

# Ecology of longidorid nematodes

Bernhard Weischer\* and Maria Teresa M. Almeida\*\*

\* Biologische Bundesanstalt, Institut für Nematologie und Wirbeltierkunde, Toppeheideweg 88, D-48161 Münster, Germany.

\*\* Universidade do Minho, Departamento de Biologia, Campus de Gualtar, P-4709 Braga, Portugal.

Accepted for publication 10 September 1994

**Summary.** This review demonstrates how the main aspects of a nematode's biology are influenced by major ecological factors. Global distribution of longidorids is determined by natural geological events (e.g. continental drift) and by man-made dissemination with plant material. The present regional distribution is due to quaternary glaciation, post-glacial spread, climate and soil properties. Local occurrence is essentially governed by microclimate, soil and vegetation. Depth distribution depends mainly on soil texture, soil moisture and host roots. Soil texture is particularly important for migration because large nematodes such as longidorids are unable to force a passage through the soil as roots do. Main factors influencing population development are the reproductive capacity of a species, the climate, host plants and antagonists. Some longidorids have developed strategies for survival in plant-free soil and under adverse conditions.

**Key words:** *Longidorus*, *Xiphinema*, *Paralongidorus*, distribution, ecology, survival, host interactions.

After the recent synonymisation of *Longidoroides* with *Paralongidorus* by Siddiqi et al. (1993) the family Longidoridae is comprised of the four genera *Longidorus*, *Paralongidorus*, *Xiphinema* and *Xiphidorus*. Its members are large ectoparasitic nematodes with relatively long life-cycles and thus are more susceptible to the influence of various ecological factors than are most other phytonematodes. Longidorids are of particular interest because several species can transmit plant viruses (Weischer, 1993). In this review we discuss how some aspects of nematode biology are influenced by major edaphic, biotic and intrinsic factors.

Since the publication of a comprehensive review by Weischer (1975) numerous research papers have contributed to a better understanding of longidorid ecology although considerable gaps in our knowledge still remain. In part this is the result of a rapid increase in the number of new species described and to the many changes in longidorid taxonomy during the last 20 years. Furthermore, little is known about the biological and ecological parameters of longidorids. Some species are extremely difficult to culture under controlled conditions *viz.* *X. americanum* - group spp.,

and for the majority of species this has not yet been attempted. Consequently, most data available and presented here were obtained from research done with a limited range of species, mainly those which transmit viruses.

*Xiphinema americanum* Cobb, 1913 is probably the most intensively studied longidorid nematode with numerous publications describing various aspects of its biology and ecology. For more than 50 years it was considered to be a widely distributed, highly adaptable species. However, after a taxonomic revision by Lamberti & Bleve-Zacheo (1979) it is now considered to be a complex of 39 different species (Lamberti & Ciancio, 1993). Ecological data published for *X. americanum sensu lato* are now being re-examined (Robbins, 1993). In our paper only data for *X. americanum sensu stricto* are given unless indicated otherwise.

## GLOBAL DISTRIBUTION

The world-wide distribution of nematodes results from two different factors: natural geological events such as plate tectonics and continental drift, and man-made dissemination through international trade. The

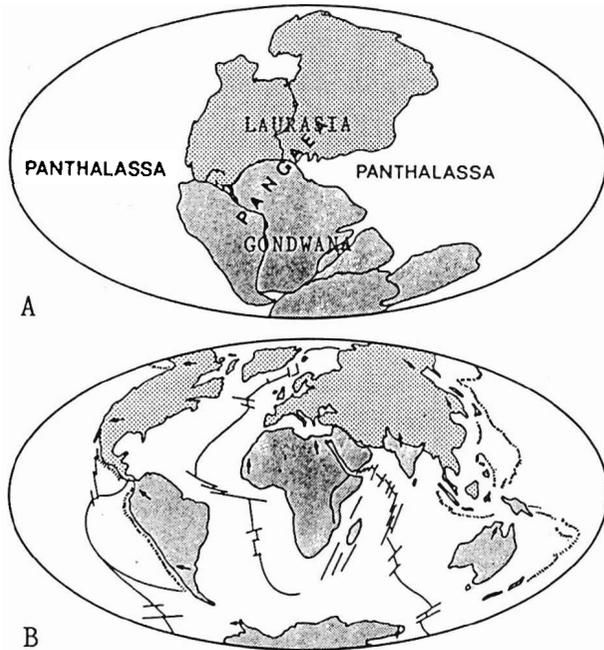


Fig. 1. Continental drift. A. Pangaea (220 million years ago) and its future division into Laurasia and Gondwana, with the present continents indicated. B. Present situation: coarse stipling, continents derived from Laurasia; fine stipling, continents derived from Gondwana.

most reliable information about natural occurrence can be gained from surveying natural undisturbed habitats. Until now this has been done only to a limited extent (Alphey & Taylor, 1986; Brown & Taylor, 1987; McNamara & Flegg, 1981; Navas et al., 1990).

Coomans (1985) studied the classification of Longidoridae using phylogenetical and biogeographical criteria. From the present global distribution he concluded that *Xiphinema* is a cosmopolitan genus originating in Gondwanaland during the Permian period. From there it spread to Laurasia before the break up of Pangaea some 180 million years ago (Fig. 1). Subsequently, speciation (species formation) took place in Africa from where today the majority of species have been reported. The genus *Xiphidorus* is restricted to South America with four species described from Argentina and four from Brazil. These species probably originate from their ancestors after the separation of South America from Africa during the cretaceous period.

From the present distribution of *Paralongidorus* and *Longidorus* it may be concluded that they probably originated in South-East Africa and India

prior to the separation of these continents. In these regions the main speciation in *Paralongidorus* took place whilst the main speciation of *Longidorus* occurred in Europe following a spread to Laurasia.

World-wide man-made distribution is clearly demonstrated by *X. index* with its close connection with viticulture. This species has been found only rarely under indigenous vegetation, mainly in the vicinity of vineyards. Obviously *X. index* has been disseminated to all continents with planting material from its centre of origin in Iran (Martelli & Taylor, 1989).

## REGIONAL DISTRIBUTION

The term 'regional' is used here in contrast to 'global' and is used in a broad sense. For Europe and the Mediterranean region Brown & Taylor (1987) and Brown et al. (1990) provided a thorough survey on the occurrence of longidorids. The present regional occurrence can partly be attributed to geological events. Topham & Alphey (1985) related the scarcity of longidorids in Northern Europe to the influence of quaternary glaciation. Similarly, Dalmaso (1970) connected the present distribution of longidorids in France with glaciation. Based on their actual occurrence this author distinguishes between Atlantic species (e.g. *X. diversicaudatum*) and Mediterranean species (e.g. *X. italiae*, *X. pachtaicum*) thus indicating the direction of post-glacial spread as well as preferences in climate (Fig. 2). Also, Navas et al. (1990) recognised Euroatlantic and Mediterranean species of longidorids. In a detailed analysis of the distribution of *Longidorus* species in the Euromediterranean region Navas et al. (1993) determined centres of distribution within distinct geographical areas. They suggested that after the period of glaciation species such as *L. africanus*, *L. congoensis* and *L. intermedius* were the origin of dispersive speciation in this region.

