THE GENUS *NACOBBUS* THORNE & ALLEN, 1944 (NEMATODA: PRATYLENCHIDAE): SYSTEMATICS, DISTRIBUTION, BIOLOGY AND MANAGEMENT

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*Miguel Costilla died (July, 2001) before this review was completed. The review is dedicated to his memory.

ABSTRACT

Manzanilla-López, R. H., M. A. Costilla, M. Doucet, J. Franco, R. N. Inserra, P. S. Lehman, I. Cid del Prado-Vera, R. M. Souza, and K. Evans. 2002. The genus *Nacobbus* Thorne & Allen, 1944 (Nematoda: Pratylenchidae): Systematics, distribution, biology and management. Nematropica 32:149-227.

The two known species of *Nacobbus*, *N. aberrans* and *N. dorsalis*, are sedentary root endoparasites that occur in the Americas. The parasitic habits of these two so-called "false root-knot nematode" species include similarities to both root lesion and root-knot nematodes. The migratory and vermiform juveniles and immature adults behave like lesion nematodes, causing cavities and lesions inside the root tissues, whereas the mature females are sedentary and obese and induce root galls and specialized feeding sites as do true root-knot nematodes. Limited information is available on the less well-known species *N. dorsalis*, which is present only in California where it has negligible economic importance and parasitizes only a few non-cultivated plants without evidence of attack on agricultural crops. In contrast, many studies have examined the biology, economic impact, and management of the more economically important *N. aberrans*, which occurs in temperate and subtropical latitudes of North and South America. This false root-knot (or potato rosary) nematode has a wide host range, which includes at least 84 plant species. Many common weeds are good hosts. The results of host and field studies conducted in North and South America indicate that *N. aberrans* populations can be separated into bean, potato and sugarbeet groups. The populations of each group have distinct host preferences and do not reproduce on graminaceous species or on leguminous species of the genera *Medicago* and *Lupinus*. The yield losses reported on staple and industrial crops infected by *N. aberrans* average 65% for potato in the Andean region of Latin America, 55% and 36% for tomato and bean in Mexico, respectively, and 10-20% for sugarbeet in the United States (Nebraska). Different levels of resistance, varying according to the nematode population, have been found in bean, chilli pepper, potato, and tomato. Most research on crop rotation, mixed cropping, and chemical and non-chemical strategies for management of *N. aberrans* has been conducted on bean, chilli pepper, and tomato in Mexico, potato in Argentina, Bolivia and Peru, and sugarbeet in the United States.

Key words: biology, diagnostics, distribution, false root-knot nematode, histopathology, host range, life cycle, management, morphology, *Nacobbus aberrans*, *Nacobbus dorsalis*, potato rosary nematode, quarantine, races, systematics, thermal requirements, yield losses.

RESUMEN

Manzanilla-López, R. H., M. A. Costilla, M. Doucet, J. Franco, R. N. Inserra, P. S. Lehman, I. Cid del Prado-Vera, R. M. Souza, and K. Evans. 2002. El genero *Nacobbus* Thorne y Allen, 1944 (Nematoda: Pratylenchidae): Sistemática, distribución, biología y manejo. Nematrópica 32:149-227.

Las dos especies conocidas de *Nacobbus*, *N. aberrans* y *N. dorsalis*, son parásitas sedentarias de raíces que ocurren en el continente Americano. Los hábitos de parasitismo de estas dos especies denominadas "falso nematodo del nudo de la raíz" incluyen similitudes tanto con los nematodos lesionadores de la raíz como con los nematodos noduladores o agalladores. Los juveniles vermiformes migratorios y los adultos inmaduros se comportan como los nematodos lesionadores, produciendo cavidades y lesiones dentro de los tejidos radicales, mientras que las hembras maduras son sedentarias y obesas e inducen agallas radicales y sitios de alimentación especializados como lo hacen los verdaderos nematodos agalladores de las raíces. Existe información limitada sobre la especie *N. dorsalis*, la cual sólo está presente en California, donde su importancia económica no es significativa y únicamente parasita unas cuantas plantas no cultivadas, no existiendo evidencias de ataque a cultivos agrícolas. En contraste, numerosos estudios han examinado la biología, el impacto económico y el manejo de la especie económicamente más importante *N. aberrans*, la cual ocurre en las latitudes templadas y subtropicales de América del Norte y del Sur. Este nematodo falso nodulador (o nematodo del rosario de la papa) posee una amplia gama de hospedantes, que incluye a 84 especies de plantas. Muchas malezas comunes son hospedantes eficientes. Los resultados de los estudios sobre hospedantes y de campo conducidos en Norte y Sudamérica indican que las poblaciones de *N. aberrans* pueden ser separadas en los grupos de frijol, papa y remolacha. Las poblaciones de cada grupo tienen preferencias por hospedantes diferentes y no se reproducen sobre especies de gramíneas o sobre especies de leguminosas de los géneros *Medicago* y *Lupinus*. Las pérdidas de rendimiento reportadas en cultivos alimenticios e industriales promedian un 65% en papa en la región Andina de América Latina, 55% y 36% en tomate y frijol en México, respectivamente, y 10-20% en remolacha en los Estados Unidos (Nebraska). Diferentes niveles de resistencia, que varían de acuerdo a la población del nematodo, han sido encontrados en frijol, chile o ají, papa y tomate. La mayoría de las investigaciones sobre rotación de cultivos, cultivos asociados, y estrategias químicas y no químicas para el manejo integrado de *N. aberrans* han sido conducidos en frijol, chile o ají, y tomate en México, papa en Argentina, Bolivia y Perú y remolacha en los Estados Unidos.

Palabras claves: biología, diagnósticos, distribución, nematodo falso nodulador, histopatología, gama de hospedantes, ciclo de vida, manejo, morfología, *Nacobbus aberrans*, *Nacobbus dorsalis*, nematodo del rosario de la papa, cuarentena, razas, sistemática, requisitos térmicos, pérdidas en rendimiento.

INTRODUCTION

The genus *Nacobbus* Thorne & Allen, 1944 contains species of a predominantly endoparasitic habit with sedentary, swollen females inhabiting galls that they induce in the roots of their hosts. According to Sher (1970) the genus contains only two valid species: *Nacobbus dorsalis* Thorne & Allen, 1944 and *N. aberrans* (Thorne, 1935) Thorne & Allen, 1944, the latter being an important parasite of vegetables such as bean, chilli pepper, potato, tomato and sugarbeet with estimated losses as high as 65% in potato (Otazú *et al.*, 1985), 55% in tomato (Zamudio, 1987), 36% in bean (Silva-Jaramillo, 1989) and 10-20% in sugarbeet (Inserra *et al.*, 1996). *Nacobbus aberrans* is indigenous to the Americas and occurs in the USA, Mexico, Ecuador, Bolivia, Peru, Chile and Argentina. Other records and quarantine interceptions (some of which have not been confirmed) include England (Franklin, 1959), The Netherlands (de Bruijn and Stemerding, 1968), Finland and the former USSR (Kir-

janova and Lovanova, 1975), India (Prasad *et al.*, 1965) and China (Yin and Feng, 1981).

Nacobbus aberrans is adapted to a wide range of climatic conditions (Alarcón and Jatala, 1977), the life cycle being strongly influenced by temperature (Prasad and Webster, 1967; Quimí, 1979) and many aspects of the ecology remain poorly understood. The ability of *N. aberrans* to become established in different environmental conditions complicates the management of this nematode, which is subject to international phytosanitary quarantine regulations in an effort to limit its introduction to other countries (CABI and EPPO, 1997).

Its morphology and host range show great variability between populations from the majority of the geographical areas where it has been found. These observations have led to the suggestion that *N. aberrans* could be considered as a species complex (Jatala and Golden, 1977) with a series of biotypes or physiological races.

Host range has been the main criterion to support and designate races of *N. aberrans*, but discordance in the data and non-reproducible results frequently occur (Boluarte and Jatala, 1993; Toledo *et al.*, 1993; Ortuño *et al.*, 1997). The situation is further complicated by a poor understanding of the taxonomy of the group, which remains controversial with the validity of species and subspecific groups inadequately resolved (Baldwin and Cap, 1992).

The problems caused by *N. aberrans* differ according to the crop and location where it occurs. In the USA, sugarbeet is the most important crop affected. The description, in 1956, of *Nacobbus batatiformis* (= *N. aberrans*), from sugarbeet, resulted in the subsequent recognition of *Nacobbus* as an important plant parasite and a threat to the establishment of new areas for production of the crop (Johnson, 1971). In Latin America, affected crops may include staple foods (potato, bean) and the few commercial crops available for the small-scale producer (chilli pepper, tomato), and considerable areas of infested land may be made unavailable for the production of seed and export crops (e.g., potato).

Economically acceptable recommendations, such as rotation or other cultural practices, are linked with specific identification of the nematode, determination of host range, ecological studies, estimation of infestation levels prior to cropping, etc. These requirements demand research to provide the information necessary to help increase production, preferably through co-existence with the parasite by means of an acceptable and appropriate integrated pest management approach.

Ninety-five countries produce potatoes in the developing world (CIP, 1984) and, in an era of intensive international trade, *N. aberrans* has become a major concern. This nematode has potential social and economic impacts on producers as well as the many nations who might import infected crops.

Being endemic to the Americas, the importance of *N. aberrans* in staple crops is highest in South America, where the most severe yield losses occur in potato. This nematode can also be very damaging to non-staple crops, such as tomato in Mexico, and there is a great need to reduce associated losses. Intensive research (often limited to specific areas) has been conducted in countries such as Argentina, Bolivia, Peru and Mexico. Much of this useful information is not readily accessible to the international community of nematologists, being written in Spanish in reports and publications that lack English summaries and which are often of limited distribution. The present review is an attempt to summarize knowledge of the taxonomy, biology, ecology and management of the genus *Nacobbus*.

MORPHOLOGY AND SYSTEMATICS OF *NACOBBUS* SPECIES

The first illustrations of *Nacobbus* sp. (a male and a second-stage juvenile, collected from sugarbeet, *Beta vulgaris* L., in Colorado) were published by Cobb in 1918, when he mis-identified them as *Heterodera schachtii* Schmidt, 1871. In 1935, morphological and biological information on *Nacobbus* was provided by Thorne with the description of the species *Anguillulina aberrans* collected in Utah from shadscale (*Atriplex confertifolia* Torr. & Frem.), a member of the Chenopodiaceae, i.e., the same family as sugarbeet. Subsequently, Filipjev (1936) considered *Anguillulina* Gervais & van Beneden, 1859 (= *Tylenchus* Bastian, 1865) a very diverse genus and transferred *A. aberrans* to *Pratylenchus* Filipjev, 1934. This new combination resulted in the binomen *Pratylenchus aberrans* (Thorne, 1935) Filipjev, 1936. Thorne and Allen established the genus *Nacobbus* in 1944 as a consequence of the discovery in California of a new species, *N. dorsalis* Thorne & Allen 1944, which was designated as the type of this new genus. There was some confusion in labelling the illustrations of *N. dorsalis,* because the posterior body regions of *Pratylenchus* Filipjev, 1934 and *Heterodera* Schmidt, 1871 specimens were indicated as belonging to *N. dorsalis.* In the same paper, Thorne and Allen (1944) transferred the species *A. aberrans* to the new genus, which was included in the family Tylenchidae Örley, 1880.

The taxonomic status of *Nacobbus* has been controversial because, unlike most sedentary endoparasites, all juvenile stages, vermiform females, and males can behave as migratory parasites, although the mature, swollen, females are sedentary endoparasites that establish permanent feeding sites and incite galls in host roots. Thorne (1949) placed *Nacobbus* in a new subfamily Pratylenchinae within the family Tylenchidae. Chitwood and Chitwood (1950) placed *Nacobbus* in a new subfamily, the Nacobbinae, within the family Heteroderidae Filipjev & Schuurmans Stekhoven, 1941 (Skarbilovich, 1947) amend. Wouts, 1973. In 1963, Siddiqi transferred the Nacobbinae to another family, the Pratylenchidae, and this grouping was followed by other authors (Wouts, 1973; Maggenti, 1981; Maggenti *et al.*, 1987; Luc, 1987). Golden (1971) placed the Nacobbinae in the family Nacobbidae (Chitwood & Chitwood, 1950 n. rank) within the superfamily Heteroderoidea (Filipjev & Schuurmans Stekhoven, 1941). Andrássy (1976) kept *Nacobbus* in the Nacobbinae along with *Nacobbodera* but in the superfamily Hoplolaimoidea Filipjev, 1934 (Paramonov, 1967). The most recent, widely accepted, classification, proposed by Luc (1987), indicates *Nacobbus* as the only genus, with two valid species (*N. aberrans* and *N. dorsalis*), in the subfamily Nacobbinae, which, with the Pratylenchinae, is included under the family Pratylenchidae.

Diagnosis of the genus: The genus *Nacobbus* is characterized by: strong sexual dimorphism (Fig. 1) with a swollen, irregularly distended adult female having a single ovary and subterminal vulva; vermiform males with a small bursa enveloping the tail tip; a well developed stylet in both sexes; cuticle annulated; lateral field with four incisures irregularly areolated; deirids absent; phasmids in anterior position on tail; labial area rounded, continuous with three to four annuli; median bulb rounded with prominent valve; oesophageal glands overlapping the intestine dorsally; young or immature (vermiform) and mature (swollen) females inducing galling in the roots of their host. The classification of species in the genus is based on biological and morphological characteristics of adult stages, especially those of the vermiform immature female.

