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FOOD LOSSES IN FIELD AND STORE

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Nematode injury to crops

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Eelworms or nematodes are worm-like, translucent creatures with tough, protective cuticles. Those that feed upon or parasitize plants are about 1 mm long (Christie, 1959; Filipjev & Schuurmans Stekhoven, 1941; Jones, 1959). Their worm-like form and movement fit them to live in the labyrinth of passages in the soil, between the folded leaves of plant buds, in the air spaces of leaves and stems, or within plant tissues themselves. Nematodes do not have a waterproof surface and are soon inactivated if their environment begins to dry out, but some can withstand desiccation for a long time and, when dry, are more resistant to nematicides than when wet (Hague, 1959). Nematode cuticle has some protective properties and the environments in which they live also afford them much protection: they are rarely exposed and accessible to soil-surface or leaf-surface treatments with chemicals as are some insects and some fungal spores.

The life cycles of most nematodes are simple. The eggs hatch into young forms similar to the adults and, as generations follow each other quickly while conditions are favourable, numbers can increase rapidly. Most species show no obvious adaptations to parasitism but, in a few advanced parasites, the female becomes sedentary, loses the power of movement and degenerates into little more than a saccular, egg-laying machine. The cyst-forming nematodes (Franklin, 1949) are among the most advanced plant parasites known. In them, the female body wall becomes a leathery cyst or capsule giving additional protection to the eggs inside, which usually do not hatch until stimulated by a substance which exudes from host roots. The number of generations per year is limited, especially when the host crop has a short vegetative period, but very large soil populations may be built up when a host crop is grown repeatedly on the same land.

All known plant parasitic nematodes possess mouth parts adapted for piercing and sucking (Fig. 1), similar to those in aphids, leaf hoppers and other hemipterous insects. The head contains a hollow, needle-like stylet equipped with protractor muscles and able to pierce plant cells. After penetration, saliva is injected and cell sap withdrawn. Some nematodes remain external to plant tissue, others invade and

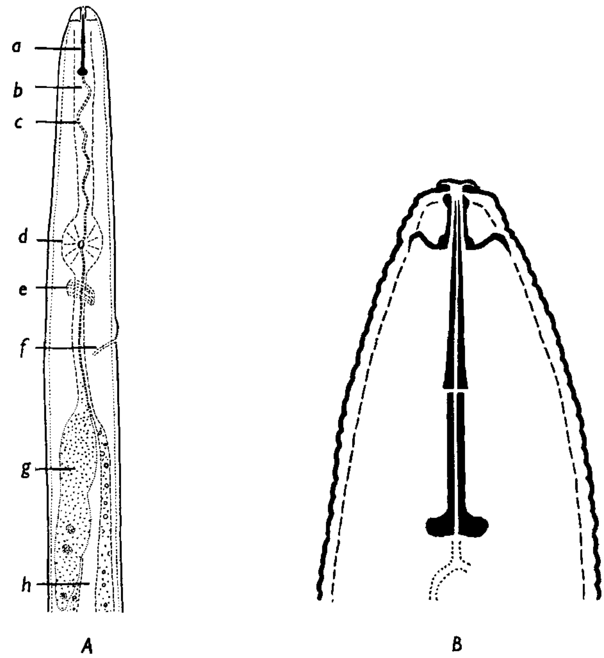

Fig. 1. Head end of plant-feeding nematode. (*A*) The structures of the pharynx: *a*, mouth spear; *b*, opening of duct of dorsal oesophageal gland; *c*, lumen of oesophagus; *d*, oesophageal bulb; *e*, nerve ring; *f*, duct and opening of excretory pore; *g*, the three oesophageal glands; *h*, lumen of the gut. (*B*) The mouth spear. Muscles are attached to the basal knobs, of which there are three. Actual size of mouth spear 13 μ. (After Franklin, 1959.)

become deeply embedded. Plants are injured partly by mechanical breakdown of cells but more by the toxic effect of nematode saliva or, as has been recently shown, by the transmission of virus diseases (Hewitt, Raski & Goheen, 1958; Jha & Posnette, 1959; Harrison & Cadman, 1959). Wounds made by nematodes also act as portals through which other pathogenic soil organisms gain entry (cf. Labruyère, den Ouden & Seinhorst, 1959) and nematodes are sometimes only one of the factors in a disease complex (Pitcher & Crosse, 1958).