Vegetation is another factor influencing regional occurrence and distribution of longidorids. Harrison & Winslow (1961) suggested that *X. diversicaudatum* is a common constituent in natural woodland in Britain and that its incidence has decreased since the advent

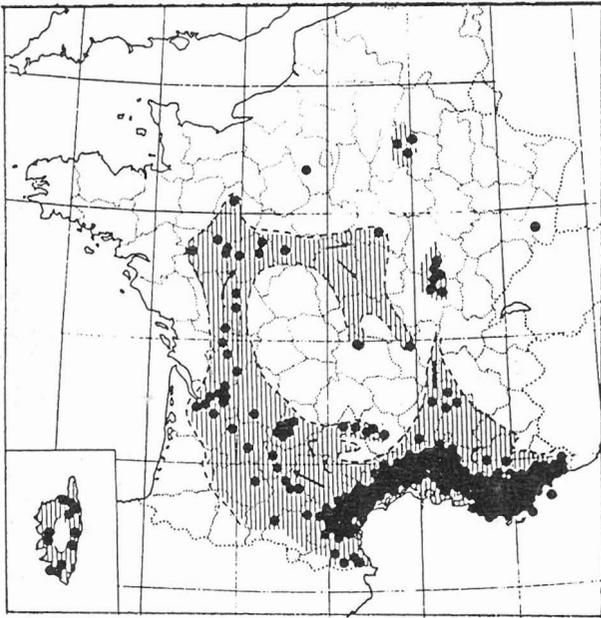


Fig. 2. Occurrence and post-glacial spread of *Xiphinema pachtaicum* in France. (From Dalmasso, 1970).

of agriculture. Similarly, McNamara & Flegg (1981), based on their studies of the present pattern of occurrence, suggested that the distribution of longidorids in the UK was determined initially by the prehistoric vegetation. Rau (1975) studied the occurrence of virus transmitting nematodes in near-natural habitats in Lower Saxony, Germany. He was able to relate some longidorids to distinct plant communities. For example, *X. diversicaudatum* was mainly found in oak-hornbeam forests, type *Stellaria-Quercus-Carpinetum* and *X. vuittenezi* in beech forests, type *Melicophagetum elymetosum*, indicating a preference for continental habitats.

The influence of soil properties on regional distribution is evident with *X. diversicaudatum*. This species is absent in Eastern Switzerland and adjacent parts of Germany but frequently found outside this area. Klingler et al. (1983) attributed this pattern to the soil i.e. to the type of original rock. In the region without *X. diversicaudatum* soils are derived by weathering of calcareous rock with an average pH of 7.8 whereas in the adjacent regions where the nematodes occur the soil is derived from siliceous rock with an average pH of 6.2 (Fig. 3). Also, in Spain this

species is frequently found in soils with pH=5-6.5 but very rarely in calcareous soils (Navas et al., 1988). However, in Great Britain it occurs in a wider range of soil types (Taylor et al., 1978).

As all ecologically active biotic and abiotic factors form a system of interconnected and interacting relationships the examination of a single factor cannot fully explain the observed distribution of nematodes. Multifactorial analyses give more satisfactory results. In Spain *X. italiae* was found in uncultivated areas with acid or slightly acid sandy soils at relatively high altitudes in a sub-humid climate. In contrast, *X. index* occurred only in cultivated areas, mostly vineyards, at lower altitudes in Mediterranean environments (Navas & Arias, 1986). The latter species seemed to be less restricted by physical environmental factors. For both species soil temperature and moisture were the main limiting factors (Arias et al., 1992). The optimum biotope for *X. coxi* was a vegetation of supramediterranean to subatlantic type, humid brown soils with a texture between sand and sandy loam and a normal to rich content of organic matter, pH=6 and an altitude of 1280 m (Arias et al., 1987). *X. diversicaudatum*, an Atlantic species, occurs in Spain in sandy siliceous soils (pH=5-6.5) with a high content of organic matter under natural vegetation at higher altitudes. This species was negatively associated with a warm continental climate. In contrast *X. pachtaicum*, a Mediterranean species, occurred most frequently in arable land on calcareous soils (pH=8) at lower altitudes and its presence was not markedly affected by climate (Navas et al., 1988). *Longidorus macrosoma* is seldom found at altitudes above 650 m and occurs most frequently in heavy calcareous clay soils with pH=7.5-8.5 (Buser, 1990).

## LOCAL DISTRIBUTION

Similar to 'regional' the term 'local' is used here in a broad sense. It comprises single sites with identical or similar biotopes (e.g. vineyards) and small areas. Local occurrence and distribution of longidorids are essentially determined by microclimate, soil properties and vegetation. Dalmasso (1970) recorded a high correlation between the presence of some



Fig. 3. Influence of soil on the regional distribution of *Xiphinema diversicaudatum*. Soils are derived from calcareous rock in the region in which this nematode is absent (hatched area). (Modified from Klingler et al. 1983).

longidorids and local climate. He found *X. vuittenezi* in areas with an annual rainfall of 500-700 mm but not in adjacent areas with higher rainfall. In contrast, *X. neovuittenezi* was found only in very warm localities with an annual rainfall of less than 500 mm. In sugarcane fields in Mauritius, Williams & Luc (1977) found *X. elongatum* mainly in latosolic reddish prairie soils and low humic latosols in lower elevations with an annual rainfall less than 2500 mm. The distribution of *X. krugi* complemented that of *X. elongatum*. *X. krugi* was widespread in latosolic brown forest soils and humic ferruginous latosols at higher elevations with an annual rainfall of more than 2500 mm. *Xiphinema*

*vulgare* was essentially confined to calcareous sandy soils whilst *X. insigne* appeared tolerant of different soil conditions.

Andres & Bello (1984) found the abundance of *L. profundorum* in a brown non-calcareous soil to be positively correlated with the sand content. Another example of the close relation between soil type and the abundance of a longidorid nematode was described by Luc & Hoestra (1960). Under coconut palms without undergrowth the population density of *X. attorodorum* was closely correlated with the soil type: 11 individuals per litre in coarse sand, 36 in red alluvial soil, 52 in fine

sand and 340 in a fine textured soil rich in organic matter (*terre de barre*).

Vegetation can exert a major influence on the local occurrence and distribution of longidorids. Rüdell (1990) reported the occurrence of *X. diversicaudatum*, *L. attenuatus* and *L. macrosoma* in vineyards in the Palatinate, Germany to primarily depend on the pre-vineyard vegetation and to a lesser extent on soil characteristics. This may change in course of time under continuous grapevine.