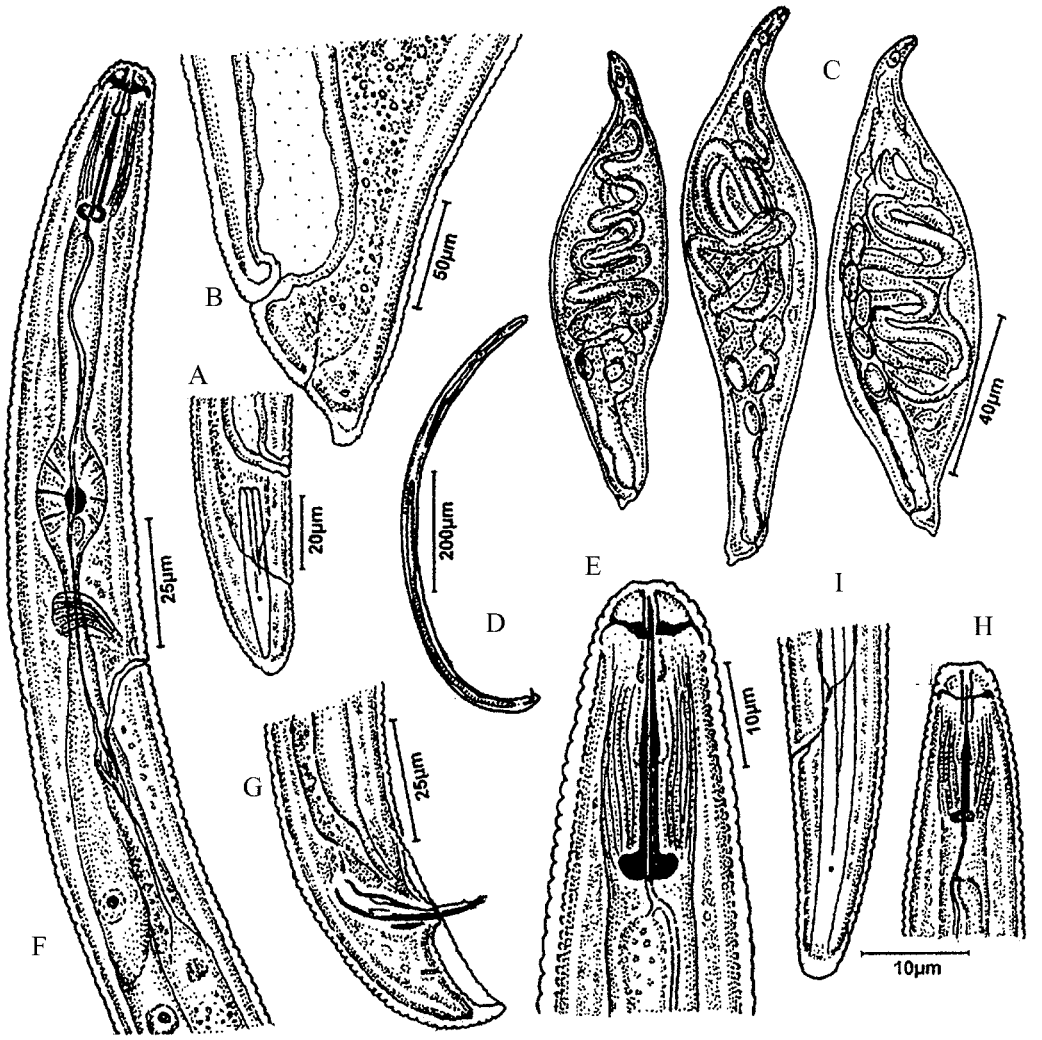

Fig. 1. *Nacobbus aberrans* (Reproduced from Crop Protection Compendium, Global module, 2nd edition© CAB International. Wallingford, UK). A. Immature female; B. Posterior region of mature female; C. Mature females; D. Male; E. Anterior region of male; F. Oesophagus of male; G. Posterior region of male; H. Anterior region of second stage juvenile (J2); I. Posterior region of J2.

Vermiform immature female: Migratory in soil and roots. Body elongate-slender, with incompletely developed reproductive tract. Cuticle annulated with anastomoses. Lateral field with four incisures (occasionally five), non-areolated or with irregular areolation (Fig. 1). Deirids absent. Phasmids on the tail, variable in position. Lip region rounded, hemispherical, continuous; with 3-4 annuli. Face, as seen with scanning electron microscopy (SEM), showing a large circular or ovoidal oral disc tending to appear slightly hexagonal or octagonal in some specimens. Oral opening dorso-ventrally oval with six distinct papillae and elongated amphidial

apertures. Dorsal and ventral lip sectors rounded, clearly separated from each other and distinct from the oral disc (see Fig. 7F in Sher and Bell, 1975). The sectors may be considered to be submedian lobes (Geraert, 1997) and are referred to as such in following sections. According to Geraert (1997), they usually bear four cephalic sensilla. Stylet strong, usually with rounded knobs. Oesophageal glands elongated, overlapping the intestine dorsally. Oesophago-intestinal junction anterior to glands (Seinhorst, 1971). Oesophago-intestinal valve present, although some authors have considered it to be undeveloped (Luc, 1987). Ovary immature, short (with few tandem oocytes), followed by the oviduct, which, at its junction with the uterus, occasionally looks like the 'spermatheca' reported by Thorne and Schuster (1956), the presence of which in the genus remains controversial (Sher, 1970). A similar anatomical structure has been observed without sperm (Cid del Prado and Manzanilla-López, unpublished) or filled with spermatozoa (see Fig. 2O in Doucet, 1989; also Martínez *et al.*, 1995). It is likely that, as the female swells, the highly developed ovary and uterus compress the oviduct cells, making them difficult to observe. Uterus elongated without eggs. Vulval aperture in the form of a transverse slit located in a transversely oval area; inner surface of vulval lips crenate. First post-vulval annulus wider; subdivided by narrower striae. Depending on species and according to Sher (1970), the vulva is located at 91-97% of body length within 0.8 to 2.3 anal body widths and 8 to 14 annuli from the anus in *N. dorsalis*, but 15 to 24 in *N. aberrans*. Anal opening poriform, 10 to 17 annuli from the posterior end in *N. aberrans* and 10 to 18 annuli in *N. dorsalis*. Tail tapering to an annulated terminus, which may be rounded, smooth or irregularly lobed.

Mature swollen female (Figs. 1 and 2)*:* Sedentary endoparasite in roots. Spindle-shaped to globose, sac-like in the central part of the body; neck region short, posterior region round (*N. aberrans*) to elongate (*N. dorsalis*), smooth or irregular margins (Figs. 1 and 2). Face with oral disc and oral opening similar to that of the vermiform immature female. Lateral lobes inconspicuous. A distinct prominence between the subdorsal and subventral lobes or in the lateral lobes has been observed in some populations of *Nacobbus* (see Fig. 4 in Baldwin and Cap, 1992; Cid del Prado, 1986). However, such a prominence is more noticeable in distorted specimens and it may be produced during processing when the lip area collapses over the cephalic framework. Oesophageal glands overlap the intestine dorsally. Oesophago-intestinal valve reportedly undeveloped (Luc, 1987). Anterior region of genital tract well developed with the uterus elongated and convoluted, with or without eggs; posterior uterine branch atrophied and obliterated. Spermatheca absent. Vulva located very posteriorly. Anal opening poriform. Phasmids punctiform. Tail short with rounded, dome-shaped, bifid or irregular terminus similar to that of the vermiform immature female (Fig. 2).

Male (Fig. 1)*:* Body vermiform. The *en face* view as seen with SEM shows a labial disc more prominent than in females. The cephalic framework is variable in development. Stylet longer than in female (Table 1), oesophageal region as in the immature female. Lateral field with four incisures with regular external areolation and fewer areolations in the central field. Testis single, outstretched but occasionally reflexed in *N. aberrans*. Spicules slightly curved ventrally with round to acute terminus. Gubernaculum simple. Bursa peloderan, well developed in *N. aberrans* and slightly less so in *N. dorsalis*. Phasmids rod-like, lying on bursal flaps (Andrássy, 1976).

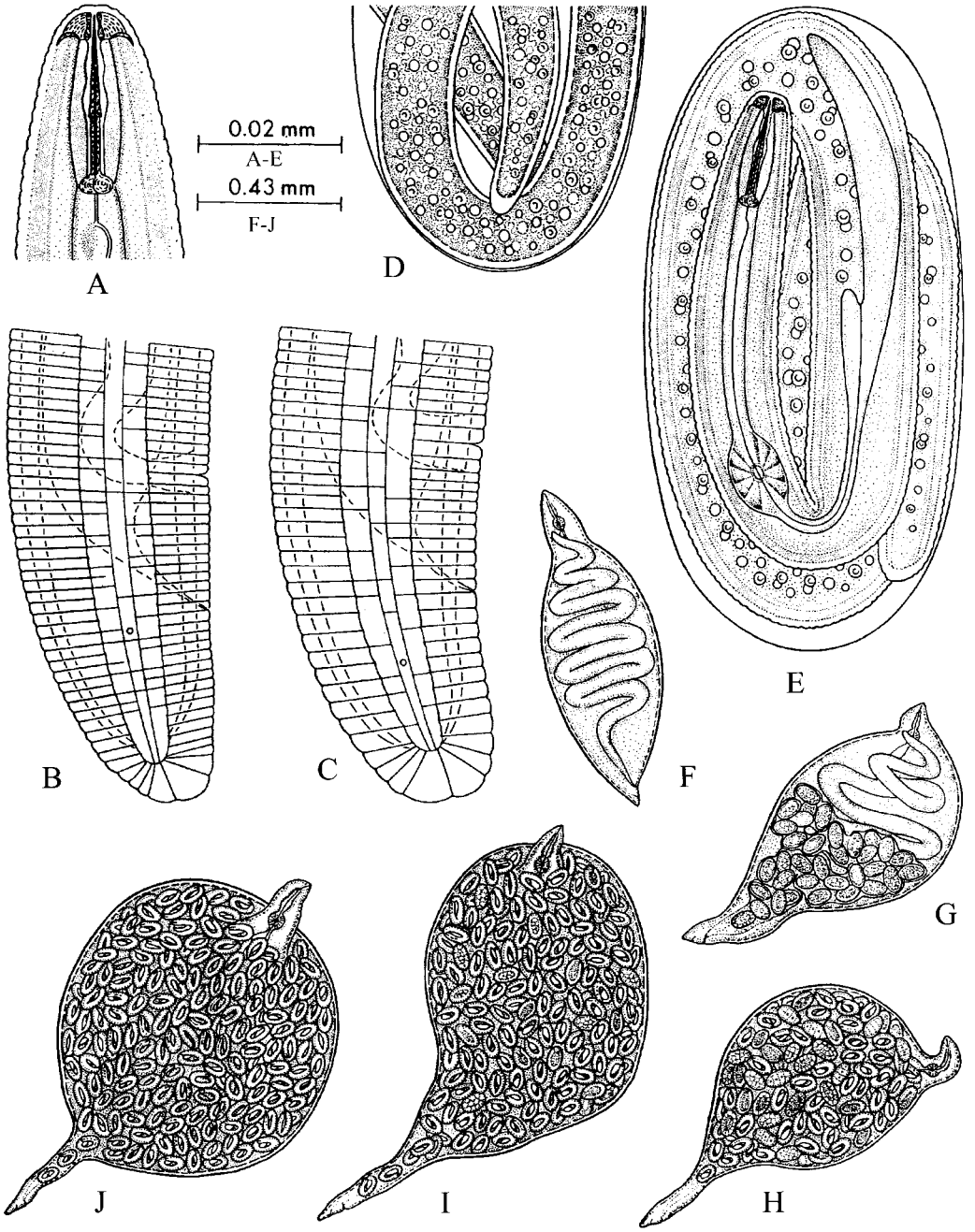

Fig. 2. *Nacobbus dorsalis* (Sher, 1970). A. Immature female, anterior region; B-C. Immature female, posterior region; D. Portion of egg with first stage juvenile; E. Egg with second stage juvenile; F-G. Early stages of mature female; H-J. Later stages of mature female.

Table 1. Combined ranges of selected morphometrics of vermiform immature and mature females, and males of *Nacobbus aberrans* from North America, Europe, and South America (Sher, 1970; Johnson, 1971; Quimí, 1979; Doucet, 1989; Doucet and Rienzo, 1991; Manzanilla-López *et al.*, 1999).

Character	Vermiform immature females	Mature females	Males
Linear (µm)			
L	476-1143	500-1660	600-1381
Stylet	15-26	13-25	18-29
Gubernaculum	—	—	5-11
Spicules	—	—	19-38
Ratios			
a	15-56	—	19-44
b	4.3-10	—	4.2-11
b'	2.0-6.6	—	2.0-8.0
c	21-48	—	24-55
c'	0.9-2.2	—	0.8-2.0
Percentages			
V	89-96	—	—
Counts			
Perineal annuli	12-36	—	—

Second stage juvenile (J2) (Fig. 1)*:* Body elongate, slender. Head slightly offset with three annuli; *en face* view similar to adults; tail blunt, curved ventrally and with a hyaline region. Oesophagus as described above, glands overlapping intestine for up to 60% or more of the body length, gland nuclei and nucleoli prominent. Lateral field with four incisures; phasmids midway along the tail. They are migratory and may be ecto- or endo-parasitic.

