establish many small plots in large but otherwise uniform fields. These can be at random, in a grid pattern, or along known trends in Pi. The plots can be split and a nematicide applied to one half. For each plot, the Pi and yield are determined. The results will produce a scatter of points, hopefully with yield decreasing as Pi increases. Much of the scatter is due to errors in estimating Pi and yield, and it can be minimized by taking the average of all the results within each error band. Such an approach needs:

1) a wide range of initial populations;
2) a uniform field;
3) a large number of plots (100 or more); and
4) the plots to be part of an otherwise uniform crop.

2.4 POPULATION DYNAMICS

Nematodes have various reproductive strategies. Some grow large and have long life cycles with low rates of population increase (K strategists); others are relatively small, have short life cycles and potentially higher reproductive rates (r strategists). An endoparasitic habit with induction of giant cells or other rich and continuously available food sources, reduces the exposure to predation and other stresses and further increases the reproductive potential. A reduction in the number of active juvenile stages further decreases the development time, thereby reducing generation time and increasing the potential for multiple generations in a season. A wide host range completes the adaptation of pathogens such as some *Meloidogyne* spp., which can be regarded as the ultimate plant-parasitic nematode r strategists. Many *Longidorus* spp. are examples of K strategists.

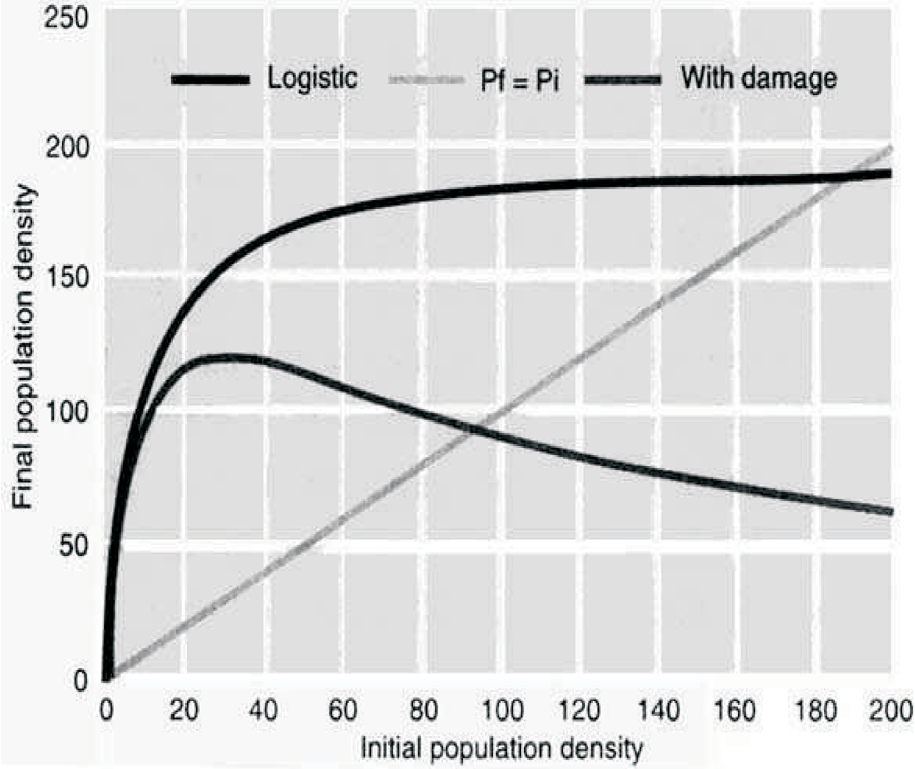

Figure 4 : *The theoretical logistic relationship between initial population density and final population density, and the relationship when roots are damaged*

space lost as a result of root damage, which increases the competition between invading nematodes, resulting in an even greater shift in the sex ratio towards male production than would otherwise be the case. Thus, the approach to the asymptote is slower, and indeed the asymptote is reduced below the theoretical level. Further increases in Pi can inflict so much root damage that the population increase becomes negative and the population size is ultimately reduced.