Nematodes are minute, and large numbers of them are usually needed to cause direct injury of economic importance. However, it is not so when they are transmitting virus, for a single nematode may infect and permanently cripple a whole plant.

Nematodes injurious to plants fall into two groups, one found in the soil down to appreciable depths and the other essentially soil-surface animals that invade plants and sometimes move up them (Wallace, 1959) or get carried up during growth to infest aerial parts. Occasionally they occur in flower heads and so may be seed-borne (Goodey, 1949). Injury by root-feeding nematodes is not at once obvious, unless large and prominent galls are formed, as by *Meloidogyne* spp. and *Nacobbus* spp., or where the roots are lined with swollen females as by *Heterodera* spp., *Rotylenchulus reniformis* and *Tylenchulus semipenetrans* (Steiner, 1953). Root feeding, whether external or internal, may stop the elongation of growing points and lead to abnormal and excessive branching and so affect the main root tips that thickened and stubby growth ensues, or cause lesions and necrotic cavities. These types of injury result in patches of stunted and wilted plants exhibiting signs similar to, and often mistaken for, those caused by drought or a deficiency of some essential element. The relationship between the degree of injury and the initial population of nematodes in the soil has been most studied in the cyst-forming nematodes (Jones, 1959). The regression of yield or growth and initial population is not linear but logarithmic (Jones, 1957). Because of intraspecific competition for root space, the number of nematodes per unit length of root required to reduce yield by a given amount rises as the population density rises. Population increase is greater at low initial population levels than at high, and is density-dependent. Population decrease, however, is density-dependent and continues at a fairly steady rate over a period of years. The eggs contained in the cysts are in large measure buffered from the environment around them and the decline in their numbers seems to result mainly from spontaneous hatch in April and May each year, and is proportional to the average number of eggs remaining in the cysts. After a host crop, populations sometimes increase to levels approaching 500 eggs/g soil (5×10^{11}/acre) and it may take from 5 to 7 years or more before a safe level is reached again.

The second group of nematodes, which affect stem and leaf structures in or above the soil surface, contains the stem and bulb eelworm (*Ditylenchus dipsaci*) the potato tuber nematode (*D. destructor*), the bud and foliar nematodes (*Aphelenchoides* spp.) and seed gall nematodes (*Anguina* spp.). Injury by these nematodes varies greatly but includes the following gross signs: abnormal growth, distortion, bloating, gall-formation and canker. Infested plants are usually stunted, misshapen, unthrifty and tend to die in patches, so that yield is greatly reduced. In arable land, especially if light and sandy, the surface tends to dry out and heat up, making conditions unfavourable for these kinds of nematode, although there may be cool, moist periods in early spring and autumn when activity is possible. Soil-surface nematodes are favoured more by cold, moist clay soils, low temperatures, irrigation and heavy rainfall. The stem eelworms, for example, are most prevalent in north temperate regions such as Great Britain, Scandinavia and parts of North America, in moist river valleys in Switzerland and some irrigated valleys in Western U.S.A.

Less is known about population levels of this second group of nematodes, and population changes do not follow the same simple trends as with the cyst-forming kinds (Seinhorst, 1956). Weed hosts, even if they do not support rapid reproduction, self-sown crop plants and ground-keepers are probably all important in maintaining low levels of infestation. Infestations may also be introduced in soil, seeds or other planting material. Under favourable conditions reproduction is rapid on susceptible crops but devastating attacks usually occur only where a susceptible crop follows one previously infested. In lucerne, in which the race of stem eelworm that attacks the crop is thought to be introduced as occasional individuals adhering to the seed, small foci of infection appear at the end of the 1st year, spread locally during the 2nd year and engulf the greater part of the crop in the 3rd year (Brown, 1957). Soil populations of astronomic size are left after devastating attacks, but numbers fall rapidly, especially when soil conditions are adverse, weeds are rigorously suppressed and susceptible crops are withheld in the following year.