Third (J3) and fourth (J4) stage juveniles: These stages are migratory endoparasites but are less motile than the J2 or vermiform adults. They can be differentiated by a 'C-shaped' body, total length, maximum body width, length of gonad and distance from the posterior end of the gonad along the center body line to the tip of the tail (Clark, 1967). The J3 is longer and wider than the J2, with the lobes of the subventral oesophageal glands shorter than in the J2 and lying on both sides of the gut in an inverted 'V' shape with a slightly longer dorsal overlap. Gut very granular and filled with lipid globules. Gonad longer in female than in male and always nearer the tail; J4 female has a convex hyaline region (the future vagina) near the tail. In males, the gonad grows towards the cloaca.

Eggs (Fig. 2)*:* Ellipsoidal, thin-walled. The eggs of *N. aberrans* (75-92 × 35-46 mm) start to segment before they are laid and in *N. dorsalis* (82-110 × 40-52 mm) they are fully embryonated in the interior of the female body. The first stage juvenile develops and molts to the second stage inside the egg in both species.

THE SPECIES OF *NACOBBUS*

The genus *Nacobbus* currently includes two valid species: *N. dorsalis* and *N. aberrans.* The type species, *N. dorsalis,* has minor economic importance because of its limited geographical distribution, being

found occasionally in a few sugarbeet fields in Monterey County, California (Steele, 1984; Baldwin and Cap, 1992). *Nacobbus aberrans* is a major pest of many cultivated vegetable and field crops in North and South America. Several characters have been used to separate the females of these two species, including the number of annuli between vulva and anus (which, according to Sher (1970), at 8-14 are fewer in *N. dorsalis* than the 15-24 in *N. aberrans*), the body shape of the swollen adults (round with an elongate posterior region in *N. dorsalis* as opposed to spindle-shaped without an elongate posterior portion in *N. aberrans*), and the retention of embryonated eggs inside the body in *N. dorsalis* as opposed to their being laid in a gelatinous matrix in *N. aberrans*. In the past, two additional species were included in this genus, *N. batatiformis* Thorne & Schuster, 1956 collected from sugarbeet in Nebraska, and *N. serendipiticus* Franklin, 1959 collected from tomato (*Lycopersicon esculentum* Mill.) grown under greenhouse conditions in England. *Nacobbus batatiformis* was separated from *N. dorsalis* by the spindle-shaped mature females and from *N. aberrans* by the anterior position of the phasmids and shorter distance between vulva and anus of vermiform females. *Nacobbus serendipiticus* was distinguished from *N. dorsalis* by the spindle-shaped mature females and from *N. aberrans* by the better developed procorpus and more anterior position of the phasmids. A subspecies of *N. serendipiticus* with large males was collected from potato (*Solanum andigenum* Juz. & Buk.) in Bolivia. This subspecies was called *N. serendipiticus bolivianus* Lordello, Zamith & Boock, 1961. Sher (1970) synonymized *N. batatiformis*, *N. serendipiticus* and *N. serendipiticus bolivianus* with *N. aberrans* because of the lack of consistent morphological differences. Many taxonomists, including Luc (1987), accept this synonymy. Siddiqi (1985) listed all the species and subspecies mentioned above as valid, without providing any explanation but later accepted *N. aberrans* and *N. dorsalis* as the only two valid species in the genus (Siddiqi, 2000). A possible new but unnamed species, with few perineal annuli in females (8-14) as in *N. dorsalis* and spindle-shaped swollen females as in *N. aberrans*, was collected from spinach (*Spinacia oleracea* L.), in Texas (Johnson, 1971).

Variability within Nacobbus aberrans*:* The morphological characteristics of *N. aberrans* are illustrated in Figure 1. The wide ranges of selected morphometrics of *N. aberrans* populations from different geographical areas (Sher, 1970; Johnson, 1971; Quimí, 1979; Doucet, 1989; Doucet and Di Rienzo, 1991; Manzanilla-López *et al.*, 1999) are shown in Table 1. Vermiform immature females of *N. aberrans* with less than 15 perineal annuli occur in Argentina and Mexico. Such variability in the number of the perineal annuli and the presence of anastomoses can complicate the separation of *N. aberrans* from *N. dorsalis* when only a small number of specimens is available for diagnosis. However, the mean values derived from populations of about 20 specimens of *N. aberrans* were always more than 16, thus confirming the diagnostic value of this character for the separation of the two species (Doucet, pers. obs.). The V ratio (distance of vulva from anterior end 100/ body length) is also a valuable character since it is independent of the number of perineal annuli. In *N. dorsalis*, V is 94-97 *versus* 90-96 in *N. aberrans*.

Morphological examination of populations of *N. aberrans* from Argentina, Bolivia, Mexico and Peru (Doucet and Di Rienzo, 1991; Manzanilla-López, 1997) indicated variability of tail shape of immature females. Tails were usually subhemispherical, bluntly pointed, or subdigitate with smooth, annulated or cleft termini. Lateral

fields were usually marked by four incisures. However, specimens with areolated lateral fields marked by five incisures were also observed in Argentinian populations.

The statement made by Jatala and Golden (1977), that ". . . all known species found in South America at present are considered to be of the *Nacobbus aberrans* complex", promoted an assessment of variation in populations. Since then, it has frequently been claimed that *N. aberrans* is a complex of species or aggregates (Jatala, 1993; Canto-Sáenz *et al.*, 1996; Doucet, 1996). In its simplest form the aggregate groups together, for convenience, a number of species (binomials), which are, in classical taxonomy, morphologically similar and difficult to discriminate. Often they are of restricted geographical distribution and frequently show little variation.

Cytogenetics has been used in the recognition of aggregates (cytospecies, microspecies, etc.) and such studies have been made for *N. aberrans* (Jatala and Boluarte, 1993; Martínez *et al.*, 1995; Canto-Sáenz *et al.*, 1996) in an attempt to discriminate several populations. Although differences in chromosome number were found in some populations, these studies were not continued.

Isozyme analyses have shown inter- and intra-population genetic variability in *N. aberrans*, often with more genetic similarity among populations from different geographical areas than from the same host (Mayorga and Jatala, 1990; Doucet and Gardenal, 1992b; Ibrahim *et al.*, 1997; Manzanilla-López *et al.*, 1997). Comparisons of populations from Mexico and South America using morphological characters and other approaches, such as isoelectric focusing and RAPD-PCR, have defined three possible groupings for *N. aberrans*: two South American groups typified by populations from Bolivia and Peru and a third from Mexico. This Mexican group shows close affinity with populations from Argentina (Ibrahim *et al.*, 1997; Manzanilla-López *et al.*, 1997, 1999).

Variability within Nacobbus dorsalis*:* As mentioned previously, this species can be separated from *N. aberrans*, according to Sher (1970), by the smaller number of annuli (8-14 *vs* 15-24) in the perineal region of immature and mature females and a more posterior vulva in the immature female (V = 94-97 *vs* 91-94). Males of *N. dorsalis* are largely indistinguishable from those of *N. aberrans*, except for a smaller body length, some differences in the lateral field (irregular, complete areolation) and a less developed bursa. The body of the mature female of *N. dorsalis* (Figs. 2 and 3) is oval or spherical and possesses a short anterior projection containing the anterior portion of the oesophagus (procorpus and metacorpus). There is also an elongate posterior portion, which remains slender and contains the vulva, part of the uterus with embryonated eggs, and the tail, the latter protruding from the root tissue (Fig. 3). The presence of embryonated eggs in the uterus has been considered a biological feature of diagnostic value to separate *N. dorsalis* females from those of *N. aberrans*, which, by contrast, usually contain unsegmented eggs. However, females of *N. aberrans* with fully embryonated eggs inside the body have been reported from different populations (Johnson, 1971; Manzanilla-López, 1997). *Nacobbus aberrans* females can also adopt a semi-endoparasitic position in the galls, leaving the vulva-tail region exposed as in *N. dorsalis* (Johnson, 1971; Inserra, 1983; Inserra *et al.*, 1983; Manzanilla-López, 1997). The ranges of selected morphometrics of *N. dorsalis* are shown in Table 2.

Relationships: Baldwin and Cap (1992) analyzed the phylogenetic relationship between *Nacobbus* and other representatives of the family Pratylenchidae and concluded that the low lip region shared by *Nacobbus* and other Pratylenchidae is a

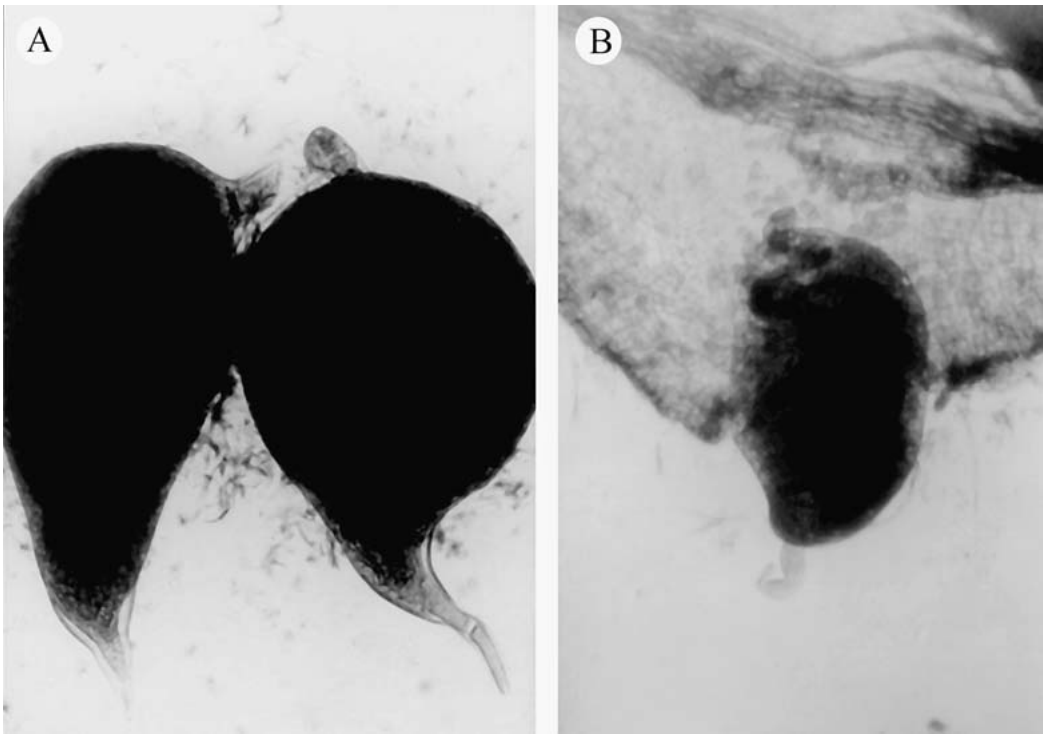

Fig. 3. *Nacobbus dorsalis* (Manzanilla-López, unpublished). A. Adult females; B. Gall and adult female.

derived character, suggesting the probability of a common ancestor. The phylogenetic relationships credited to the genus have varied due to various factors, *viz.* the poor understanding of the taxonomic importance of many characters, plus the lack of studies on embryology and ontogeny within the Pratylenchidae and related taxa that could clarify homologies or analogies and therefore their taxonomic and hierarchical value. *Nacobbus* shares with other Pratylenchidae the saccate female (*Achlysiella* Hunt, Bridge & Machon, 1989), the presence of one genital branch (*Apratylenchoides* Sher, 1973, *Hoplotylus* s'Jacob, 1960, *Pratylenchus* and some species of *Radopholus* Thorne, 1949, *sensu lato*), the dorsal overlapping of the oesophageal glands (*Achlysiella*, *Apratylenchoides*, *Hoplotylus*, *Radopholus*), and phasmids close to the anus (*Achlysiella* and *Hoplotylus*). Most of these characters are considered to be convergent within the Tylenchida and not sufficient to elevate the phylogenetic classification of the genus (Baldwin and Cap, 1992). According to Luc (1987), only the saccate female has suprageneric value and, although this character is linked with dimorphism between sexes, *Nacobbus* does not present the strong secondary dimorphism of other Pratylenchidae (*Achlysiella*, *Hoplotylus*, *Radopholus*), in which the anterior part of the male oesophagus is degenerate.

The *en face* SEM view is considered a valuable taxonomic character at the family or generic level (Luc, 1987) and the *en face* views of *Nacobbus* and *Radopholus* + *Achlysiella* are very distinct from the rest of the Pratylenchidae. The *en face* view of a *Nacobbus*

Table 2. Ranges of selected morphometrics of vermiform immature and mature females, and males of *Nacobbus dorsalis* from California, U.S.A. (Sher, 1970).

Character	Vermiform immature females	Mature females	Males
Linear (µm)			
L	590-1060	1300-1600	720-1160
Stylet	19-24	20-24	20-27
Gubernaculum	—	—	8-11
Spicules	—	—	27-35
Ratios			
a	26-34	—	25-41
b	5.1-7.3	—	5.2-8.7
b'	2.0-3.9	—	2.7-4.7
c	30-52	—	25-38
c'	0.8-1.4	—	1.4-1.8
Percentages			
V	94-97	—	—
Counts			
Perineal annuli	8-14		

female is similar to that of a *Radopholus* sp. male, but differs from other Pratylenchidae where the submedian lip sectors are either fused to each other or to the oral disc (Figs. 4 and 5; Baldwin and Cap, 1992; Geraert, 1997). The male of *Radopholus* has the submedial lobes separated by deep indentations as in *Nacobbus*. The distinctiveness of the *en face* view of *Nacobbus* was even used to support its transference from the Pratylenchidae to the Heteroderidae (Sher and Bell, 1975).