All the equations mentioned require modification by including a damage function such as that of Seinhorst, which also allows the differences in tolerance between cultivars to be taken into account. The damage functions used model proportional differences, and further modification may be required to account for absolute differences in plant size.

Another plant characteristic that affects population increase is the host status of the plant. Differences can be modeled in terms of maximum multiplication rate or the space required for successful multiplication (Seinhorst models), or in terms of fecundity or effects on the sex ratio (Jones and Perry model).

An important method of expressing and comparing the effects of different cultivars or cropping regimes is to consider the equilibrium density, i.e., the

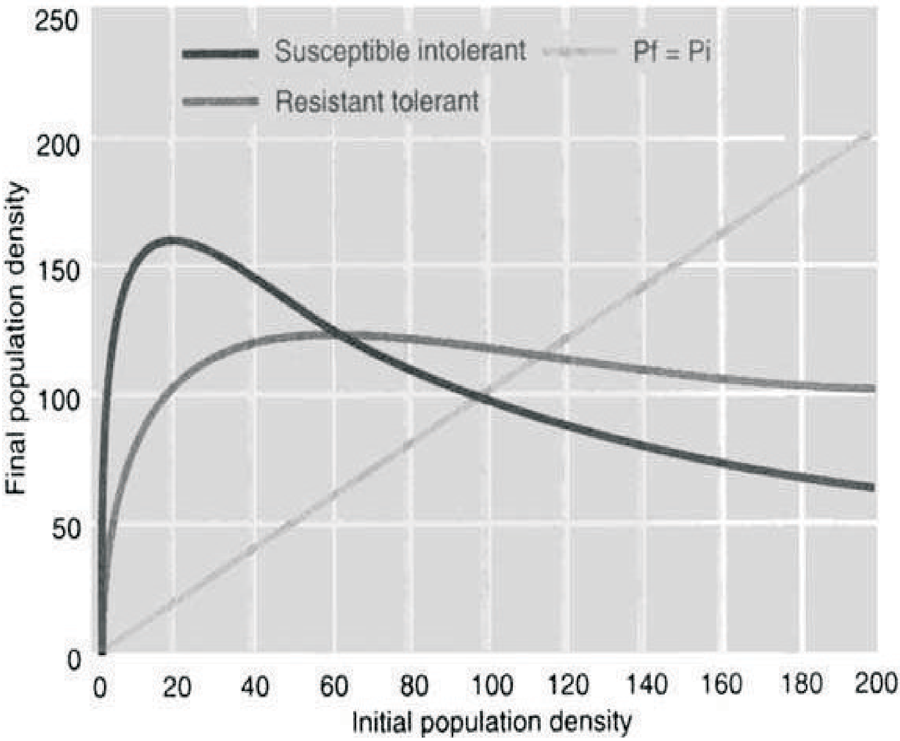

Figure 5 : *The relationship between Pf and Pi when a tolerant and an intolerant host are grown*

point at which Pf = Pi. This density is usually observed at a Pi, which is larger than that which gives the largest Pf (Fig. 5). In practice, this equilibrium density is reached after a period of oscillation about the equilibrium density. The size of the oscillations will be determined by the tolerance and resistance of the host. Tolerance and resistance will produce small oscillations, while susceptibility and intolerance can result in large oscillations. Indeed, these two factors can interact to the extent that a tolerant but partially resistant cultivar can produce a higher equilibrium density than an intolerant susceptible cultivar.

Care needs to be taken in devising management strategies for the control of nematodes to balance the benefits of tolerance against the benefits of resistance, to ensure that while yields are maximized, nematode populations are not raised to levels that are damaging to other cultivars.

Models can be used to examine and explore nematode management strategies, but need to take into account the effective population if this is less than the actual population, and the decline in the numbers of nematodes in the absence of a host crop. Annual yield losses worldwide due to plant-parasitic nematodes have been summarized in Table 1.