In Europe, cyst-forming nematodes are of great economic importance. The beet eelworm caused trouble early in the development of the beet industry in Germany but was not recognized as the cause of *Bodenmüdigkeit* until 1859. Even after the cause of the disease and the value of crop rotation in controlling it was recognized, farmers in the beet-growing areas of Europe and elsewhere continued to overcrop with beet and brassicas, and fertile land around factories went out of beet production, sometimes causing factories to close. This pattern began to repeat itself in Great Britain after the establishment of the sugar-beet industry in 1925, but fortunately a policy of crop rotation was adopted by the British Sugar Corporation from 1937 and the Sugar Beet Eelworm Order 1943 enforced crop rotation in the areas most threatened (Jones, 1959). Potato-root eelworm was introduced into Europe about 1900 or earlier and is continuing to spread in many European countries. In Britain it occurs in all the principal potato-growing areas and in gardens and allotments all over the country (Thompson, 1959). It also affects tomatoes in glasshouses. Very heavy losses occurred towards the end of World War II because of the greatly increased wartime acreage. The smaller acreage now grown, realization of the importance of crop rotation, and advice to growers based on soil sampling, have all helped to lower infestations on farms, but in gardens and allotments the pest continues to increase. Losses from cereal-root eelworm attacks on oats were worst some time after the war, possibly as a result of intensive growing of cereals (Rolfe, 1959). Here too losses appear to have declined somewhat in the last few years. The pea-root eelworm remains something of an enigma, as attacks sometimes occur on land where peas or other known host crops have not been grown for many years.

In Britain, stem-eelworm attacks on oats, clover, lucerne and onions are important locally, but more widespread and serious trouble is experienced in the Scandinavian countries.

Cyst-forming eelworms cause problems in the northern half of the U.S.A., where they are serious on sugar-beet, soya beans and shade tobacco in a number of areas. Potato-root eelworm is known only from Long Island and is a declining problem. Onions and lucerne suffer losses from stem eelworm. Various species of migratory soil-nematode affect a wide range of crops in the light, sandy soils of the south-eastern coastal plain (Christie, 1959). The citrus industry of Florida is menaced by a disease known as 'spreading decline' caused by the nematode *Radopholus similis* which attacks the root system down to 5 ft or more below the surface. Large areas have been cleared and treated with nematicide in an attempt to contain the foci of infection (Suit & Ducharme, 1957). Races of the same nematode cause 'black-head toppling' disease of banana in Jamaica (Leach, 1959), parts of central and South America and elsewhere and also 'decline' in pepper plantations in Indonesia (Kalshoven & van der Vecht, 1959) and Sarawak. The nematode *Rhadinaphelenchus cocophilus* causes red-ring disease of coconuts in the Carribean area (Fenwick, 1957). Throughout the southern U.S.A. and most other intensely cropped areas of the world with tropical or subtropical climates, root-knot nematodes, *Meloidogyne* spp., cause outstanding losses in many crops. Because there are few trained nematologists, many other important nematode problems on key food crops such as rice and paddy remain uninvestigated.

Because nematodes are soil organisms, control is especially difficult. Few satisfactory nematicides are known and these are too expensive for most agricultural crops in Europe. For these reasons, control is largely based on knowledge of host ranges, crop rotation, use of resistant varieties and eradication of weed hosts. Hot-water treatment of bulbs, stools or runners is also practised. These methods are valuable but are not always convenient or sufficiently effective. Chemical control at economic prices is the ultimate goal.

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Crop losses by insects and the problem of control

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'. . . animals which annually consume an amount of produce that sets calculation at defiance; and, indeed, if an approximation could be made to the quantity thus destroyed, the world would remain sceptical of the result obtained, considering it too marvellous to be received as truth.' (Curtis, 1860.)

'Insecticides and other pesticides will be increasingly used, because agriculture cannot forego the benefits they confer, but this carries with it the obligation to know as much as possible about the ways in which they kill and their effects on animals other than those they are immediately directed against.' (Bawden, 1960.)