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Feeding structures and parasitic properties in plant-parasitic nematodes

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Abstract
Plant-parasitic nematodes are one of the most important crop pests in the world. So far, about 4100 species of plant parasites have been identified. They can attack all parts of the plant, such as roots, stems, leaves and seeds. Plant-parasitic nematodes feed on living plant tissues and exhibit a wide variety of interactions with their hosts. In plants, they are generally fed as ectoparasitic, semi-endoparasitic, endoparasitic and mobile ecto-endoparasitic. Ectoparasites never enter the host. Semi-endoparasitic nematodes are fed embedded into the tissue, partly with a part of the body outside. Endoparasitic nematodes completely enter the roots. Immigrant endo-ectoparasite nematodes remain vermiform. The head areas are inserted into cortical cells, where only nutrients are removed. In addition, these feeding types include subgroups. The types of information that feed on plant-parasitic nematodes are important for management strategies. This investigation is started to provide an overview of feeding structures and parasitic properties of plant-parasitic nematodes.

Keywords: feeding structures, parasitic properties, plant-parasitic nematodes

1. Introduction

Nematodes are animal organisms that can live in different environmental conditions (Baldwin and Perry, 2003) [1]. They interact differently with other living things (parasitic, mutualistic, etc.) in their environments. These animals can adapt to very different habitats with different feeding behaviours in parasites, predators or free-living types. With these features, they can be found in more diverse and diverse environments than other multicellular organisms. Today, there are more than 20000 types of nematodes defined in the phylum Nematoda. It is known that the number of species damaging plants is more than 4100 (Perry and Moens, 2011) [2]. Plant parasite nematodes are obligate parasites and are mostly fed in the cytoplasms of their hosts (Jones *et al.*, 2013) [3]. However, not all of these species cause economic losses in plants. Plant-parasitic nematodes can cause damage to the underground or aboveground parts of plants.

As a result of the worldwide evaluation, nematode genus and species of economic importance are listed (in order of importance) as follows (Jones *et al.*, 2013) [3]:

1. *Meloidogyne* spp. (Root-knot nematodes)
2. *Heterodera* ve *Globodera* spp. (Cyst nematodes)
3. *Pratylenchus* spp. (Lesion nematodes)
4. *Radopholus similis* (Burrowing nematode)
5. *Ditylenchus dipsaci* (Stem and bulb nematode)
6. *Bursaphelenchus xylophilus* (Pine wood or wilt nematode)
7. *Rotylenchulus reniformis* (Reniform nematode)
8. *Xiphinema index* (Dagger nematode)
9. *Nacobbus aberrans* (False root-knot nematode)
10. *Aphelenchoides besseyi* (Rice leaf white-tip nematode)

Plant-parasitic nematodes are located in the three order: Rhabditida, Dorylaimida and Triplonchida. The species belonging to the genus such as *Helicotylenchus, Rotylenchulus, Heterodera, Globodera, Pratylenchus, Meloidogyne*, which cause damages especially in the underground parts of the plants, and the species that are found in harmful *Anguina, Ditylenchus, Aphelenchus, Aphelenchoides* in the above-ground parts of the plants are classified in the Rhabditida order, species belonging to the genus *Longidorus, Paralongidorus, Xiphinema*, which may be a virus vector, are in the Dorylaimida order; species belonging to the genus such as *Trichodorus Paratrichodorus* are classified in the Triplonchida order (Decraemer and Hunt, 2006) [4].

Plant-parasitic nematodes have three different biological periods: egg, larva and adult (Felix, 2003) [5]. The larvae hatched from the eggs turn to the plants through their root secretions. Generally, the first introduction to plants or feeding starts from the back of the root tip of the plant (Hunt *et al.*, 2005) [6]. The majority of plant-parasitic nematodes can cause damage to the roots of the hosts, and a small number of them to the aboveground parts of plants such as leaves, flowers or stems (Hussey and Davis, 2003) [7]. The plant physically damages the cell envelope primarily through the stylet (inserter-absorbent needle) and then destroys the structure of the cell wall through cellulitic and pectolitic enzymes (Abad *et al.*, 2003) [8]. These methods can be effectively used by plant-parasitic nematodes in their feeding or intercellular movement (Karssen and Moens, 2006) [9]. As a result of their nutrition, they can cause deformations in stem cells, preventing the transmission of nutrients from the soil, some soil-borne diseases due to their wounds in the roots, and deaths in plant cells due to toxic substances in stylet secretions (Schomaker and Been, 2006) [10].