For several longidorids water is the limiting factor. *Xiphidurus amazonensis*, *Xiphinema attorodorum*, *X. bergeri* and *Paralongidorus australis* occur, and are active, only in very wet to submerged soils (Uesugi et al., 1985; Luc & Hoestra, 1960; Luc, 1973; Stirling, 1985).

### DEPTH DISTRIBUTION

The main factors determining the depth distribution of longidorids are soil texture, moisture and host roots. Compared to other migratory ectoparasitic nematodes, longidorids colonise and sometimes prefer deeper soil layers. With *L. macrosoma* Flegg (1968) observed an increase in numbers with increasing depth to 70 cm and *L. profundorum* was present in even deeper layers. In contrast, numbers of *X. diversicaudatum* and *X. vuittenezi* decreased with increasing depth. In Eastern Scotland most *L. elongatus* were found in the top 10 cm of the soil while most *L. leptocephalus* were below 30 cm (Boag et al., 1987). *L. arthensis* (Brown et al., 1994) and *L. orongorongensis* (Yeates et al., 1992) were found only below 50 cm.

In old vineyards the vertical distribution of *X. index* extended to a depth of 2.4 m, single specimens occurring even at 3.6 m (Raski et al., 1965). In vineyards of Moldavia, Polinkovsky (1980) found *X. index* in all soil layers from 0-150 cm with a maximum density between 30 and 80 cm. Ferris & McKenry (1974) found *X. americanum sensu lato* in the upper 45 cm of an undisturbed soil with a maximum at 20 cm. This depth distribution was independent of the occurrence of roots. In contrast, *X. diversicaudatum* showed a significant relation to plant roots (Aboul-Eid

& de Maeseneer, 1973; Cotten, 1977) with fewer nematodes present at 40-60 cm below the four annual crops tested than below three perennial plant species. Also, differences were observed between the perennial crops in the nematodes distribution which was uniform to 40 cm under perennial ryegrass but under strawberry there were significantly more nematodes in the top 20 cm. Both plants are good hosts for the nematodes. Also, Barbez (1982) reported a definite influence of plants on the average depth distribution of some longidorids e.g. *L. leptocephalus* was found at 10-17 cm depth in a hop field and at 0-90 cm under pasture and *L. caespiticola* was present at 10-80 cm under hop and at 20-70 cm under pasture.

### SPREAD

Nematodes can colonise new sites either by active migration through the soil or by passive translocation by water, wind, animals or man. Nematodes are confined to a localised place in the soil because they are mostly unable to force a passage through the soil as do roots and earthworms. Therefore, soil texture has an important influence on large nematodes such as longidorids. The nematode's body diameter is more important than its length. Jones et al. (1969) found *X. diversicaudatum* in an untilled woodland containing much clay only in macropores between aggregates and not in the primary space between soil particles. The space available for these nematodes decreased from 13% of the total soil volume at a depth of 2 cm to 5% at a depth of 30 cm corresponding with increasing amounts of clay and thus also determining the vertical distribution of the nematodes.

The horizontal spread of *X. diversicaudatum* in woodland was estimated to be 30 cm per year by Harrison & Winslow (1961). Taylor et al. (1994) analysed the same site 30 years later and concluded that in undisturbed habitats *X. diversicaudatum* can remain for several decades without much lateral spread. Thomas (1981) observed a migration rate under near-field conditions for *L. elongatus* of 10 cm/month and 6 cm/month for *X. diversicaudatum*. Migration in the vertical plane was of a similar range. With both species, most movement occurred under

favourable hosts but very little movement occurred in plant-free soil.

The influence of soil type, temperature and moisture on the horizontal migration of *Xiphinema coxi*, *X. diversicaudatum* and *L. macrosoma* was studied by Fritzsche (1968) under laboratory conditions. In all four soils tested (heavy clay, humous loam, stony loam and light sand) the optimum temperature for nematode migration was 20-22° C and the optimum soil moisture was 18-20%. The optimal soil type for migration was different for the different species. *Xiphinema coxi* moved 2 mm/day in light sand but only 0.7 mm in heavy clay, *X. diversicaudatum* 1.8 mm in heavy clay and 0.4 mm/day in stony loam, *L. macrosoma* 1.4-mm/day in the three heavier soils but only 0.4 mm in light sand.

Soil moisture is a very important factor, especially for ectoparasites. Nematodes cannot move when the forces binding water to the soil structure are too strong and similarly are unable to move when all spaces are filled with water and aeration is blocked. In contrast, *Paralongidorus australis* migrates only in flooded and not in moist and dry, clay soils (Stirling, 1985). This inability to move in non-flooded soil is most probably related to soil structure. Large nematodes may move in very wet soils by pushing aside loosely held fine particles even when the natural pore size is smaller than their body diameter (Jones et al., 1969). The vertical movement of several nematode species was studied under near-field conditions by Rössner (1972). After two months 30% of the population of an undetermined *Longidorus* species were found at 75-100 cm depth and after three months several individuals had reached the zone between 130 and 160 cm depth.

All these data demonstrate that active movement of nematodes leads only to short range spread with greater distances only achieved by passive translocation. As already mentioned the presence of *X. index* in vineyards world-wide is obviously due to the nematode being disseminated with plant material.

The influence of rivers and irrigation water on the spread of longidorids was demonstrated in South Africa. Barbercheck et al. (1985) found *X. index* in 41

of 56 irrigated localities along the Bree River, whereas, 15 years previously it had occurred only at three sites. A similar spread was observed with *X. italiae* by van Reenen & Heyns (1986) in vineyards irrigated from the Berg River. This species had probably been introduced accidentally at the first site and subsequently spread via the river and through irrigation water.

From the very restricted distribution of *Longidorus vineicola* in Scotland and the morphological similarity between the isolated populations from some islands off the north-west coast Boag & Brown (1987) concluded that this species had been introduced by man only on one occasion and subsequently had spread. Another investigation from Scotland showed that numbers of *Longidorus elongatus* extracted from soil adhering to boots and tractor tyres were 10% of the numbers obtained in the same sample size directly from the field, thus demonstrating the efficiency of localised spread by man and by farm implements (Boag, 1985).

## POPULATIONS

Major factors influencing nematode populations are the reproductive capacity of the species, the climate (in particular the seasonal fluctuations), host plants and antagonists. For most longidorid species little is known about their reproductive capacity. However, data are available for *X. diversicaudatum* (Brown & Coiro, 1983) and *X. index* (Brown & Coiro, 1985). With *X. diversicaudatum* the estimated total reproduction of an individual female is 180-200 progeny. Under the climatic conditions of southeastern England a female had a yearly production of 68 eggs and a reproductive life-span of three years (Flegg, 1968). Females of *X. index* on *Ficus carica* had a reproductive life-span of 56 weeks at 20° C and produced a total of 150 progeny.