Characters such as the obese female and biology of sedentary members were again under scrutiny with the description of the genus *Achlysiella* (Hunt *et al.*, 1989) in establishing relationships and evolutionary trends among the Pratylenchidae. Both *Nacobbus* and *Achlysiella* have immature females (with a short ovary and few cells) that later become obese and sedentary in the host roots, but the life cycle is compressed in *Achlysiella* with non-feeding juveniles having superimposed molts (Hunt *et al.*, 1989). Although juveniles of *Nacobbus* retaining old cuticles have been reported (Clark, 1965; Manzanilla-López, 1997) and knowledge of its ontogeny has progressed (Souza and Baldwin, 1998), the value of a totally or partially compressed life cycle is still to be assessed. These findings suggest that future discoveries of taxa may be made that will reveal a transformation series between the sedentary *Nacobbus* and a vermiform genus of Pratylenchidae (Baldwin and Cap, 1992).

There remains a need for studies on embryology, ontogeny, development of the female gonad, morphology of spermatozoa, biology of reproduction, systematics and molecular approaches for interpretation of the phylogeny of the genus *Nacobbus*.

NACOBBUS ABERRANS (THE FALSE ROOT-KNOT NEMATODE OR POTATO ROSARY NEMATODE) GEOGRAPHICAL DISTRIBUTION

Nacobbus aberrans has been found in association with numerous crops and native

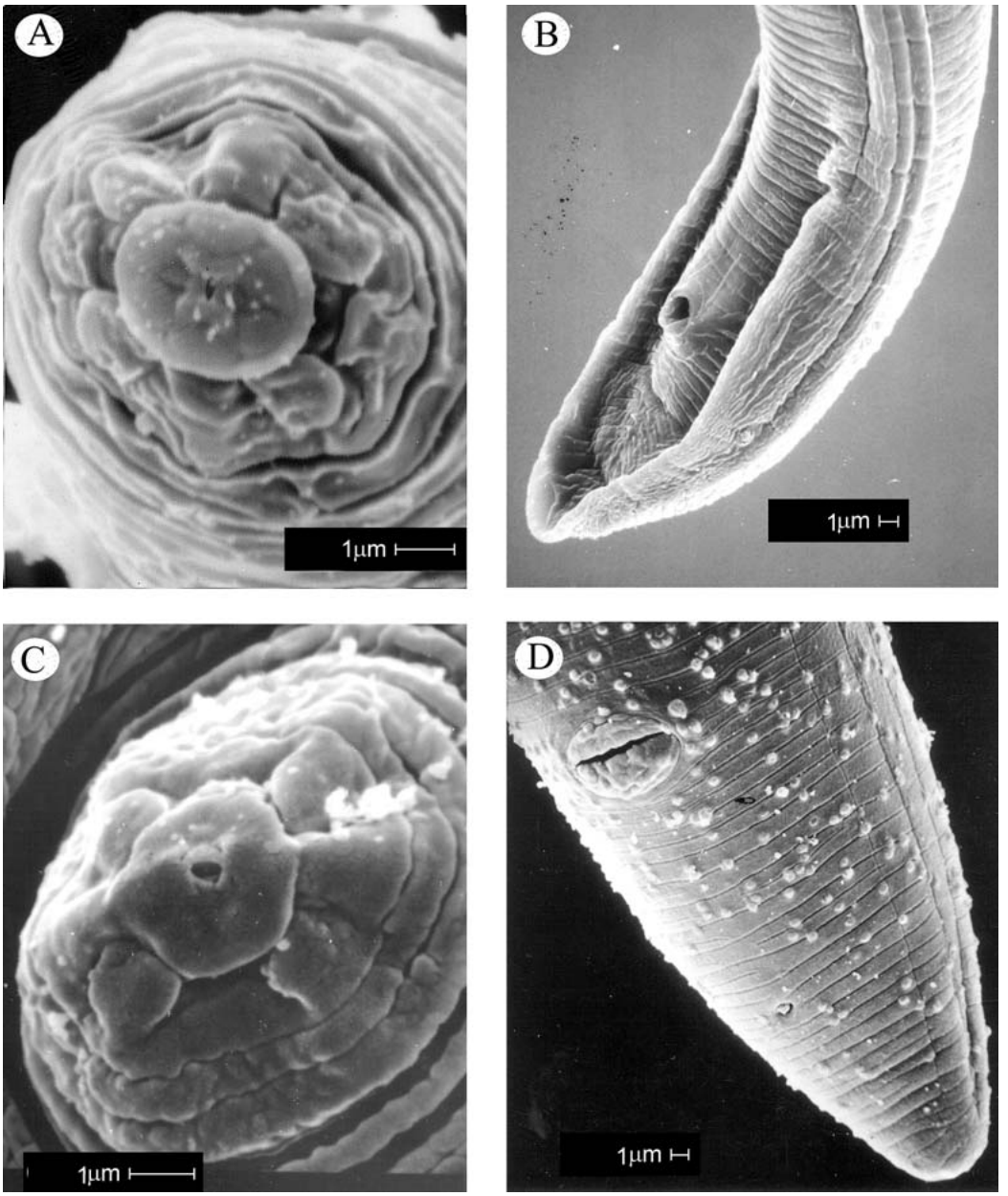

Fig. 4. SEM of *Nacobbus dorsalis* (I. Cid del Prado-Vera). A. En face of male; B. Posterior region of male; C. En face of female; D. Immature female (tail).

plants in temperate and subtropical areas of North and South America. In North America, it has been reported in the USA and Mexico. In the USA, it attacks sugarbeet, other field vegetable and weed hosts, but not potato, and is localized in the cen-

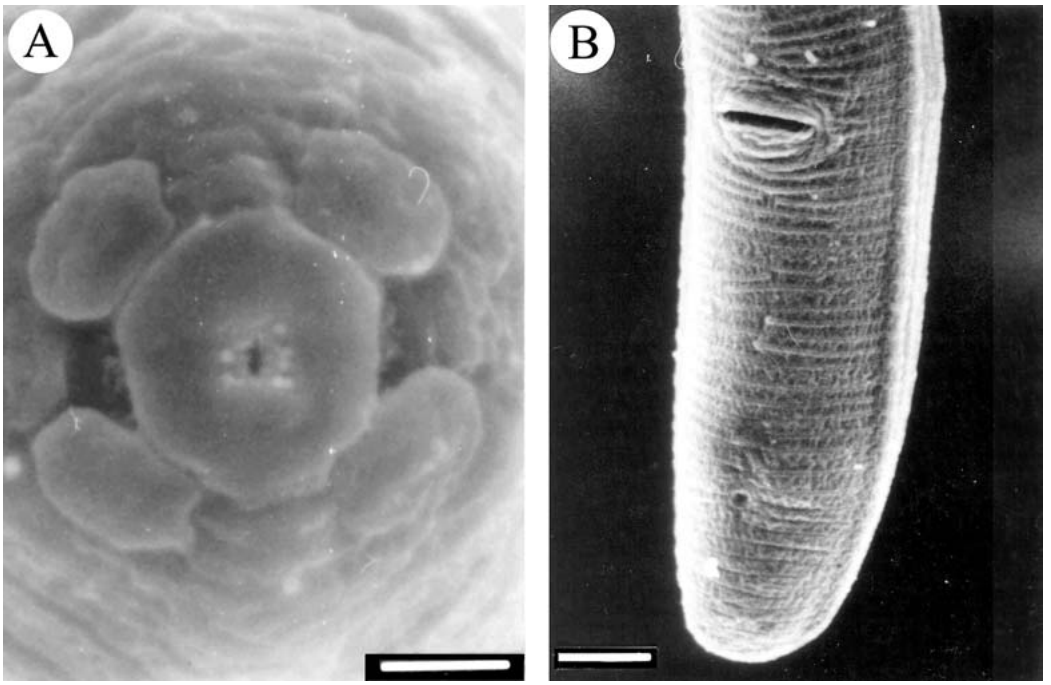

Fig. 5. SEM of *Nacobbus aberrans* (R. Manzanilla-López). A. En face of mature female (scale bar = 1.48 µm); B. Posterior region of immature female (scale bar = 6.1 µm).

tral and north-western states, specifically in Arkansas, Colorado, Kansas, Montana, Nebraska, South Dakota, Utah, and Wyoming (Caveness, 1959; Robbins, 1982). In Mexico, it has been found in the states of Coahuila, Guanajuato, Hidalgo, Mexico, Morelos, Puebla, Oaxaca, San Luis Potosí, Tlaxcala and Zacatecas (Cid del Prado, 1986; Cruz *et al.*, 1987; Cid del Prado *et al.*, 1993; Toledo *et al.*, 1993; Torres *et al.*, 1994; García-Camargo and Trejo, 1995). In these Mexican states, the nematode causes economic losses on tomato, bean and chilli (Toledo *et al.*, 1993). Nematode populations from Hidalgo, Morelos and Mexico are able to attack both sugarbeet and potato, thus differing from the sugarbeet race of the nematode from the USA, which does not infect potato. A race that infects bean is reported in Guanajuato and Zacatecas states. In South America, *N. aberrans* has been detected mainly in the western countries, including Ecuador, Peru, Bolivia, northern Chile, and Argentina. With the exception of Ecuador, where there are no confirmed reports of infections on potato, *N. aberrans* is a major pest of potato and also of vegetable and field crops (including sugarbeet) in these South American countries (Franco, 1994). In the temperate highlands of the Andean regions of southern Peru, Bolivia, northern Chile and northern Argentina (Jujuy, Salta, and Tucuman provinces), *N. aberrans* is the most common pest of potato and other local tuber crops such as mashua, oca, and olluco. In Argentina, it damages vegetable crops in Catamarca, Cordoba, Mendoza, and San Juan provinces, and also in the subtropical lowlands in Buenos Aires, Rio Cuarto, and Santa Fe provinces (Doucet, 1989). There are no reports from countries from the central

part of South America (Brazil, Colombia, Guyana, Paraguay, Surinam, Venezuela and Uruguay) or from Central America. Outside the American continent, *N. aberrans* infestations have been reported in England (UK) and The Netherlands under greenhouse conditions and these very probably originated from infected propagative plant material introduced from the American continent (Franklin, 1959; de Bruijn and Stemerding, 1968). Reports from Russia and Finland relate to *N. aberrans* detection in potato tubers introduced from Peru (Kirjanova and Lobanova, 1975). The detection of *Nacobbus* in India has not been confirmed (Prasad *et al.*, 1965) but a detection is reported from China (Yin and Feng, 1981). So far, there is no evidence of established *N. aberrans* infestations under field conditions outside the Americas.

The wide distribution of *N. aberrans* in the Americas has probably resulted from its broad host range, which includes many weeds, and from the passive transport of the nematode with propagative plant material such as seed potatoes and other tuber-forming hosts (Jatala and de Scurrah, 1975). The practice of returning unsanitized sugarbeet tare soil from the collection centers to fields has favored the spread of cyst forming, lesion, and root-knot nematode pests of sugarbeet in Idaho and Oregon (Hafez *et al.*, 1993). This practice may have also played an important role in the dissemination of the sugarbeet race of *N. aberrans* in agricultural areas of the northwestern USA and in Mexico.

BIOLOGY

Life cycle: The life cycle of *N. aberrans* is similar on all of its non-tuber-forming hosts. The first life cycle study on *N. aberrans* (*N. batatiformis*) was by Thorne and Schuster (1956) on sugarbeet. Other studies (Clark, 1967; Prasad and Webster, 1967) were done on the development from egg to maturity on tomato with a population introduced into England. Doncaster (1971) and Doncaster and Seymour (1973) published observations on feeding and juvenile migratory behavior. Life cycle studies have used the population introduced into England, North American (Mexico and USA) and South American (Argentina, Bolivia and Ecuador) populations (Clark, 1967; Prasad and Webster, 1967; Johnson, 1971; Quimí, 1981b; Inserra *et al.*, 1983; Costilla, 1985a; González *et al.*, 1989; Jatala and Haddad, 1993b; Manzanilla-López, 1997, 1999; Souza and Baldwin, 2000). Although agreeing in many respects, these studies also show some important differences. *Nacobbus aberrans* appears to have two main strategies to develop to the adult stage: (1) after penetration of the roots by the J2, development may occur inside and outside the root, with repeated penetration and emigration until the adult stages are attained; (2) after penetration by the J2, development may proceed inside the root until the young immature female or male stage is attained (Fig. 6).