Table 1 : *Summary of estimated annual yield losses due to damage by plant-parasitic nematodes worldwide*

Life sustaining crops	Loss (%)	Economically important crops	Loss (%)
Banana	19.7	Cacao	10.5
Barley	6.3	Citrus	14.2
Cassava	8.4	Coffee	15.0
Chickpea	13.7	Cotton	10.7
Coconut	17.1	Cowpea	15.1
Corn	10.2	Eggplant	16.9
Field bean	10.9	Forages	8.2
Millet	11.8	Grape	12.5
Oat	4.2	Guava	10.8
Peanut	12.0	Melons	13.8
Pigeon pea	13.2	Miscellaneous	17.3
Potato	12.2	Okra	20.4
Rice	10.0	Ornamentals	11.1
Rye	3.3	Papaya	15.1
Sorghum	6.9	Pepper	12.2
Soybean	10.6	Pineapple	14.9
Sugar beet	10.9	Tea	8.2
Sugar cane	15.3	Tobacco	14.7
Sweet potato	10.2	Tomato	20.6
Wheat	7.0	Yam	17.7
Average	**10.7**	**Average**	**14.0**

Overall average 12.3 %

2.4.1 Nematode Population Dynamics and Economic Thresholds

Patterns in the population dynamics of nematodes are determined by the intrinsic characteristics that regulate rates of births and deaths of individuals and modified by conditions of the environment in which the population functions. Intrinsic factors include the productive capacity of the gonad in relation to resource demands of somatic tissues, the rate and length of the reproductive period, and the life history strategy. Modifying factors include availability of food, sperm and other driving resources, and environmental conditions. Various models have been used to describe the dynamics of populations; some are primarily descriptive of observed trends, others are more explanatory and mechanistic. All may be relevant in prescribed situations.

Economic thresholds are management tools for minimizing economic losses due to nematodes (Tables 1 and 2). They are based on projections of expected crop performance in relation to population levels at a critical point in time or at multiple points in time. The economic threshold is that level to which the population of the target nematode species should be managed under prevailing economic and environmental conditions. In its most comprehensive sense, the economic threshold is based on the integral of expected returns from the current crop and from future crops, given the expected trajectory of the nematode population at this level of management.

Table 2 : *Estimated crop losses due to major plant-parasitic nematodes in India*

Sl.No.	Crop	Nematode	Estimated loss (Rs)/Avoidable field loss
1.	Barley	*Heterodera avenae*	Rs. 30 million
2.	Black gram	*Meloidogyne incognita*	8.7%
3.	Brinjal	*M.incognita*	33.7%
4.	Citrus	*Tylenchulus semipenetrans*	15%
5.	Coffee	*Pratylenchus coffeae*	Rs. 20 million
6.	Cotton	*M.incognita*	17.7-19.9%
7.	Cowpea	*M.incognita*	28.6%
8.	Finger millet	*M.incognita*	4.8%
9.	French bean	*M.incognita*	43.5%
10.	Groundnut	*M.arenaria*	51%
11.	Maize	*Rotylenchulus reniformis*	6%
		M.incognita	6%
12.	Okra	*M.incognita*	28.1%
13.	Pigeonpea	*Heterodera cajani*	14.2%
14.	Pea	*M.incognita*	20%
15.	Potato	*Globodera rostochiensis*	Total failure of the crop
16.	Rice	*Aphelenchoides besseyi*	12.2%
		Hirschmaniella oryzae	30-87%
		H.macronata	43%
17.	Tobacco	*M.incognita*	50%
18.	Wheat	*Heterodera avenae*	Rs. 40 million

a. Economic Threshold Based on Initial Nematode Population (Pi)

At its simplest, if the control cost is $100, it makes sense (in the short term) to apply the control only when the expected crop loss is >$100. So, the economic threshold is the population level of nematodes at which the cost of control is equal to the value of the crop loss. If the population is above that threshold, the value of loss is greater than the cost of control. So, apply the control; if not, take the loss.

The above reasoning assumes that the applied control will reduce the population to a non-damaging level. If that is not the case, the economic threshold is that population at which the cost of control is equal to the difference between the crop value with and without the control. So, if the cost of control