The actual reproduction rate of a population is greatly influenced by the climate. Although many longidorids can survive in frozen soil for some time they generally need higher temperatures for activity, especially for feeding and reproduction. At 10° C very few *X. index* fed on fig and tomato and reproduction

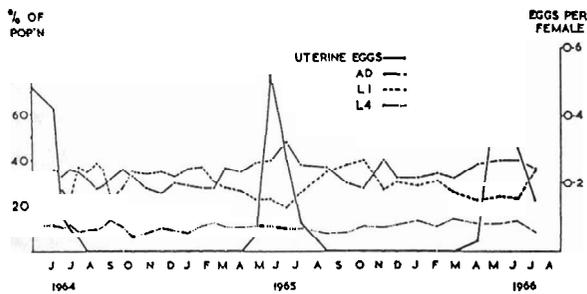


Fig. 4. Egg production by *Xiphinema vuittenezi* occurs only during the early summer (peaks). (From Flegg, 1968).

did not occur. At 13° C most nematodes fed but only 14% of the females produced eggs whereas at 23° C all females reproduced (Coiro et al., 1991). Similarly, *L. elongatus* showed no development at 10° C (Wyss, 1970). Under greenhouse conditions at 20° C *X. index* completed its life cycle within six weeks whereas it took up to one year in the field (Dalmasso, 1970). Coiro & Agostinelli (1991) calculated the minimum temperature required for each stage of *X. index*: for egg to J<sub>1</sub> = 168 day/C; for J<sub>1</sub> = 56 day/C; for J<sub>2</sub> = 54 day/C; for J<sub>3</sub> = 56 day/C; for J<sub>4</sub> = 112 day/C; for young to gravid female 112 day/C. From these data the proportions of the life-cycle can be estimated as 3:1:1:1:2:2, with the J<sub>4</sub> stage taking twice as long to develop as the three other juvenile stages.

In temperate climates where there are distinct seasons egg production in most longidorids is limited to a short period of early summer when temperatures are adequate and suitable fresh roots are available (Fig. 4). A second period can occur in early autumn when perennial plants produce a second flush of new roots as shown by Taylor (1967) and Thomas (1969). The duration of each juvenile stage is greatly influenced by temperature. Consequently, the proportion of juvenile and adult stages in a population has no regular annual cycle.

Recently it has been reported that some species of the *X. americanum*-group have only three instead of the usual four juvenile stages (Halbrendt & Brown, 1992, 1993). It is not yet known whether this has any bearing on the duration of the development.

The influence of soil type on the population density of *X. vuittenezi* was demonstrated by Rüdél (1975). Under grapes the average densities of the nematode were three individuals/250 ml in slate derived soils, 25 in loam, 35 in sand and 125 in sandy loam.

The presence and quality of hosts are the most important factors governing population development. Populations of *L. elongatus* increased rapidly on *Fragaria vesca*, *Stellaria media*, *Mentha sativa* and *Lolium perenne* and slightly under turnip; but on raspberry they declined at the same rate as in fallow soil (Taylor, 1967). *Xiphinema diversicaudatum* increased under perennial ryegrass, raspberry and strawberry but decreased under hop, potato, sugar beet, cabbage and some cereals (Cotten, 1977). With the same species Griffiths & Trudgill (1983) reported a 32-fold increase on strawberry but only an 8-fold increase on raspberry within one generation. With *L. elongatus* they recorded a 34-fold and an 8-fold increase on strawberry and turnip respectively. These differences in population increase were partly due to a prolonged generation time on the poorer hosts. Another example of how hosts can influence population development was shown by Brown & Coiro (1985) and Coiro et al. (1987): the reproductive capacity of *X. index* under tomato was only 20% of that under fig.

Rüdél (1975) studied the influence of different hosts on the population development of *X. vuittenezi*. Within five months the average numbers per 250 ml of soil increased from 30 to 61 on grapevine, from 36 to 275 on barley and from 34 to 503 on potato. When comparing reproductive capacities of species under different hosts it is important to note the differences in feeding behaviour within the longidoridae. Some are strict root-tip feeders whereas others can also attack other sites. Therefore, the density of roots and root-tips which differs with different plants can significantly influence the results obtained.

Not only species but also populations of the same species can have differences in their host ranges. A population of *X. index* from USA reproduced well on tomato cv. Haubners Vollendung whilst a population

from Italy did not (Coiro et al., 1990). In this case the cultivar was the decisive factor. In addition, the US-population had a greater reproductive capacity and a shorter life cycle. With *P. australis* the presence of host roots alone is not sufficient to incite a population increase (Stirling, 1985), only when the soil is flooded does reproduction begin (Fig. 5).

Many antagonists can affect longidorid populations e.g. species of the bacterium genus *Pasteuria* are known to infest nematodes. Species and isolates of these bacteria are highly specialised and have restricted host ranges. In their review Sayre & Starr (1988) listed 11 *Xiphinema*, five *Longidorus* and one *Paralongidorus* species as hosts of *Pasteuria* spp. The number of new associations is increasing and it is likely that several new *Pasteuria* species associated with nematodes, including longidorids, remain to be discovered. However, their effect on longidorid populations is limited. In an orchard naturally infested with *P. penetrans* the degree of parasitism proved to be density dependant and the maximum rate of parasitised individuals of *X. diversicaudatum* was only 22.3% over a period of two years (Ciancio, 1994). Jaffee (1986) and Jaffee & Shaffer (1987) studied the parasitism of *X. americanum* and *X. rivesi* by zoosporic fungi. Both species were attacked by several fungi e.g. *Catenaria anguillulae*, *Lagenidium caudatum*, *Aphanomyces* sp. and *Leptolegnia* sp., but none of the fungi was able to significantly reduce the nematode numbers in the soil. *Xiphinema rivesi* was more susceptible than *X. americanum* to *C. anguillulae* and isolates of this fungus differed in their virulence to the nematodes. In the experiments of Dürschner (1983) *X. index* was not infected by *Drechmeria coniospora*, *Cephalosporium balanoides*, *Nematoctonus leiosporus*, *Haptoglossa heterospora* and *H. zoospora*. However, individuals in a greenhouse population were naturally infested with *Pythium middletoni*, so far only known from India. Perkins & Atkinson (1992) reported nematophagous fungi exerting a seasonal influence on the density of *L. elongatus*.

Among predators, some acari are reported to attack longidorids. Sturhan & Hampel (1977) reported that the bulb mite, *Rhizoglyphus echinopus* fed on *X.*

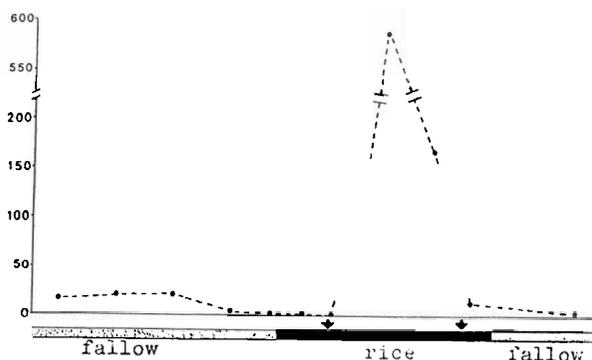


Fig. 5. In the presence of the main host, rice, reproduction by *Paralongidorus australis* only occurs when the soil is flooded (interval between arrows). (Modified from Stirling, 1985).