According to Thorne and Schuster (1956) and Clark (1967), the life cycle of *N. aberrans* begins with eggs laid in a gelatinous matrix secreted by the female. The first stage juvenile (J1) develops inside the egg, one week after the first cellular division at a temperature of 20°C (Clark, 1967). The first molt occurs within the egg and can last from an hour to several days, depending on temperature. After hatching, the J2 penetrates a root, where it may remain or leave to re-enter the root at another site (Clark, 1967). Several juveniles may enter at the same penetration point (Prasad and Webster, 1967; Castillo, 1982; Inserra *et al.*, 1983). Within the root they move intracellularly, penetrating terminal and lateral cell walls and causing necrotic lesions. Root penetration may be regulated by temperature: Prasad and Webster (1967)

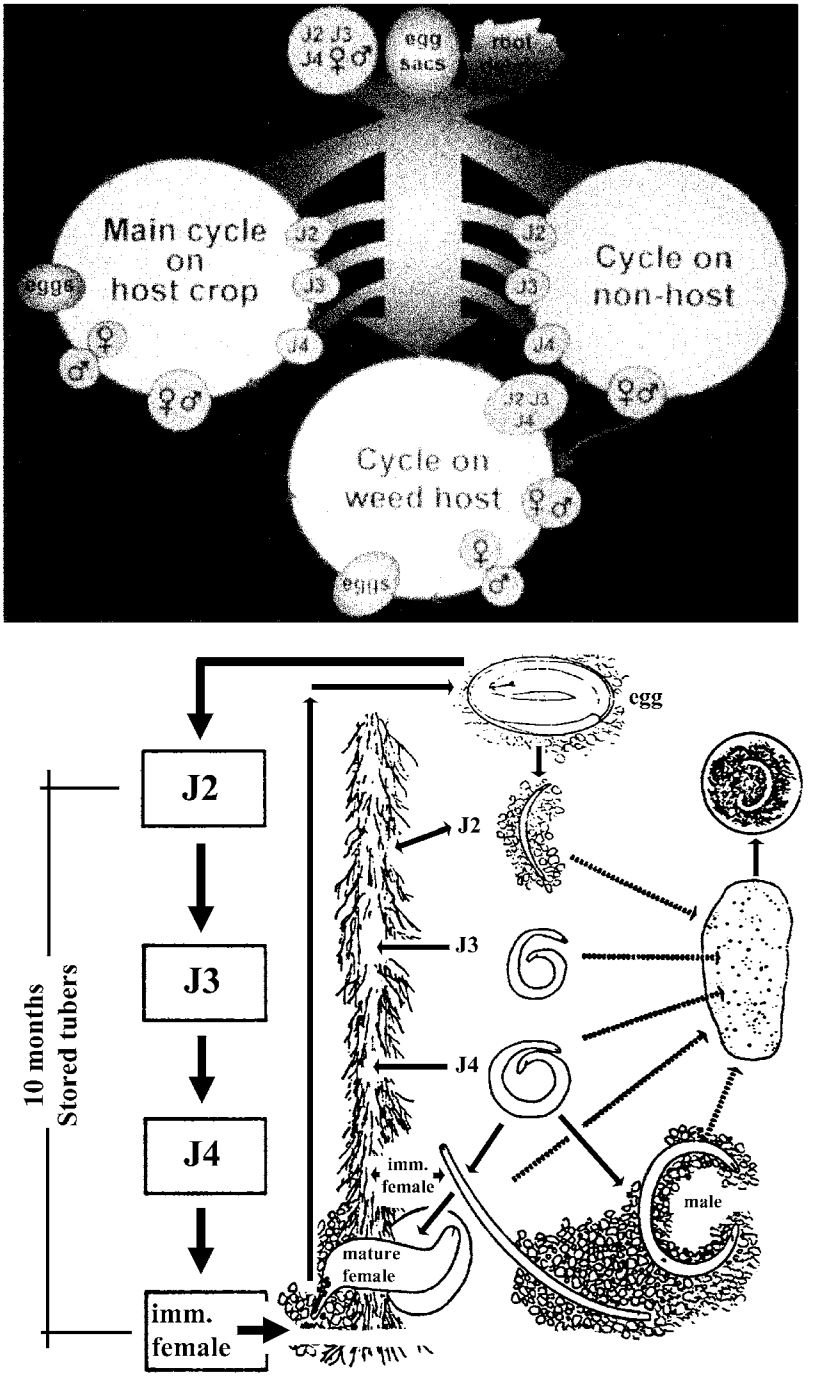

Fig. 6. Life cycle—general (Manzanilla-López, 1997); potato (Costilla, 1985a).

observed more juveniles penetrating at 15, 20 and 25°C, with fewer at 30°C but penetrating more rapidly than at lower temperatures. The J2 molts either in the root or in the soil to J3, which is less active and tends to remain coiled in the root cortex.

The J3 initially resembles the J2 but tends to adopt a 'C' shape or to coil up as it feeds and enlarges, and a notable reduction occurs in the length of the oesophageal glands. Gender can be distinguished shortly after the molt to the J3 stage: the juvenile female is shorter than the male, with an elongated genital primordium located nearer to the tail than in the male. Late J3 females show the developing vulva as a clear patch within the dark, granular body contents, close to the tail. The molt to female or male J4 can occur in the root or in the soil (Quimí, 1979; Manzanilla-López, 1997) although, according to Clark (1967), the male J4 is restricted to the root cortex. The J4 externally resembles the J3, the female gonad developing anteriorly from the vulva whereas in the male it grows posteriorly towards the cloaca. Molting of the J4 to the adult may take place inside or outside the root, immature females being vermiform. J3 and J4 maintained in water agar are able to complete their development and attain the adult stage without feeding (Quimí, 1979). Juveniles may retain their shed cuticles (Clark, 1965), a trait that can also be observed in the recently molted adults of both sexes, which often retain the J4 cuticle (Manzanilla-López, 1997). Clark (1967) suggested that, after the J4 female molts in the cortex, the adult migrates to the vascular system, a move forced either by cell necrosis (Quimí, 1979) or by sloughed off cells within the cavities occupied by the nematodes (Johnson, 1971). Newly molted females were reported exploring the surfaces of *Agrobacterium rhizogenes* transformed tomato roots (TTR, which have numerous fast-growing lateral roots and grow well in axenic culture, being referred to as "hairy roots"). The nematodes retained the shed cuticle and, after entering the root, burrowed along the vascular system (Manzanilla-López, 1997).

Adult males may be found in roots or soil. They are believed to leave the roots after molting in order to search for females (Clark, 1967). On TTR they have been observed exploring and probing epidermal cells and moving intracellularly within the root cortex (Manzanilla-López, 1997).

In contrast to the juvenile migratory behavior described above, Johnson (1971), working with a population from Texas, did not observe any migration until the J2 had developed to young males, some seven weeks after inoculation on tomato roots kept *in vitro*. Vermiform immature females typically establish themselves near the vascular cylinder and induce syncytia and galls before developing into sedentary endoparasites, although semi-endoparasitism has also been recorded (Johnson, 1971; Inserra, 1983; Inserra *et al.*, 1983, 1985; Manzanilla-López, 1997). Males and vermiform immature females may occur together in the soil but do not mate (Manzanilla-López, 1997). Mating in soil has, however, been considered a possibility and, in a root tip inoculation experiment with one vermiform immature female, eggs were produced (González *et al.*, 1989), implying that the female had mated in the soil if it is assumed that the species is amphimictic. However, it is likely that fertilization usually occurs after the female has become established in the root. Sedentary females build up lipid reserves and produce a gelatinous matrix that attracts the males. Up to 16 males may surround galls containing unfertilized females on TTR; they can also be found in the egg mass (one to 18) or within the gall next to the female tail (Manzanilla-López, 1997).

The egg sac is produced inside the gall and discharges to the root surface through a small channel, which is presumed to be formed during root penetration by the vermiform immature female. The number of eggs per egg sac is variable: 37 to 833 (Costilla, 1985a; Inserra *et al.*, 1985) but with many eggs retained inside the galls (Manzanilla-López, 1997). In contrast, the female of *N. dorsalis* does not shed eggs into an egg sac and can contain 1000-1500 eggs (Thorne and Allen, 1944). Most eggs are laid in various stages of embryogenesis but, as with *N. dorsalis*, *N. aberrans* can retain inside the female's body a few eggs that contain vermiform juveniles (Manzanilla-López, unpublished). It is not known how the gelatinous matrix is produced (Geraert, 1994). It is first extruded as a soft, colorless string of jelly, but hardens and becomes brownish with age (Canto-Sáenz, 1992; Manzanilla-López, 1997). The vermiform immature female stimulates gall formation (Prasad and Webster, 1967; Inserra *et al.*, 1983). The whole life cycle is completed in 28 to 95 days, depending on temperature (Clark, 1967; Prasad and Webster, 1967; Quimí, 1979; Inserra *et al.*, 1985; Manzanilla-López, 1997, 1999; Souza and Baldwin, 2000).

The life cycle of *N. aberrans* on potato (Costilla, 1985a) is somewhat different from that on tomato and sugarbeet (Fig. 6B). Because tubers are harvested and stored for different periods of time, *Nacobbus* populations in the Andes (where temperatures can be below -10°C) developed an extended survival strategy. The nematode overwinters in the lenticels of stored crops or wild tubers in the ground. When conditions improve in the following spring, the life cycle resumes on either planted crops or sprouting wild tubers. The juveniles, vermiform immature females and males can be found in tubers of different age and in underground stems, roots and stolons. The same stages can be recovered from soil in small numbers throughout the year, although in summer the numbers are greater. Mature females with egg sacs are rarely found in tubers. The greatest invasion of new tubers occurs when the plant foliage is reduced, either by natural senescence or by physical removal.

Under experimental conditions, the life cycle can be completed in 22 days if tubers that are planted contain J4s about to molt, vermiform immature females and males. Under field conditions, where eggs and other stages that have developed on weeds and "volunteers" make up the bulk of the primary inoculum, it is estimated that two generations may be completed and a third started within the growing period of six to seven months. The third of these generations, represented by J3s, J4s and possibly vermiform immature females, may be found in the lenticels on the tubers and may not be completed until the following growing season as a result of the tubers being harvested and stored under conditions of reduced temperature and moisture.

Parasitic habits and physiology: Manzanilla-López (1997, 1999) and Souza and Baldwin (1998) concluded that *N. aberrans* has a combination of pratylenchid and heteroderid strategies for invasion, feeding and establishment in the host (reflected in the migratory behavior of the juveniles and vermiform immature females and males, and the sedentary endoparasitic habit of the mature females).

The highly motile J2 has more dispersion potential than other stages and is likely to be the crucial pre-parasitic and parasitic stage of the life cycle. It feeds either at different sites on the same root or on different roots, and displays remarkable changes in its oesophageal glands and lipid content as it builds reserves before molting to the next stage (Schuster *et al.*, 1979; Manzanilla-López, 1997, 1999).

Quimí (1979) observed that J2s placed on nutrient water agar without tomato roots died without further development but that, under the same conditions, J3s and J4s reached the young male or female stages. More J4s than J3s survived and Quimí concluded that both J2 and J3 need to feed in the cortex until they have accumulated sufficient reserves to develop further. Because of their greater lipid content (Schuster *et al.*, 1979) the J3 and J4 are more likely than the J2 to survive adverse conditions, such as dehydration (Manzanilla-López and Pérez-Vera, 1999) and low temperature (Costilla, 1985a).

Souza and Baldwin (1998) used light microscopy and transmission electron microscopy (TEM) to estimate the level of oesophageal gland activity of the seven developmental phases of *N. aberrans*, i.e., pre-parasitic second-stage juveniles (J2), parasitic J2, J3, J4, vermiform immature females, young sedentary females (with up to 10 laid eggs), and mature sedentary females (with large egg masses). They showed that all three oesophageal glands were metabolically active in all J2 examined, although only in parasitic J2 were there numerous secretory granules in the oesophageal gland extensions and ampullae. No evidence was reported of secretory activity in the oesophageal glands of the J3 and J4, or in migratory females, suggesting that these stages do not feed. Reserves stored by the J2 must therefore sustain three molts and the migratory female's search for a feeding site and induction of a syncytium (Souza and Baldwin, 1998). Feeding activity resumes in young and mature sedentary females, where the dorsal gland is highly active and enlarged. The subventral glands are metabolically active, but with little synthesis of secretory granules, suggesting that in sedentary females they may have physiological roles other than digestion.

In other model plants, such as TTR or *Arabidopsis thaliana* (L.) Heynh. inoculated with *N. aberrans*, the J2s displayed remarkable migratory behavior, probing root hairs and penetrating roots as they moved inside or left the roots, but also showed periods of inactivity marked by occasional stylet thrusting and body movement (Manzanilla-López, 1997, 1999). They induce necrosis, cavities and cell hypertrophy in gall-like swellings and root hairs (Schuster and Sullivan, 1960; Manzanilla-López, 1997). In *A. thaliana*, affected cells showed strong cytoplasmic streaming, possibly related to injection of secretions by the nematodes. The J3 and J4 were less active than the J2 and did not migrate long distances from roots—they are commonly described as sluggish but may move and rest next to the root hairs. They have also been observed penetrating the roots and producing longitudinal channels, mainly by moving into the cortex, often coiling or folding within a small area. Pumping of the metacorpus has been observed inside cells, suggesting ingestion (Manzanilla-López, pers. obs.).