2. Feeding Structures

Nutrition is one of the basic behaviours necessary for living things to continue their vital activities. Plant-parasitic nematodes need living plant tissues to survive. In nematodes with different feeding habits, it is widely used as stoma or mouth feeding apparatus. In addition, expression of organs such as stylet (inserter-absorbent needle or chisel), mural tooth (wall tooth), buccal cavity (mouth cavity) and tooth can be used to prevent confusion within the feeding mechanisms (Bilgrami and Gaugler, 2004) [11].

The structure and function of the feeding apparatus is based on the feeding style of the nematode and also gives information about the nutritional and nutritional habits (Karakas and Bolukbasi, 2019) [12]. The basic feeding apparatus is expressed in different names in different nematode groups with its structure, shape and dimensions. For example; Nutritional apparatus called buccal cavity in predatory nematodes has specialized structures like dorsal-ventral teeth and small teeth. In nematodes fed with plant parasites or fungi, the organs used to break down the tissue and remove the food are called stylets. This structure is movable back and forth and connects to the esophagus with a narrow lumen. Morphological and physiological changes in stylet and esophagus according to nematode type are differences in nutritional behaviour. In this process, especially stylet took its final form independently in three basic groups of plant- parasitic nematodes (Hunt *et al.*, 2005) [6]. Thus, the main feeding apparatus observed in plant-parasitic nematodes are stylet (Stomatostylet) in *Tylenchida*; Odontostylet (Odontostyle) in *Longidoridae*; In *Trichodoridae*, it is called Onchiostylet (Onchiostyle) (Figure 1).

Stylets observed in *Longidoridae*; It consists of an end section called Odontostylet and Odontophore that carries this part or acts as a support to Odontostylet (Figure 1-A).

Stylet or Stomatostylet observed in *Tylenchida*; It consists of a conical head, an intermediate section called a shaft or a handle, and the last region of the basal lumps to which the muscles that connect the stylet are attached (Figure 1-B).

The stylets observed in *Trichodoridae*; Onchium (Onchiostylet), which has a fold in its ventral and qualifies as a stylet-like tooth, and Onchiophore, which supports or carries this structure (Figure 1-C).

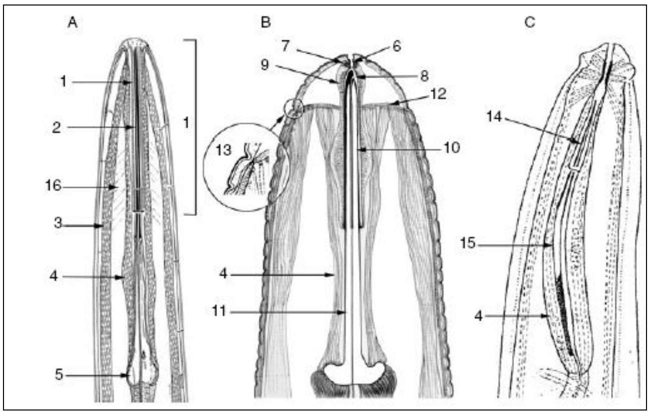

Fig 1: Types of stoma region and feeding apparatus (stylet) in plant-parasitic nematodes A. Odontostylet and odondophore (*Longidoridae*) B. Stomatostylet (*Tylenchomorpha*) C. Onchiostylet (*Trichodoridae*) 1. Cheliostom 2. Odontostylet 3. Somatic muscles 4. Stylet protractor muscles 5. Flange odontophore 6. Stoma tip 7. Cuticular area before stoma 8. Stylet opening 9. Stoma 10. Stylet connus 11. Stylet extension and knobs 12. Basal head frame 13. Detailed body cuticle (Details of the median and basal region of the head region cuticle). Striped basal zone of the head region. The median layer has disappeared 14. Onchium 15. Onchiophore 16. Dilatores cavity.