*index* and *L. elongatus*. However, the efficiency of such predators is generally low.

Interspecific competition also can influence population development of longidorids. Norton (1969) showed that the root-knot nematode, *Meloidogyne hapla*, reduced the population development of *X. americanum sensu lato*. Similarly, inoculated *Pratylenchus vulnus* quickly superseded in numbers an established population of *X. index* on grapes (Pinochet et al., 1976). In both cases the higher multiplication rate of the tylenchid competitors and the changes they induced in the plant tissue are probably the main causes of the longidorid decline. The influence of soil type on reproduction was demonstrated by Coiro et al. (1987). In sand and loam the population densities of *X. index* were similar, but were generally lower and increased more slowly in clay soil.

## SURVIVAL

Longidorids have comparatively low multiplication rates and long life-cycles. Therefore, individual survival is important for the persistence of a species. Survival strategies are important for species in habitats with fluctuating conditions such as substantial changes in temperature and moisture. Also, nematodes with long life-cycles must be able to survive in plant-free soil for extended periods of time by using food reserves or slowing their physiological processes. The maximum period of survival of longidorids recorded in plant-free soil occurred with *L. macrosoma*

when individuals survived for up to five years in host-free soil (Buser, 1990).

Survival in fallow soil can be greatly influenced by temperature and moisture. *Xiphinema bakeri* survived best at 4° C and moisture pressure of pF=2.4 and worst at 30° C and pF=4.2. Mortality increased with increasing temperature or moisture, the early development stages being more susceptible than pre-adults and adults (Sutherland & Slugget, 1974). The importance of soil moisture for survival of *X. index* was shown by Raski & Hewitt (1960) when nematodes survived for five months in moist, sterile, sandy loam, and for 35 days in the same soil when dry.

Studying the influence of soil moisture and particle size on the survival of *X. index* under greenhouse and laboratory conditions, Sultan & Ferris (1991) found that maximum survival in host-free soil was not more than 60 days even under favourable moisture conditions. Survival was very low in both saturated and dry soils. The comparatively high susceptibility of *X. index* to adverse ecological conditions must probably be seen in relation to the high multiplication rate due to a short life-cycle and parthenogenicity in this species.

Several longidorids are able to survive unfavourable conditions by entering stages of inactivity and arrested development. The review by Antoniou (1989) on this subject shows that information on longidorid survival is scarce.

A simple adaptation to water loss is shown by *P. maximus*. In slowly drying soil individuals coil tightly thus reducing the area of the outer body surface and water loss (Sturhan, 1963). With *X. pachtaicum* summer quiescence with reduced metabolism is a regular phenomenon (Dalmaso, 1970). This species is well adapted to moderate desiccation and can remain quiescent for more than one year whereas it does not survive in very wet soil. *Paralongidorus australis* has various ways to survive adverse conditions (Stirling, 1985). In slowly drying soil these nematodes assume a coiled form and become quiescent. Initially, inactive females still produce eggs indicating an only slightly reduced activity. In this stage the nematodes can be quickly reactivated by water. Continued drying leads

to an anhydrobiotic status which enables the nematode to survive for five months in a dry concrete-like soil. Surprisingly, *P. australis* can also survive in wet micro-aerobic and anaerobic environments for several months. The physiological mechanisms responsible for this phenomenon are not known.

A 'survival factor' was reported for *L. profundorum* and *X. diversicaudatum* (McNamara, 1978, 1980a,b). Nematodes stored in plant-free, heat-treated soil became translucent and died within a few weeks whilst nematodes stored in plant-free field soils retained their opacity and survived for more than 22 weeks (observation period). In translucent individuals of *X. diversicaudatum* the intestinal cells had lost their storage lipids and were heavily vacuolated. The intestine became extended and developed a large empty lumen. Furthermore, the concentrations of several fatty acids from other parts of the body decreased. In opaque individuals the intestinal lumen was small and the cells full of lipid globules. Closer study revealed that the 'survival factor' was destroyed by heating over 65° C and by lyophilisation but survived -40° C, drying, high vacuum and sonication. It was absent from soil leachings and could pass through a 50 µm aperture sieve. From his results McNamara (1980b) concluded that the 'survival factor' could be a microorganism which induced partial quiescence' in the nematode. For *L. macrosoma* a similar factor has been suggested (Buser, 1990).

## HOST INTERACTIONS

As already shown, host plants are a major ecological factor influencing many aspects of nematode life. Cohn (1975) reviewed the relations between longidorid nematodes and their hosts. All longidorids are ectoparasites feeding below rhizodermal cells. The basic pattern consists of several steps: exploration of the root surface, penetration of the root tissues by rapid thrusting of the stylet usually 2-3 cell layers deep, injection of secretions of the oesophageal glands (salivation) and ingestion of the cell contents by pumping of the basal bulb. Wyss (1981) has reviewed the available information and shown that there are only small variations from this basic pattern. The

*Longidorus* species studied so far all fed on root-tips, or just behind, causing damage to the meristematic tissue. *Xiphinema* species have a similar feeding behaviour but can also attack other parts of the root e.g. the root hair region. Therefore, the density of roots and root-tips in the rhizosphere of a plant has a direct influence on host quality and on the multiplication of a nematode species. A closer analysis of the changes induced by *X. diversicaudatum* in root-tip galls of strawberry and ryegrass showed that the metabolism of the two host plants responded differently to the feeding of this nematode thus indicating that host interactions in longidorids are far from being uniform (Griffiths & Robertson, 1988). There is strong circumstantial evidence that longidorids need to feed on modified giant cells for reproduction.

Out of a total of about 300 species of longidorids eight *Longidorus*, one *Paralongidorus* and seven *Xiphinema* species are at present known to be vectors of plant viruses. Available data show that the natural occurrence of longidorid-transmitted plant viruses (nepoviruses) and their vectors is restricted to temperate climates in the northern hemisphere, particularly Europe, the Mediterranean region and North America. Due to the limited mobility of their vectors the actual geographical distribution of nepoviruses corresponds most probably to their areas of origin or differentiation where hosts and vectors are available (Martelli & Taylor, 1989). In North America longidorid vectors and the nepoviruses they transmit are widespread whereas in Europe their occurrence is more restricted to smaller areas. This has led to very specific associations in Europe where most nepoviruses have only one vector and populations of a nematode species can vary in their vector efficiency. In North America most nepoviruses have more than one vector and species of the *X. americanum*-group can transmit more than one nepovirus (Brown et al, 1993; Martelli & Taylor, 1989; Weischer, 1993). Nothing definite is known how and why some longidorid nematodes became virus vectors. One can, however, speculate that some of their basic characters discussed earlier in this review favoured the evolution of virus-vector-host plant associations such as long persistence of

populations due to a year long individual life span and several periods of reproduction, wide host range, ability to live in different soil types and tolerance of a considerable range of temperatures. As far as can be said at present longidorid nematodes do not profit from any association with a virus nor have the virus particles retained in a nematode a negative influence on the virus carrying individual.