Quiescence and survival stages: Nematodes react to adverse environmental stimuli through physiological strategies generally known as dormancy, a term which comprises diapause and quiescence (Jones *et al.*, 1998). Quiescence is usually a facultative response, occurring only when the stress factor is present, but it can be an obligatory part of the life cycle and may lead to cryptobiosis. Diapause includes strategies such as developmental arrest by environmental or endogenous factors and differs from quiescence in being temporarily irreversible, requiring other "triggers" to break the dormancy even when all the environmental factors are favorable (Womersley *et al.*, 1998). Quiescence and diapause in eggs and other stages have been suggested to occur in *N. aberrans*

(Clark, 1967; Inserra *et al.*, 1983; Manzanilla-López, 1997; Souza and Baldwin, 2000). Clark (1967) noted that the egg was better adapted to survive unfavorable conditions such as low temperature or absence of a host, and that the juveniles became quiescent with their development apparently slowed or even stopped when overcrowded (Clark, 1967). Eggs of the Nebraska population of *N. aberrans* incubated at 15°C produced a 10% hatch, the unhatched J2 remaining quiescent in their eggs; a further 6% hatched when the eggs were re-incubated at 25°C (Inserra *et al.*, 1983). It is not known whether other populations retain quiescent J2 in their eggs at lower temperatures, although Peruvian and Bolivian populations can tolerate temperatures of -13°C for up to one year (CIP, 1979, 1981). According to Inserra *et al.* (1983), temperature has a stronger effect on hatching than root exudates, and low temperature may be one of the factors involved in triggering diapause.

There is still a gap in our knowledge of how *N. aberrans* tolerates and survives a broad spectrum of adverse conditions for long periods. Soils retain a significant level of inoculum, even under conditions of prolonged rotation without a crop host (The Beet Sugar Development Foundation, 1957). Possible factors involved include: the polyphagous nature of *N. aberrans* and its broad range of weed hosts (Costilla, 1985a; Canto-Sáenz, 1992), plus anatomical and physiological features of the nematode (i.e., gelatinous matrix, egg shell, cuticle) and root debris or anatomical structures (i.e., tuber lenticels) of the host (Jatala and Kaltenbach, 1979; CIP, 1979; Costilla, 1985a), which may provide protection to the eggs and juveniles. The survival and infectivity of juveniles, males, vermiform females and egg masses of a Mexican population (Montecillo) were assessed using water-glycerin mixtures (to produce conditions of 0, 20, 40, 50, 60, 80, 98.8 and 100% RH) for different periods of time (one to 30 days) at 20°C. The J2 was the least tolerant of the juvenile stages to dehydration. The J3 and J4 tolerated up to three weeks of dehydration (20-98.8% RH), with the J4 having the greatest recovery (85%) at 50% RH. Both J3s and J4s were infective after recovery. Vermiform females survived for a few days at 40-98.8% RH, but males were very intolerant of dehydration and soon died. Egg masses tolerated treatments of 60-98.8% RH and hatched J2s were infective to tomato plants (Manzanilla-López and Pérez-Vera, 1999). Further experiments (Manzanilla-López *et al.*, 2000; López and Pluma, 2000) under similar conditions corroborated the tolerance and infectivity of the J3, J4 and the J2 hatching from egg masses when dehydrated gradually either in water-glycerin mixtures (20, 40, 60, 98.8, 100% RH) or in soil contained in glass columns (75.5, 86, 96, 100% RH).

Cristóbal *et al.* (2001b) tested different development stages of the same Mexican population for resistance to adverse conditions in the field. Stages tested included whole egg masses, eggs free of the egg mass, J2s, J3s, J4s, and infected root fragments. After 50 days in soil in microplots, only inoculation with J3s, J4s and root fragments resulted in the production of galls on tomato plants, reinforcing the conclusion that the surviving quiescent stages were the J3s and J4s.

Dormancy can be triggered by various cues, such as photoperiod, which, by acting via the host plant, may have a strong influence on the induction and length of the diapause (Womersley *et al.*, 1998). Souza and Baldwin (2000) studied the life cycle and response of the J3 and J4 stages of *N. aberrans* from two populations (one from Mexico and one from Argentina) on tomato plants grown in soil-less pouches

with nutrient solution under two controlled regimes (optimal and sub-optimal) of photoperiod and temperature. The J3 did not molt to the J4 under sub-optimal conditions but molted immediately when optimal conditions were restored. According to Souza and Baldwin (2000), there is a certain time when the development of the J3 can no longer be interrupted by sub-optimal conditions occurring late in their development. However, some of the J4 remained quiescent and did not molt to the adult stages under either sub-optimal or optimal conditions. This behavior was considered to protect the more vulnerable adults from facing unsuitable conditions (Souza and Baldwin, 2000).

Although some studies of physiological processes during the life cycle of *N. aberrans* have been made, further research is needed, particularly in areas such as reproduction, survival, and the role of oesophageal gland secretions, together with studies of metabolic processes such as lipid accumulation (Schuster *et al.*, 1979; Manzanilla-López, 1997; Manzanilla-López and Pérez Vera, 1999), especially in the egg stage (Storey, 1983). Such research is essential before definitive conclusions about survival strategies of this nematode can be made.

ENVIRONMENTAL FACTORS

Effect of temperature: Temperature is one of the most important factors regulating the development and survival of plant parasitic nematodes. In South America, *N. aberrans* is found mainly in the highlands (Ortuño, 1990). Keeping infested soil at 5°C apparently stimulates activity and infection potential (CIP, 1979). In Argentina, however, it occurs in areas where mean annual temperatures vary from 22 to 24°C (Costilla, 1985a). In Ecuador, it occurs in Guayllabamba (Quimí, 1979) at mean annual temperatures of 17°C and in the inter-Andean region of El Valle de Chota where temperatures are higher (Triviño *et al.*, 1998). Under glasshouse conditions, parasitic activity accelerates during summer. At temperatures of 24 to 26°C, potato resistance to *N. aberrans* fails although the mechanisms involved are not known, so the nematode becomes even more important as a limitation to growing potatoes in the warmer zones of South America (Alarcón and Jatala, 1977). In Mexico, *N. aberrans* has been recorded from places such as Tecamachalco (State of Puebla), with a minimum temperature of 3.5°C and maximum of 29.5°C (Zamudio, 1987). Its wide distribution in Mexico means that it is likely to tolerate temperatures below zero and up to 30°C. It can damage crops at cool temperatures of 15-18°C in the highlands of Andean regions and also at warmer temperatures of 20-26°C in the subtropical lowlands of Argentina and Ecuador (Franco, 1994).

Crop damage caused by the nematode has been related to soil temperatures: winter-grown vegetables were more severely damaged than those grown during the late spring, summer and early fall and the growth of spinach was significantly reduced at relatively cool soil temperatures (20 and 24°C), but this effect was less apparent at higher soil temperatures. Although development of the nematode was completely inhibited at 29°C on spinach, there was some development on tomato (Johnson, 1971).

Thermal requirements and degree days: Data for the minimum thermal requirements for embryogenesis (from egg to second stage juvenile) or the completion of one whole generation are useful in estimating the number of generations which may occur in a crop season (Koshy and Evans, 1986), assessing potential distribution (Dao, 1970; Tiilikkala, 1987; Lahtinen

et al., 1988), consideration of the existence of geographical races (Daulton and Nusbaum, 1961; Rivoal, 1978; Langeslag *et al.*, 1982), development of simulation and yield loss models (Ferris, 1978; Caswell and Thomason, 1991), understanding population dynamics (Singh and Sharma, 1984; Tzortzakakis and Trudgill, 1996) and in the implementation of cultural control strategies (Mugniery, 1978; Langeslag, *et al.*, 1982; Griffin, 1988).

Embryogenesis: The duration of the life cycle in poikilothermic organisms such as nematodes is usually linearly related to temperature between lower and upper thresholds, and back projection of the linear part of the relationship provides the theoretical base temperature (T_b) (Trudgill, 1995). In a study of the time required for the completion of embryogenesis in two *N. aberrans* populations at temperatures from 12 to 30°C, it was observed that data may fit not only a linear but a sigmoid relationship. The best fit ($r^2 = 0.96$) was achieved using a quadratic model, the T_b being estimated at 13.4°C for a Mexican population (Manzanilla-López, 1997).

Thermal requirement studies must not be done during periods when organisms are in diapause or when they are influenced by environmental factors such as hatching factors, chilling, photoperiodism, etc. (Trudgill, 1995). The effects of these factors on *N. aberrans* embryogenesis and generation time are unknown and may interfere with the fitting of linear models and calculation of accurate basal temperature and thermal constant values. However, some calculations can be made from values in the literature for temperature ranges tolerated by the nematode and the duration of different biological processes.

The eggs of the *N. aberrans* sugarbeet race from Nebraska hatched at temperatures as low as 5°C, although less than 1% of the eggs hatched at this temperature. Less than 3% hatched at 10°C and the optimal temperature for egg hatch was 25°C (Inserra *et al.*, 1983). The small hatch at 5 and 10°C indicates that these are extreme temperatures for hatching and may not allow further nematode development. As significantly more eggs hatched at 15°C (about 12%) than at 5 and 10°C (<3%), it is reasonable to assume that the minimum threshold temperature (MTT) for the embryogenesis of *N. aberrans* is around 13°C. The results of this study of the sugarbeet race, and another in England (Clark, 1967), indicate that the duration of embryogenesis of *N. aberrans* from egg deposition to J2 emergence is 51, 12-17, and 9-10 days at 15, 20, and 25°C, respectively (Clark, 1967; Inserra *et al.*, 1983). The calculated day-degrees (DD, = temperature of the experiment – MTT (13°C) × duration of embryogenesis in days) required at these temperatures were very similar at 102, 84-119, and 108-120 DD at 15, 20, and 25°C, respectively.

Postembryogenic development: No root penetration by J2 of the sugarbeet race of *N. aberrans* occurred at 5°C and very little at 10°C (Schuster *et al.*, 1966; Inserra *et al.*, 1983), suggesting that even 10°C is an extreme temperature for post-embryogenic development. Taking into consideration the fast development of nematode juveniles at 20°C, the MTT for the post-embryogenic development of *N. aberrans* must lie between 10 and 20°C, and probably close to 15°C. The duration of the post-embryogenic development of the *N. aberrans* sugarbeet race from root penetration by the J2 until the appearance of the swollen females with eggs is 75 and 38 days, or 375 and 380 DD above 15°C, at 20 and 25°C, respectively (Inserra *et al.*, 1983). The duration of the nematode life cycle from egg to egg for the sugarbeet race of *N. aberrans* is 48 days at 25°C, requiring 480 DD (Inserra *et al.*, 1983). Different workers

inoculated host plants with egg masses containing eggs at different stages of embryogenic development (Prasad and Webster, 1967; Costilla, 1985a) or with the J2 (Quimí, 1981b). In experiments that used egg masses, the computation of the duration of the nematode life cycle includes an unknown duration of embryogenic development but, interestingly, the duration of the nematode life cycle in these experiments is similar to that of the post-embryogenic development of the sugarbeet race by Inserra *et al.* (1983). On potato in Argentina, the potato race completed its life-cycle in 48 and 37 days at 22 and 24°C, respectively (Costilla, 1985a), equivalent to 336 and 333 DD compared with 375 and 380 DD for the post-embryogenic development of the sugarbeet race. On tomato in England, *N. aberrans* took 36 days at 25°C to complete its life-cycle (Prasad and Webster, 1967), equivalent to 360 DD and therefore almost identical to the post-embryogenic development of the sugarbeet race. However, this same population from England, in an experiment on tomato, took 70 days at 19°C or 280 DD to complete its life cycle (Quimí, 1981b). A population from Ecuador at the same temperature took 80 days or 320 DD (Quimí, 1981b), an intermediate value. Adding together the DD calculated for the completion of the life cycle and that required for embryogenesis (102 and 110 DD at 20 and 25°C, respectively) in these experiments gives totals very similar to those calculated for the life-cycle of the sugarbeet race. The full life cycle of the potato race in Argentina would require 438 and 443 DD at 20 and 25°C, respectively. The potato race (on tomato) in England would require 470 DD at 25°C, and this same race on tomato in Ecuador would require 382 DD at 19°C, and 485 DD at 25°C. Most of these values are not very different from the 480 DD calculated for the completion of the life cycle of the sugarbeet race. Differences in values for the basal development temperature are to be expected, depending on the climate and habitat conditions to which different populations are adapted. However, it is unlikely that MTT values lie much outside 13 to 15°C, as greatly different values would cause great variation in the calculated DD values for the development of *N. aberrans* at different temperatures, as reported by Inserra *et al.* (1996).

The numbers of DD required by *N. aberrans* to complete its life-cycle in these experiments, with an assumed MTT of 15°C, are greater than those required by other nematode pests, such as *Heterodera schachtii* (280-350 DD; Raski, 1950) and *Globodera rostochiensis* (266-358 DD; Greco and Moreno, 1992), which share sugarbeet and potato as hosts in common with *N. aberrans*.

Effect of soil: Although soil characteristics, such as texture, humidity, cationic exchange capacity, pH, salinity, litter layer, etc., are important factors for development of, and changes in, nematode populations over time, not much is known about their effects on *N. aberrans* and very few data are available from the literature. Adaptation to different temperatures and soil types has been related to the wide distribution of *N. aberrans* (Alarcón and Jatala, 1977). Sandy, medium and fine-textured soils, poor in organic matter (1.5%) and with a pH moderately acid (pH 5.7-6.1) to alkaline (7.6-7.8), all favor its development and occurrence (Costilla, 1985a; Yáñez-Juárez, 1997). In Mexico, *N. aberrans* has been found thriving in impoverished soils with a "caliche" layer (porous, permeable and saline), like those of the Mezquital Valley (State of Hidalgo), or sandy soils (xerosol type) as in Tecamachalco (State of Puebla).