3. Feeding Habits and Parasitic Properties

All plant-parasitic nematodes carry stylets to feed or enter their hosts. These properties distinguish them from most of the other nematode groups (Perry and Moens, 2006) [13]. Plant- parasitic nematodes are obligate parasites and they obtain the nutrients necessary for their development from different parts of the plants. The differences observed in nutritional habits are the adaptations they have created in order to survive in their habitats (Robinson, 2003) [14]. In the classifications made about the nutritional habits of these pests, the differences in their lives in various periods may cause inaccuracies (Zuckerman, 1971) [15]. Therefore, it classifies by taking into consideration the changes observed after the process of establishing the nutrition relationship. As seen in Table 1 and Figure 2, plant-parasitic nematodes can be divided into four different groups as ectoparasitic, endoparasitic, semi-endoparasitic and mobile ecto-endoparasitic according to their feeding habits (Wyss, 1997; Decreamer and Hunt, 2006) [16, 4]. Although there is consensus about the other three groups in the definitions, there are different opinions about the type of mobile ecto-endoparasitic nutrition (Hunt *et al.*, 2005). Some researchers can be defined as semi-endoparasitic or mobile ecto-endoparasitic nutrition. In this review, it is considered as a separate group to make the reader more understandable. In addition, these basic groups can be divided into subtypes depending on their diet (Wyss, 1997; Wyss, 2002) [16, 25].

Table 1: Parasitic Properties in Plant-parasitic Nematodes

<table>
<tr><th colspan="2">Types of Parasitism</th></tr>
<tr><td rowspan="2">Ectoparasitic</td><td>Mobile Ectoparasitic</td></tr>
<tr><td>Constant Ectoparasitic</td></tr>
<tr><td colspan="2">Semi-Endoparasitic</td></tr>
<tr><td rowspan="2">Endoparasitic</td><td>Mobile Endoparasitic</td></tr>
<tr><td>Constant Endoparasitic</td></tr>
<tr><td colspan="2">Mobile Ecto-Endoparasitic</td></tr>
</table>

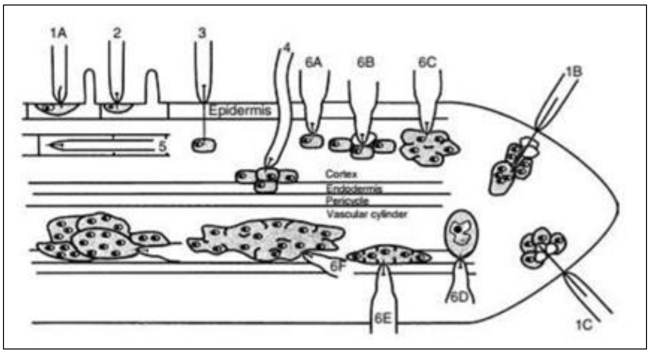

Fig 2: Nutritional types of important plant-parasite nematodes. [1A, 1B and 1C *Dorylaimid* nematodes (mobile ectoparasite); all others are *Tylenchid* nematodes]. 1 A. *Trichodorus* spp. 1B. *Xiphinema index* 1C. *Longidorus elongatus*. 2.*Tylenchorhynchus dubius* (mobile ectoparasite) 3. *Criconemoides xenoplax* (constant ectoparasite) 4. *Helicotylenchus* spp. (mobile ecto-endoparasite) 5. *Pratylenchus* spp. (mobile endoparasite) 6A. *Trophotylenchulus obscurus* 6B. *Tylenchulus semipenetrans* 6C. *Verutus volvingentis* 6D. *Cryphoder autahensis* 6E. *Rotylenchulus reniformis* 6F. *Heterodera* spp. 6G. *Meloidogyne* spp. (6A-6G constant endoparasites).

3.1 Ectoparasitic Nutrition

The nematodes with ectoparasitic nutrition remain in the soil during their lifetime and do not enter into the plant tissue. Nematodes use their stylets to pierce and feed plant tissues. These nematodes have a long and strong stylet and can be fed in deeper cells. Ectoparasitic nematodes can be divided into two subgroups as mobile and constant ectoparasites, depending on their feeding types (Hunt *et al.*, 2005; Decreamer and Hunt, 2006) [6, 4].

3.1.1 Mobile ectoparasitic nutrition
Many of the ectoparasitic fed species have the feature of traveling ectoparasitic nutrition. The nematode species in this type of nutrition remain filamentous-vermiform. They carry out their feeding in selected cells in a very short time. Nematode species that have longer stylets, such as *Belonolaimus*, *Trichodorus*, and *Xiphinema*, are nematode species associated with *Tylenchorhynchus* genus, which have stylet relatively shorter than the endodermal cells, while nematodes that depend on *Psilenchus*, *Tylenchus* and *Atylenchus* species are fed only. As a result of feeding of the nematodes belonging to this group, they can cause necrosis in stem cells, gall-likes welling at the root tips and gall-likes welling, and the formation of syncytia as a result of prolonged feeding periods (Van Ghelder *et al.*, 2015) [17]. Another group in this feeding is the species that can cause damage to the aboveground parts of the plants. These species, which are found in genera such as *Aphelenchoides*, *Ditylenchus*, *Bursaphelenchus*, and *Rhadinaphelenchus*, especially in leaves, flowers, plant stems or stems during certain periods of their lives; they can cause various damages such as gal, necrosis or curl in leaves (Chanu *et al.*, 2013) [18].