## CONCLUDING REMARKS

Longidoridae are a comparatively small group of phytonematodes with only four genera and a total of about 300 species. Furthermore, their general morphology and their mode of life are more or less uniform. However, in their ecology they show a high degree of differentiation as we have tried to demonstrate in this review. For the majority of species detailed ecological data are not available therefore future studies will undoubtedly reveal many insights into the ecology of these nematodes.

## REFERENCES

- Aboul-Eid, H. Z. & de Maeseneer, J. 1973. Effects of fallowing and use of copper sulphate on population dynamics and biology of *Longidorus elongatus* and *Xiphinema diversicaudatum*. *Mededelingen van de Faculteit Landbouwwetenschappen, Rijksuniversiteit Gent* 38: 67-72.
- Alphey, T.J.W. & Taylor, C.E. 1986. *European Atlas of the Longidoridae and Trichodoridae*. Scottish Crop Research Institute, Dundee, Scotland, 123 p.
- Andres, M.F. & Bello, A. 1984. Influencia del suelo y metodos de cultivo sobre *Longidorus profundorum*, nematodo fitoparásito de interés en las áreas cerealistas de la región central. *Anales de Edafología y Agrobiología* 43: 727-734.
- Antoniou, M. 1989. Arrested development in plant parasitic nematodes. *Helminthological Abstracts (Series B)* 58: 1-19.
- Arias, M., Fresno, J., Rey, J.M. & Bello, A. 1992. Virus vector nematodes and grapevine fanleaf virus in Spanish vineyards. *Nematologica* 38: 397.
- Arias, M., Navas, A. & Andres, M. 1987. Studies on morphometrics, distribution and ecology of the *Xiphinema coxi* complex in Spain. *Revue de Nématologie* 10: 377-380.
- Barbercheck, M., Smith, P.C. & Heyns, J. 1985. Occurrence and distribution of *Xiphinema* in vineyards of the Bree River valley. *Phytophylactica* 17: 27-20.
- Barbez, D. 1982. The occurrence of virus vector nematodes in hops in Poperinge (Belgium) with notes on vertical and horizontal

- distribution, population structure and population density. *Mededelingen van de Faculteit Landbouwwetenschappen, Rijksuniversiteit Gent* 47: 741-755.
- Boag, B. 1985. The localised spread of virus-vector nematodes adhering to farm machinery. *Nematologica* 31: 234-235.
- Boag, B. & Brown, D.J.F. 1987. The occurrence of *Longidorus vineacola* in Scotland with notes on its distribution in Europe. *Nematologia mediterranea* 15: 51-57.
- Boag, B., Brown, D.J.F. & Topham, P.B. 1987. Vertical and horizontal distribution of virus-vector nematodes and implications for sampling procedures. *Nematologica* 33: 83-96.
- Brown, D.J.F. & Coiro, M.I. 1983. The total reproductive capacity and longevity of individual female *Xiphinema diversicaudatum* (Nematoda: Dorylaimida). *Nematologia mediterranea* 11: 87-92.
- Brown, D.J.F. & Coiro, M.I. 1985. The reproductive capacity and longevity of *Xiphinema index* (Nematoda: Dorylaimida) from three populations on selected host plants. *Revue de Nématologie* 8: 171-173.
- Brown, D.J.F., Grunder, J., Hooper, D.J., Klingler, J. & Kunz, P. 1994. *Longidorus arthensis* sp.n. (Nematoda: Longidoridae), a vector of cherry rosette disease caused by a new nepovirus in cherry trees in Switzerland. *Nematologica* 40: 133-149.
- Brown, D.J.F., Halbrendt, J.M., Robbins, R.T. & Vrain, T.C. 1993. Transmission of nepoviruses by *Xiphinema americanum* group nematodes. *Journal of Nematology* 25: 349-354.
- Brown, D.J.F. & Taylor, C.E. 1987. Comments on the occurrence and geographical distribution of longidorid nematodes in Europe and the Mediterranean region. *Nematologia mediterranea* 15: 333-373.
- Brown, D.J.F., Taylor, C.E., Choleva, B. & Romanenko, N.D. 1990. The occurrence of Longidoridae (Nematoda: Dorylaimida) in Western USSR with further comments on longidorid nematodes in Europe and the Mediterranean Basin. *Nematologia mediterranea* 18: 199-207.
- Buser, A. 1990. Untersuchungen über die Pfeffingerkrankheit der Süßkirsche und deren Vektor *Longidorus macrosoma* (Nematoda: Longidoridae). *Diss. ETH Zurich* Nr. 9194, 204 pp.
- Ciancio, A. 1994. Population dynamics of *Xiphinema diversicaudatum* in a *Pasteuria penetrans* naturally infested soil. *Journal of Nematology* 26: 96.
- Cohn, E. 1975. Relations between *Xiphinema* and *Longidorus* and their host plants. In: *Nematode Vectors of Plant Viruses*. (F. Lamberti, C.E. Taylor & J.W. Seinhorst. Eds.) pp. 365-386. London, Plenum Press.
- Coiro, M.I. & Agostinelli, A. 1991. The development of juvenile stages of *Xiphinema index* (Nematoda: Dorylaimida) on *Vitis vinifera*. *Revue de Nématologie* 14: 181-182.
- Coiro, M.I., Serino, M. & Agostinelli, A. 1991. Feeding and reproduction of *Xiphinema index* (Nematoda: Dorylaimida) on two hosts at three temperatures. *Nematologia mediterranea* 19: 101-102.
- Coiro, M.I., Taylor, C.E. & Lamberti, F. 1987. Population changes of *Xiphinema index* in relation to host plant, soil type and temperature in southern Italy. *Nematologia mediterranea* 15: 173-181.
- Coiro, M.I., Taylor, C.E. & Lamberti, F. 1990. Reproduction of two populations of *Xiphinema index* in relation to host and temperature. *Nematologia mediterranea* 18: 117-118.
- Coomans, A. 1985. A phylogenetic approach to the classification of the Longidoridae (Nematoda: Dorylaimida). *Agriculture, Ecosystems and Environment* 12: 335-354.
- Cotten, J. 1977. Effect of annual and perennial cropping regimes in microplots on the population density and vertical distribution of *Xiphinema diversicaudatum* and on soil porosity. *Annals of Applied Biology* 86: 397-404.
- Dalmasso, A. 1970. Influence directe de quelques facteurs ecologiques sur l'activité biologique et la distribution des espèces françaises de la famille des Longidoridae (Nematoda: Dorylaimida). *Annales de Zoologie-Ecologie animale* 2: 163-200.
- Dürschner, U. 1983. Pilzliche Endoparasiten an beweglichen Nematodenstadien. *Mitteilungen aus der Biologischen Bundesanstalt für Land- und Forstwirtschaft Berlin-Dahlem*, H. 217, 83 p.
- Ferris, H. & McKenry, M.V. 1974. Seasonal fluctuations in the spatial distribution of nematode populations in a California vineyard. *Journal of Nematology* 6: 203-210.
- Flegg, J.J.M. 1968. The occurrence and distribution of *Xiphinema* and *Longidorus* species in southeastern England. *Nematologica* 14: 189-196.
- Fritzsche, R. 1968. Beitrag zum Wanderungsverhalten von *Xiphinema diversicaudatum* (Micoletzky) Thorne, *X. coxi* Tarjan und *Longidorus macrosoma* Hooper sowie der Ausbreitung des Rhabarbermosaic-Virus im Feldbestand. *Biologisches Zentralblatt* 87: 481-488.
- Griffiths, B.S. & Robertson, W.M. 1988. A quantitative study of changes induced by *Xiphinema diversicaudatum* in root-tip galls of strawberry and ryegrass. *Nematologica* 34: 198-207.
- Griffiths, B.S. & Trudgill, D.L. 1983. A comparison of the generation times of and gall formation by *Xiphinema diversicaudatum* and *Longidorus elongatus* on a good and a poor host. *Nematologica* 29: 78-87.
- Halbrendt, J.M. & Brown, D.J.F. 1992. Morphometric evidence for three juvenile stages in some species of *Xiphinema americanum sensu lato*. *Journal of Nematology* 24: 305-309.