Effect of water: Nacobbus aberrans is considered to be well adapted to dry climates, being capable of surviving up to eight

months in air dried soils (RH 7 to 9%) as the egg or vermiform female (Jatala and Kaltenbach, 1979). Dry soil carried by the wind is an important means of egg dissemination. Water stress increased damage to potato cvs Guaycha and Gendarme in Cochabamba (Bolivia), although cv. Gendarme produced the higher tuber yield and fewer galls and females per gall (Instituto Boliviano de Tecnología Agropecuaria, 1994). Excessive soil moisture (caused by frequent watering) reduced the reproduction of the nematode, but also reduced the number and size of tubers.

Effect of cations: Calcium or sodium salts added to soil infested with a population of *N. aberrans* from Texas appeared to increase galling or the multiplication of *Nacobbus* on Rutgers tomato plants. Interestingly, nematode-infested plants did not suffer salt toxicity, whereas control plants demonstrated terminal root burn due to excessive salt uptake. It was suggested that the presence of the nematodes either tied up the nutrients in some way or reduced their uptake so that toxic concentrations were not established in the plants (Johnson, 1971).

Population dynamics: There are a few reports on the population dynamics of *N. aberrans* that include data on reproduction rate, number of generations, sex ratio, etc., and the effects of both biotic and abiotic factors on population growth and development (Clark, 1967; Costilla, 1985a; Caballero and Muñoz, 1987; Franco *et al.*, 1992; Manzanilla-López, 1997). The presence of overlapping generations was first noted by Clark (1967) in observations made at a constant temperature of 20°C. Bravo-Baldeón (1977) recorded that, in naturally infested soils in Bolivia, the greatest numbers of juveniles in soil occurred 48 and 96 days after the potatoes emerged and that these peaks coincided with the greatest numbers of juveniles, males and females in roots. Also under field conditions, there were several peaks (three to four) of motile stages occurring in soil and roots until the end of the crop cycle, thus producing overlapping generations (Cid del Prado *et al.*, 1995, 1996c, 1997a; Manzanilla-López *et al.*, 1998). The migratory and endoparasitic habits of this species mean that fluctuations in numbers of the different stages of development can be better quantified from roots than from soil.

The reproductive capacity of *N. aberrans* ensures that a substantial number of eggs and juveniles are returned to the soil, either as naked egg masses or in the root debris once the crop has senesced, thus acting as the primary inoculum for the next crop. However, studies in Bolivia showed a strong influence on population dynamics of "dormancy stages", which must be reactivated before gall formation proceeds (Franco *et al.*, 1992a). It is not known for most host crops how initial densities of the nematode and other environmental factors affect the nematode's rate of reproduction. A negative linear correlation has been found experimentally between initial and final population densities by Inserra *et al.* (1984a and b), the maximum rate of increase (around 32 times) occurring at the lowest initial population density (0.25 J2/cm^3 of soil). Caballero and Muñoz (1987) reported a negative relationship between precipitation (and the consequent reduction of temperature) and the number of eggs produced by *N. aberrans* on spinach in naturally infested soils in Mexico.

Interactions with other organisms: Although *N. aberrans* has been found under natural conditions in association with important soil-borne plant pathogens and microorganisms, few interactions are documented. Interactions, depending on their effect on *N. aberrans*, may be classed as competitive (Inserra *et al.*, 1984c), synergistic (Pérez and Pérez, 1988; Hernández, 1990; Hernández Anguiano *et al.*, 1992;

Montalvo *et al.*, 1993; Vargas *et al.*, 1996), neutral (Gómez *et al.*, 1987a) or deleterious (Mareggiani *et al.*, 1985; Balderrama *et al.*, 1993; Méndoza-de Gives *et al.*, 1994; Eguiguren-Carrión, 1995).

Competition between two or more nematode species on a plant may or may not occur, depending, for example, on factors such as their initial densities, parasitic habits, pathogenicity, host susceptibility, environmental conditions and period of exposure (Eisenback and Griffin, 1987). Combined inoculations of *H. schachtii*, *Meloidogyne hapla* Chitwood, 1949 and *N. aberrans* at densities of 12 J2/cm^3 of soil, significantly suppressed the growth of sugarbeet cv. Tasco AH14 and, over time, *Nacobbus* was antagonistic to the reproduction of *H. schachtii* and *M. hapla*, particularly the latter (Inserra *et al.*, 1984c). Conversely, reproduction of *N. aberrans* was not affected by the presence of the other two genera. It was considered to be a less "aggressive" species than root-knot or cyst nematodes because of its slow development and low reproductive rate, which allowed better sugarbeet seedling growth (Inserra *et al.*, 1984c). Simultaneous root infection resulted in different spatial distributions of the adult females of the three species. *Meloidogyne hapla* females were located in the external tissue layers of the galls, females and cysts of *H. schachtii* were found at the base of *N. aberrans* induced swellings or galls, and syncytia of *N. aberrans* were in the central part of the root while those of *H. schachtii* were in a more peripheral position.

Other plant parasitic nematodes reported along with *N. aberrans* on different crops are: *Pratylenchus* sp. on tomato (De la Jara *et al.*, 1983); *M. hapla* and *Meloidodera mexicana* Cid del Prado-Vera, 1991 on chili pepper (Manzanilla-López and Cid del Prado, unpublished); *Pratylenchus andinus* Lordello, Zamith & Boock, 1961 (Lordello *et al.*, 1961), *Meloidogyne* sp. (Jatala, 1985), *Globodera pallida* Stone, 1973 (Canto-Sáenz, 1992) and *Globodera* spp. on potato (Ramos *et al.*, 1998). *Nacobbus aberrans* and *Globodera* spp. are responsible for important losses on potato in the Andean region of Bolivia where they may occur together or alone, their impact depending on initial density, climatic conditions, soil type and potato cultivar. Yield losses caused by *N. aberrans* are more pronounced than those caused by *Globodera* spp., even at low initial densities of *Nacobbus* (Ramos *et al.*, 1998). Potatoes bred for resistance to *Meloidogyne* spp. and *Globodera* spp. may reduce competition for *Nacobbus* (Jatala, 1985). However, it is not known what sorts of interactions occur between *Nacobbus* and the species listed above.

Studies of interactions between *N. aberrans* and fungi have sometimes included more than one species of fungus. As interactions become more complex, they cannot be so easily assigned to a single category (i.e., additive, synergistic, neutral or deleterious). Pérez and Pérez (1988) evaluated the responses of one *N. aberrans* susceptible (Mulato V-2) and four resistant (CM-355, CM-329, BG-1504, L-29) cultivars of *Capsicum annuum* L. to *Phytophthora capsici* Leo. and *N. aberrans*. When the nematode (1500 eggs/plant) and the fungus (180 000 zoospores/plant) were inoculated concomitantly, infection and plant mortality occurred due to the nematode breaking the plant's resistance to *P. capsici*. This synergistic interaction between *Nacobbus* and *Phytophthora* was later confirmed and further studies on the physiological and biochemical mechanisms involved have been conducted (Hernández, 1990; Hernández *et al.*, 1992; Vargas *et al.*, 1996).

Under field conditions, *N. aberrans* occurs on tomatoes infected with *Fusarium oxysporum* Schlechtendal and *F. roseum* Link: Fries (De la Jara *et al.*, 1983). Because these pathogens are important in Mexico,

Gómez *et al.* (1987a) assessed the pathogenicity of *F. oxysporum* (Schl.) f. sp. *lycopersici* (Sacc.) Snyder & Hansen and *N. aberrans* (alone or combined) on tomato under glasshouse conditions, at three different densities of inoculum. No statistically significant differences were found. In another study, the effects of *Paecilomyces lilacinus* (Thom) Samson on the two pathogens (alone or combined) were evaluated (Gómez *et al.*, 1987b). *Paecilomyces lilacinus* did not reduce the gall index or fungal damage (neutral interactions), but *Fusarium* wilting and root rotting were reduced in the treatment *Fusarium* + *Paecilomyces* + *Nacobbus*; galling was only reduced (60%) when *F. oxysporum* f.sp. *lycopersici* and *N. aberrans* occurred simultaneously.

Nacobbus aberrans and *Synchytrium endobioticum* (Schilb.) Perc. have been reported on potatoes grown in Bolivia. Montalvo *et al.* (1993) inoculated cvs Waych'a and Imilla Blanca with five densities of *N. aberrans* and *S. endobioticum* alone or combined. The fresh weights of roots and foliage, and the numbers and weights of tubers were reduced in both cultivars. A synergistic effect was noted on tuber weight, although the presence of the nematode caused the greatest effect. There was no antagonistic or stimulatory effect of the pathogens on each other. Another important pathogen of potatoes, *Spongospora subterranea* (Wallr.) Lagerh., has also been reported on the galls induced by *N. aberrans* (Jatala, 1985).

Some interactions with microrganisms have a deleterious effect on *N. aberrans* and, because of their potential use in management strategies, these are commented upon in the section on biological control.

EFFECTS ON THE HOST

Symptoms of attack: Patches of poor growth are a common feature of affected crops (Fig. 7A). Above-ground symptoms include a reduction of apical growth (stunting), chlorotic leaves with rolled margins, wilting and, in tomato, the production of small fruits. The main underground symptoms on the various hosts (Fig. 7B-E) are the presence on the roots of galls, which may bear lateral roots, and the cessation of growth of tertiary and fibrous roots. The wounds and necrosis caused by the juveniles on sugarbeet interfere with the function of the smaller branch roots of the taproots, often causing complete loss of stand. Plants that remain usually are stunted (Schuster *et al.*, 1965).

On potato roots (Fig. 7D), galls produced by *N. aberrans* tend to be distributed along the root axis, which acquires the appearance of a rosary (Canto-Sáenz, 1992). Galls on tomato and chilli pepper roots are more elongate and contain more than one female, whereas galls on potato roots generally contain only one. Severely affected potato plants are chlorotic and weak, with slower growth and earlier maturity than healthy plants (Costilla, 1985a). The number of galls increases considerably when tubers begin to form (Otazú *et al.*, 1985). Potato tubers do not show visible symptoms, but freshly harvested infected tubers have spongy tissue in the lenticels, the large cells producing an inflated appearance. The lenticels later become flatter and suberized. Nematodes are found 0.5-3 mm below the tuber skin (La Rosa and Jatala, 1977).

Symptoms on beans are similar to those described on other hosts but care must be taken to distinguish *Nacobbus* galls from *Rhizobium* nodules.

Cytopathology and histopathology: Cellular and tissue alterations related to invasion of juveniles and the histopathology of the syncytium have been studied on several crop and weed hosts using a variety of techniques. The types of lesion and damage are related to the stage of the nematode

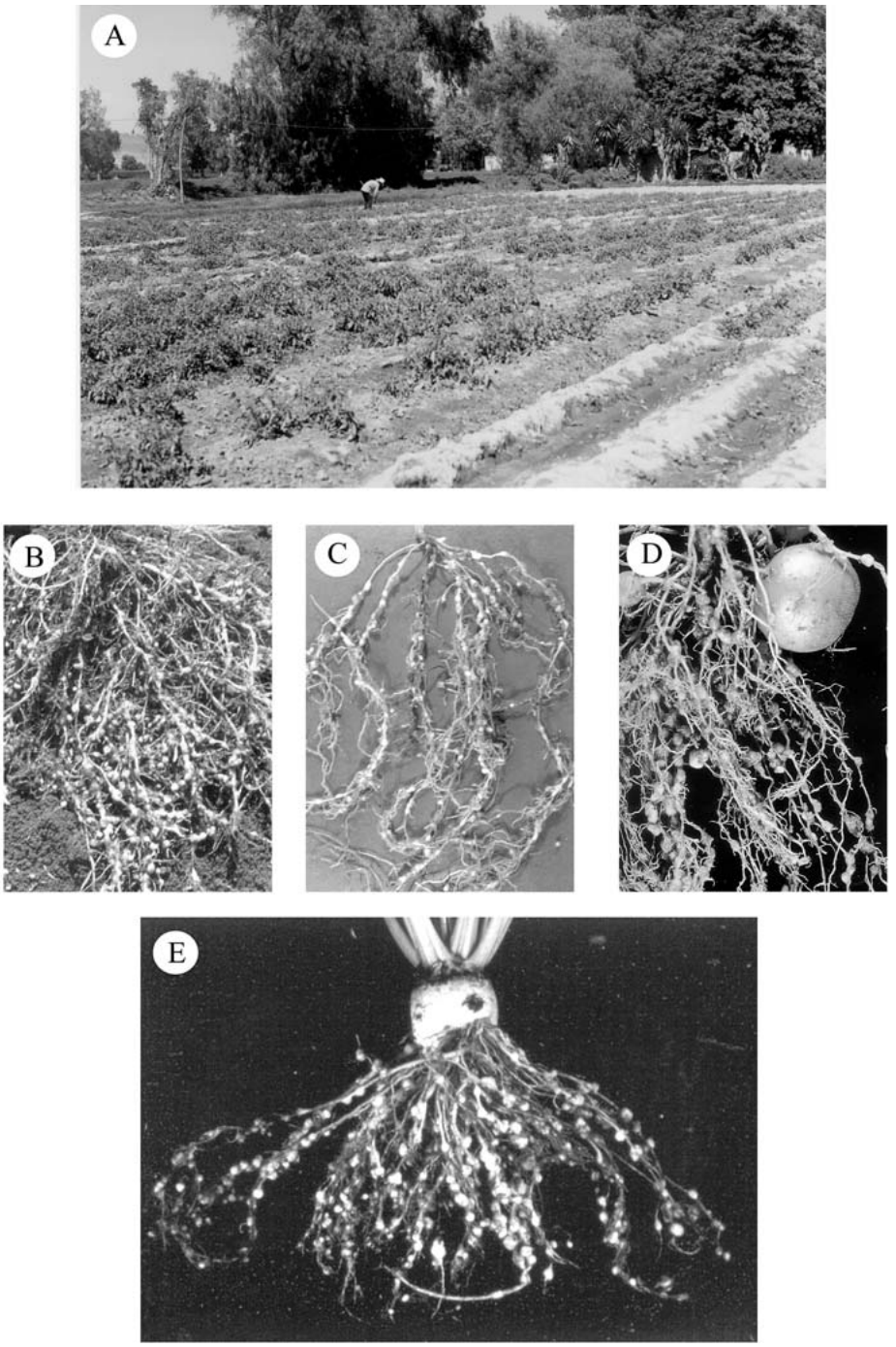

Fig. 7. Symptoms of *Nacobbus aberrans* attack. A. Tomato field (Tecamachalco, Puebla, J. Cristóbal-Alejo); B. Tomato root (Tecamachalco, Puebla, J. Cristóbal-Alejo); C. Beans (R. Manzanilla-López); D. Potato roots (J. Franco); E. Sugarbeet (Rothamsted Research).

and to the crop. Some alterations may occur in tissue culture but not in soil-grown roots. Cellular alterations (i.e., hypertrophy) tend to extend gradually outwards from the site where the juveniles are located or from the original point of induction of the syncytium (i.e., mitotic stimulation). Cellular and histological modifications in the affected roots suggest that the nematodes incite a series of physical, chemical and physiological changes.