3.1.2 Constant ectoparasitic nutrition
This type of nutrition is less frequently observed. Nematode species related to the genus such as *Cacopaurus* and *Criconemella* are in this nutrition group. Nematodes insert their stylets into deeper plant tissues and fixation at the feeding point is achieved in this way. Unlike other ectoparasitic nematodes, this type of feeding nematodes can be fed for only a long time in one of the root cortical cells (Bilgrami and Gaugler, 2004) [11]. In this feeding process, the nutrients come from cells whose cytoplasm in contact with the stylet opening has been adapted for nutrient uptake and from other cells connected to these cells with plasmodesmata (Wyss, 1997; Wyss, 2002) [16, 25].

3.2 Semi-Endoparasitic Nutrition
It is a form of feeding where only a certain part of the bodies of larvae or non-adult females enter the root tissue. In this type of nutrition, individuals are fed in the cells of the root cortex and continue their lives permanently in the feeding areas. Apart from the root tissue, the tail parts remain and bulge (Manzanilla-Lopez *et al.*, 2004) [19]. This type of nutrition can be observed in nematodes of the genus *Rotylenchulus*, *Telotylenchus* and *Tylenchulus* (Rashidifard *et al.*, 2015) [20].

3.3 Endoparasitic Nutrition
It is a form of nutrition in which the entire nematode body enters the root tissue of the plant and nutrition occurs in the tissue. The nutritional type of endoparasitic feature is divided into two subgroups: mobile and constant endoparasite (Decraemer and Hunt, 2006) [4].

3.3.1 Mobile endoparasitic nutrition
In this type of nutrition, which is observed in *Pratylenchus*, *Anguina*, *Radopholus* species, individuals continue their movement within the tissue and maintain their filamentous structure after they enter the plant tissue. Nutrition takes place from stem cortical cells. As a result of parasitism, cell turgor pressure decreases and as a result of prolonged feeding periods, deaths can be observed in cells (George *et al.*, 2016) [21]. In addition, the nematodes in this feeding type, which have a partially strong stylet, can enter and exit the roots (Manzanilla-Lopez *et al.*, 2004) [19].

3.3.2 Constant endoparasitic nutrition
In this type of nutrition, it is observed that selected endodermal cells are transformed into specialized nutrition cells such as giant cells, syncytia or nurse cells. In this type of nutrition, which occurs in economically important species such as *Heterodera*, *Globodera*, *Meloidogyne*, *Sphaeronema* or *Nacobbus*, female individuals fix themselves, and the nutrition that they have left with the replacement of the second shirt resumes and thus their body volumes increase (Strajnar *et al.*, 2011) [22]. Plants form galls with hyperplastic cells around the feeding cells formed in response to this type of feeding, and females are embedded in the tissue. There is an active period in fixed endoparasitism before it is fixed in the feeding cell. In root-knot and cyst nematodes, only second period larvae or juvenile (J2) and adult males are in movable form; In *Nacobbus* species, the mobile process can be observed in all larval periods, males and immature threadlike females (Souza and Baldwin, 2000) [23].

3.4 Mobile Ecto-Endoparasitic Nutrition
The nematodes in this feeding type remain filamentous and are fed ectoparasitically from the stem cortical cells. However, in feeding processes, they can insert their head regions only up to the root cortical cells (Talezarı *et al.*, 2015) [24]. In this type of nutrition, which is observed especially in the *Hoplolaimidae* family, the individual does not remain fixed in the tissue it feeds and does not extend to the deeper cells, as in the semi-endoparasitic nutrition. Feeding from several cells in the surrounding area associated with the feeding cell and plasmolemma can continue for days through the feeding tube created in the cell where the nematode is in contact (Wyss, 1997) [16].

4. Conclusion
Plant parasitic nematodes have very different types of nutrition. These types of nutrition show which tissue of the nematode can be fed, how it can cause damage to these tissues. The difference in nutritional strategies of plant parasitic nematodes is directly related to the harm caused by these animals in plants. Therefore, knowing the nutritional strategies of plant parasitic nematodes can help develop pest recognition and struggle strategies.

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