- Halbrendt, J.M. & Brown, D.J.F. 1993. Aspects of biology and development of *Xiphinema americanum* and related species. *Journal of Nematology* 25: 355-330.
- Harrison, B.D. & Hooper, D.J. 1963. Longevity of *Longidorus elongatus* (de Man) and other nematodes in soil kept in polythene bags. *Nematologica* 9: 158-160.
- Harrison, B.D. & Winslow, R.D. 1961. Laboratory and field studies on the relation of arabis mosaic virus to its nematode vector *Xiphinema diversicaudatum* (Micoletzky). *Annals of Applied Biology* 49: 621-633.
- Jaffee, B.A. 1986. Parasitism of *Xiphinema rivesi* and *X. americanum* by zoosporic fungi. *Journal of Nematology* 18: 87-93.
- Jaffee, B.A. & Shaffer, R.L. 1987. Parasitism of *Xiphinema americanum* and *X. rivesi* by *Catenaria anguillulae* and other zoosporic fungi in soil solution, Baermann funnels, or soil. *Nematologica* 33: 220-231.
- Jones, F.G.W., Larbey, D.W. & Parrot, D.M. 1969. The influence of soil structure and moisture on nematodes especially *Xiphinema*, *Longidorus*, *Trichodorus* and *Heterodera* spp. *Soil Biology and Biochemistry* 1: 153-169.
- Klingler, J., Güntzel, O. & Kunz, P. 1983. *Xiphinema*- and *Longidorus*-Arten im schweizerischen Mittelland. *Vierteljahresschrift der naturforschenden Gesellschaft in Zürich* 128: 89-114.
- Lamberti, F. & Bleve-Zacheo, T. 1979. Studies on *Xiphinema americanum sensu lato* with description of fifteen new species (Nematoda, Longidoridae). *Nematologia mediterranea* 7: 51-106.
- Lamberti, F. & Ciancio, A. 1993. Diversity of *Xiphinema americanum*-group species and hierarchical cluster analysis of morphometrics. *Journal of Nematology* 25: 332-343.
- Luc, M. 1973. Redescription de *Xiphinema hallei* Luc 1958 et description de six nouvelles espèces de *Xiphinema* Cobb 1913 (Nematoda: Dorylaimoidea). *Cahiers Orstom série Biologie* 21: 45-63.
- Luc, M. & Hoestra, H. 1960. Les nématodes phytoparasites de cocoteraie du Togo. Essai d'interprétation du peuplement. *L'Agronomie tropicale* 15: 497-512.
- Martelli, G.P. & Taylor, C.E. 1989. Distribution of viruses and their nematode vectors. *Advances in Disease Vector Research* 6: 151-189.
- McNamara, D.G. 1978. Survival of nematodes in fallow soil. *Annual Report East Malling Research Station*, 130.
- McNamara, D.G. 1980a. Survival of nematodes in fallow soil. *Annual Report East Malling Research Station*, 105.
- McNamara, D.G. 1980b. The survival of *Xiphinema diversicaudatum* in plant-free soil. *Nematologica* 26: 170-181.
- McNamara, D.G. & Flegg, J.J.M. 1981. The distribution of virus vector nematodes in Great Britain in relation to past and present natural vegetation. In: *Pests, Pathogens and Vegetation*. (J.M. Thresh, Ed.) pp. 225-235. London, Pitman.
- Navas, A. & Arias, M. 1986. On the distribution and ecology of *Xiphinema index* and *X. italiae* in Spain. *Nematologia mediterranea* 14: 207-215.
- Navas, A., Baldwin, J.G., Barrios, L. & Nombela, G. 1993. Phylogeny and biogeography of *Longidorus* (Nematoda: Longidoridae) in Euromediterranea. *Nematologia mediterranea* 21: 71-88.
- Navas, A., Bello, A. & Arias, M. 1988. Ecology and potential distribution of *Xiphinema diversicaudatum* and *X. pachtaicum* (Nematoda: Longidoridae) in continental Spain. *Nematologica* 34: 314-330.
- Navas, A. Feandres, M. & Arias, M. 1990. Biogeography of Longidoridae in the Euromediterranean area. *Nematologia mediterranea* 18: 103-112.
- Norton, D.C. 1969. *Meloidogyne hapla* as a factor in alfalfa decline in Iowa. *Phytopathology* 59: 1824-1828.
- Perkins, E.M. & Atkinson, H.J. 1992. Nematophagous fungi with a seasonal influence on the density of *Longidorus elongatus*. *Nematologica* 38: 428.
- Pinochet, J., Raski, D.J. & Goheen, A.C. 1976. Effects of *Pratylenchus vulnus* and *Xiphinema index* singly and combined on vine growth of *Vitis vinifera*. *Journal of Nematology* 8: 330-335.
- Polinkovsky, A.I. 1980. [Bioecological characteristics of the nematode *Xiphinema index* Thorne & Allen, 1950 in Moldavian vineyards]. *Virusnye, mikoplaxmennye i bakterial'nye bolezni poldovykh kul'tur i vinograda v Moldavii*, 106-111.
- Raski, D.J. & Hewitt, W.B. 1960. Experiments with *Xiphinema index* as a vector of fanleaf of grapevine. *Nematologica* 11: 349-352.
- Raski, D.J., Hewitt, W.B., Goheen, A.C., Taylor, C.E. & Taylor, R.H. 1965. Survival of *Xiphinema index* and reservoirs of fanleaf virus in fallowed vineyard soil. *Nematologica* 11: 349-352.
- Rau, J. 1975. Das Vorkommen virusübertragender Nematoden in ungestörten Biotopen Niedersachsens. *Diss. Technische Universität Hannover*, 169 p.
- van Reenen, E. & Heyns, J. 1986. A survey of Longidoridae in vineyards along the Berg River system. *Phytophylactica* 18: 203-207.
- Robbins, R.T. 1993. Distribution of *Xiphinema americanum* and related species in North America. *Journal of Nematology* 25: 344-348.
- Rössner, J. 1972. Vertikalverteilung wandernder Wurzelnematoden im Boden in Abhängigkeit von Wassergehalt und Durchwurzelung. *Nematologica* 18: 360-372.
- Rüdel, M. 1975. Untersuchungen über den Wirtspflanzenkreis des Nematoden *Xiphinema vuittenezi*. *Wein-Wissenschaft* 30: 21-27.

- Rüdel, M. 1990. Nematode transmitted virus diseases of grapevines in the Palatinate, Germany. *Nematologica* 36: 388-389.
- Sayre, R.M. & Starr, M.P. 1988. Bacterial diseases and antagonisms of nematodes. In: *Diseases of Nematodes*. (G.O. Poiner & H-B. Jansson. Eds.) pp. 69-101. Boca Raton, CRC Press.
- Siddiqi, M.R., Baujard, P. & Mountport, D. 1993. Description of *Paratylenchus pernoxius* sp.n. and *Paralongidorus duncani* sp.n. from Senegal, and the synonymization of *Longidoroides* with *Paralongidorus*. *Afro-Asian Journal of Nematology* 3: 81-89.
- Stirling, G.R. 1985. Observations on the biology and ecology of *Paralongidorus australis* on rice in North Queensland. *Nematologica* 31: 218-228.
- Sturhan, D. 1963. Der pflanzenparasitische Nematode *Longidorus maximus*, seine Biologie und Ökologie, mit Untersuchungen an *Longidorus elongatus* und *Xiphinema diversicaudatum*. *Zeitschrift für angewandte Zoologie* 50: 129-193.
- Sturhan, D. & Hampel, G. 1977. Pflanzenparasitische Nematoden als Beute der Wurzelmilbe *Rhizoglyphus echinopus* (Acarina, Tyroglyphidae). *Anzeiger für Schädlingskunde, Pflanzenschutz, Umweltschutz* 50: 115-118.
- Sultan, S.A. & Ferris, H. 1991. The effect of moisture and soil particle size on the survival and population increase of *Xiphinema index*. *Revue de Nématologie* 14: 345-351.
- Sutherland, J.R. & Slugget, L.J. 1974. Time, temperature and soil moisture effects on *Xiphinema bakeri*: nematode survival in fallow soil. *Phytopathology* 64: 507-513.
- Taylor, C.E. 1967. The multiplication of *Longidorus elongatus* (de Man) on different host plants with reference to virus transmission. *Annals of Applied Biology* 59: 275-281.
- Taylor, C.E., Alphey, T.J.M. & Brown, D.J.F. 1978. The distribution of nematode virus-vectors in Great Britain. In: *Plant Disease Epidemiology*. (P.R. Scott & A. Bainbridge. Eds.) pp. 265-273. London, Blackwell Scientific Publications.
- Taylor, C.E., Brown, D.J.F., Neilson, R. & Jones, A.T. 1994. The persistence and spread of *Xiphinema diversicaudatum* in cultivated and uncultivated biotopes. *Annals of Applied Biology* 124: 469-477.
- Thomas, P.R. 1969. Population development of *Longidorus elongatus* on strawberry in Scotland with observations on *Xiphinema diversicaudatum* on raspberry. *Nematologica* 15: 582-590.
- Thomas, P.R. 1981. Migration of *Longidorus elongatus*, *Xiphinema diversicaudatum* and *Ditylenchus dipsaci* in soil. *Nematologia mediterranea* 9: 75-81.
- Topham, P.B. & Alphey, T.J.W. 1985. Faunistic analysis of longidorid nematodes in Europe. *Journal of Biogeography* 12: 165-174.
- Uesugi, C.H., Huang, C.S. & Cares, J.E. 1985. *Xiphidorus amazonensis* n.sp. (Nematoda: Longidoridae) from the Brazilian Amazon Basin. *Journal of Nematology* 17: 310-313.
- Weischer, B. 1975. Ecology of *Xiphinema* and *Longidorus*. In: *Nematode Vectors of Plant Viruses*. (F. Lamberti, C.E. Taylor & J.W. Seinhorst. Eds.) pp 291-307. London, Plenum Press.
- Weischer, B. 1993. Nematode-virus interactions. In: *Nematode Interactions*. (M.W. Khan. Ed.) pp. 217-231. London, Chapman & Hall.
- Williams, J.R. & Luc, M. 1977. The species of *Xiphinema* Cobb, 1913 (Nematoda: Longidoridae) in the sugarcane fields of Mauritius. *Occasional Paper No. 30, Mauritius Sugar Industry Research Institute*, 19 pp.
- Wyss, U. 1970. Untersuchungen zur Populationsdynamik von *Longidorus elongatus*. *Nematologica* 16: 74-84.
- Wyss, U. 1981. Ectoparasitic root nematodes: Feeding behaviour and plant cell responses. In: *Plant Parasitic Nematodes*. (B.M. Zuckerman & R.A. Rhode. Eds.) Volume 3. pp. 325-351. New York, Academic Press.
- Yeates, G.W., van Etteger, H. & Hooper, D.J. 1992. *Longidorus orongorongensis* n.sp. (Nematoda: Dorylaimida) from subsoil of conifer/broadleaved forest. *New Zealand Journal of Zoology* 19: 25-31.

**Weischer B., Almeida M. T. M.** Экология лонгидорид.

Резюме. В обзоре анализируются основные экологические факторы, влияющие на биологию лонгидорид. Существующие особенности всемирного распределения этих нематод обусловлены как геологическими явлениями (к примеру, дрейф материков), так и хозяйственной деятельностью человека, в первую очередь, распространением посадочного материала. Особенности регионального распределения лонгидорид связаны с воздействием последних периодов обледенения, климатом и формированием почв в послеледниковый период. Локализация лонгидорид в почвах обуславливается в основном особенностями микроклимата и растительным покровом. Вертикальное распределение лонгидорид зависит от структуры почвы, ее влажности и распространения корней растений-хозяев. Структура почвы важна в особенности потому, что такие крупные нематоды, как лонгидориды, неспособны проникать через толщу почвы, как это делают корни растений. Основными факторами, определяющими развитие популяций лонгидорид, можно считать репродуктивную способность данного вида нематод, климатические условия, особенности растений-хозяев и наличие антагонистов. Некоторые виды лонгидорид в значительной степени приспособились к выживанию в почве, где нет растений хозяев, а также при весьма губительных для нематод условиях окружающей среды.