The J2 invades the cortex intracellularly, breaking down end walls and passing through rows of cells, forming cavities adjacent to the hypodermis. The affected cells frequently show dense cytoplasm, hypertrophied nuclei and cell walls, vacuolation, formation of starch granules and cell lysis (Schuster and Thorne, 1956; Schuster *et al.*, 1965; Inserra *et al.*, 1983; Castillo and Marbán-Méndoza, 1984; Jatala and Haddad, 1993d). In some cases, cavities spread from the cortical parenchyma towards the vascular cylinder, destroying up to 50% of the tissue (Inserra *et al.*, 1983). The cavities are usually limited by necrosis, the J3 and J4 stages usually being found inside them (Quimí, 1979). Juvenile stages can cause deterioration and death of small roots (Jatala, 1985).

Pronounced hypertrophy of the cortical cells and development of callus-like tissue occur under tissue culture conditions. Epidermal cells tend to be spherical and nematode feeding causes hypertrophy of the root hairs. The root tip may become swollen and further apical growth may be inhibited. Pendulum-like galls occur near the ends of the roots and are more frequent in tissue culture than in soil-grown root conditions (Schuster *et al.*, 1965). On excised tomato roots formation of root hairs at the site of the gall is prevented, although secondary root development is induced in soil tests. The incitant factor may be similar in both cases (Schuster and Sullivan, 1960).

Gall formation by hypertrophy, but not hyperplasia, is stimulated by the juveniles (Schuster and Sullivan, 1960; Schuster *et al.*, 1965). However, hypertrophy and hyperplasia of the pericycle and endodermis, as well as damage to the vascular system, have been associated with the female J4 (Castillo, 1982).

The permanent establishment of the nematode stimulates mitosis in the pericycle and formation of lateral roots in galled areas (Fig. 8A). On sugarbeet, stem buds ("rootlings") arise from the pericycle and produce typical leaf appendages. According to Schuster *et al.* (1965), stem bud induction may be due to an increase in the adenine/indoleacetic acid ratio within the tissue.

Syncytia are induced by the vermiform immature female, (Prasad and Webster, 1967; Inserra *et al.*, 1983) and also by the J4 female (Castillo and Marbán-Méndoza, 1984). The syncytium structure has been described as a spindle-, heart- or crescent-shaped mass of cells (Fig. 8B-D). It can measure 2 to 8 mm in size and strongly disrupts the organization of the stele causing root asymmetry (Finetti, 1990), although vascular continuity is retained by xylem and phloem cells. Where syncytia contact these cells, no wall in-growths are laid down. The nuclei of syncytia are large and irregular and the chromatin and nucleolus may be disorganized (Castillo, 1982). Numerous mitochondria and Golgi bodies are also present and the syncytial walls are thickened due to polysaccharide deposition (Jones and Payne, 1977; Ponce de León and Doucet, 1989). Crystal formation occurs in the gall tissue and starch granules (Fig. 8D) are common both inside and outside the syncytia (Schuster *et al.*, 1964).

In sugarbeet, the syncytium is formed by the merging of protoplasts due to the gradual dissolution of cell walls. It is located within the cortex and is bounded

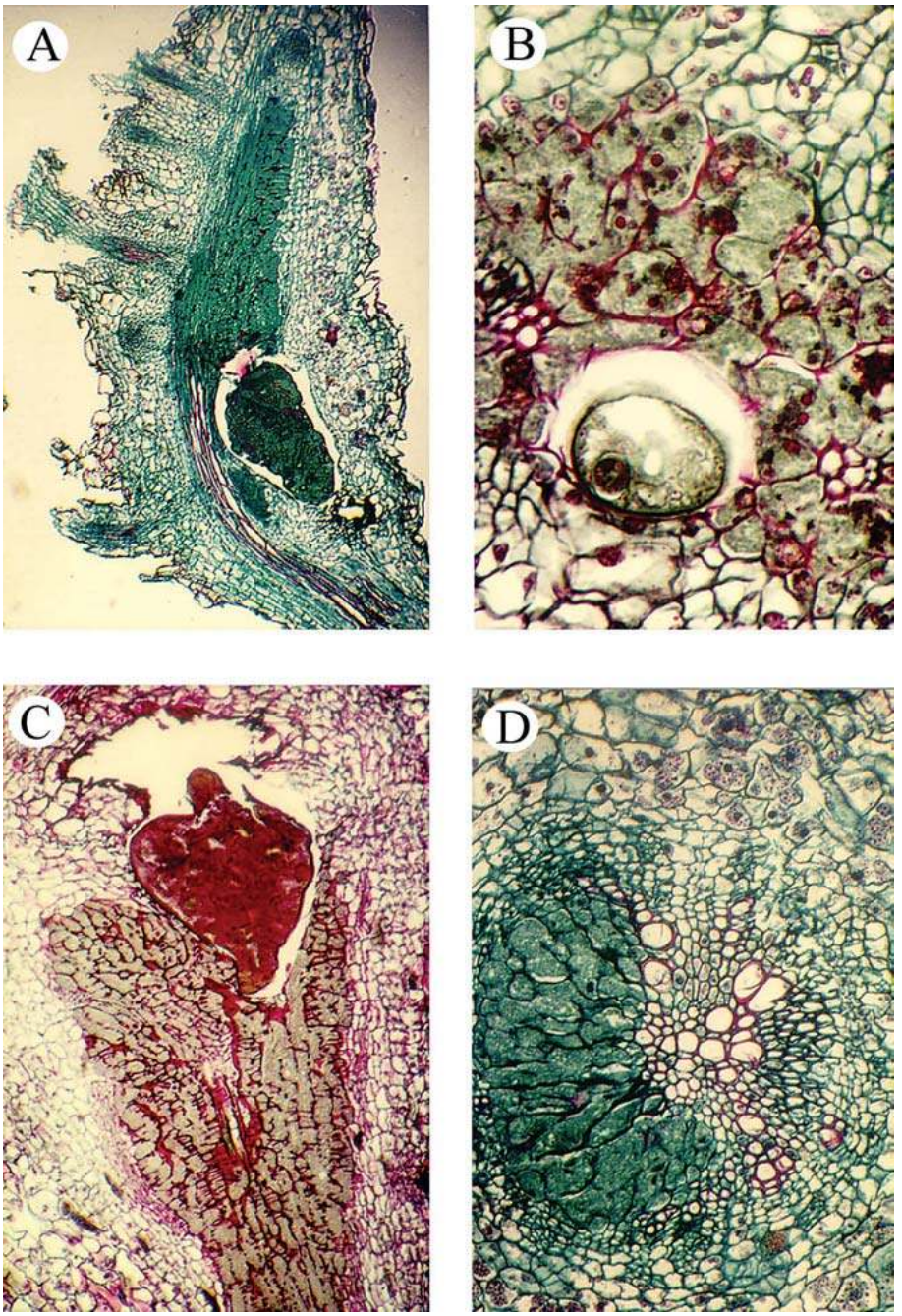

Fig. 8. Histological sections (*Nacobbus aberrans* on *Capsicum* spp.). Johansen quadruple stain modified by Castillo (1982). A. Longitudinal section of gall showing the nematode, syncytium and lateral roots (25×); B. Syncytium occupying a large area of the vascular system (100×). Note starch granules and small groups of phloem cells being displaced by the syncytium; C. Longitudinal section of gall and syncytium showing the head of the adult female directed towards the vascular cylinder (40×); D. Initial phase of syncytium development (100×).

by the endodermis or, occasionally, by the xylem elements. Budding nucleoli with concomitant invagination of the nuclei, in what according to Schuster *et al.* (1965) appeared to be an amitotic rather than mitotic division, were reported in sugarbeet galls. Budding nuclei were also found in *Kochia scoparia* (L.) Schrad. and *Opuntia tortispina* Nutt. gall sections, leading to the suggestion that a multinucleate condition in *Nacobbus*-induced syncytia arises by amitotic division rather than by pooling of nuclei (Schuster *et al.*, 1965). A multinucleate condition has been reported in some syncytia cells in potato (Finetti, 1990) and *Spergula arvensis* L. (Doucet *et al.*, 1994).

SEM observations made on tomato (Jones and Payne, 1977) showed the syncytium and cavity occupied by the nematode to be located in the gall cortex, where the parenchyma cells are larger. Air spaces between the parenchyma cells may facilitate gas exchange, thus preventing an anaerobic condition. Syncytium development occurs within the stele by wall digestion at pit-fields and by fusion of neighboring protoplasts. A stimulation of cell mitosis occurs before cell incorporation into the syncytium, tiers of cells in some regions indicating an active division of cambial cells. There is a strict demarcation between cells inside and outside the syncytium. Although cell identity is maintained, cytoplasmic contents move between the cells of the syncytium through extensive gaps and perforations in the walls. Differentiation of vascular elements occurs in the syncytium area. Xylem elements develop both within the mass of smaller cell layers away from the syncytium and also adjacent to syncytial cells. Similar groups of phloem cells (looking like vascular bundles of minor veins in leaves) are usually found well outside the syncytium, although sometimes immediately adjacent. Numerous gall cells differentiate into wound-type sieve elements, and numerous plasmodesmata are found in the pit-fields between the sieve elements and syncytial cells (Jones, 1981).

Although there are some similarities between syncytia induced by *Nacobbus* and those induced by *Heterodera* spp., significant differences also occur. Wall ingrowths (typical of transfer cells) occur in cells transformed by *Heterodera* and *Meloidogyne,* but not in syncytia induced by *Nacobbus* or *Rotylenchulus* (Jones and Payne, 1977). Enzymes were responsible for wall degradation (Jones and Payne, 1977) but questions remain about whether these enzymes are of plant or nematode origin, and what controls or regulates their production, targeting and switching and the extent to which other parts of the wall are affected. In cyst and root-knot nematodes, the enzymes probably responsible for the development of wall ingrowths are of plant origin (Goellner *et al.*, 2001).

The earliest report of histological changes in potato galls caused by *N. aberrans* (Lordello *et al.,* 1961) mentions a partial disorganization of the central cylinder, the cambium producing parenchyma instead of conducting elements, and the presence of isolated groups of vascular bundles (arising from adventitious cambium). Lordello *et al.* (1961) also found groups of hypertrophied parenchymatous cells (full of cytoplasm) lacking vacuoles but with large nuclei (secretory cells), a hypertrophied cortex with abundant starch, and a much more developed periderm. Studies of cryofractured samples of potato galls using SEM confirmed the secondary wall thickening of the syncytial cells noted using light microscopy studies. Silica deposition was reported from endodermal cells near or surrounding the syncytial cells (Jatala and Haddad, 1993d). Studies using sequential histopathology sections of an *in vitro* infection of suscepti-

ble potato roots, caused by juveniles and vermiform immature females, showed that the invasion process and symptomatology was, except for the vacuolation present in affected cells, similar to that found in other hosts. The vermiform immature females caused more extensive necrosis than the juveniles and were capable of inducing galling and deformation of the vascular system 2-3 days after inoculation (Jatala and Haddad, 1992).

Resistance of potato cultivars is generally associated with necrotic cells, which surround the nematodes and present physical barriers to constrain and reduce nematode invasion and feeding site formation. Finetti (1990) studied the responses of susceptible cultivars and clones of potato species to the nematode, and found that syncytia can be formed 5 days after inoculation of vermiform immature females on sprouted tuber pieces (3-day-old root tips) of the susceptible cv. Revolucion (*S. tuberosum*) kept in 2% water agar under growth chamber conditions, and that the syncytia formed in *S. sparsipilum* 7601217.7 were smaller, with cells having a more granular cytoplasm and bigger starch granules than in cv. Revolucion. No feeding site developed in the resistant hybrid B-25 (*S. tuberosum andigena*), despite root invasion. An early hypersensitive reaction occurred before the vermiform immature females reached the vascular cylinder. This reaction was attributed to a component of the nematode cuticle and/or secretions or excretions produced by the nematode, which could also be associated with induction of the syncytia. No lateral root formation occurred on the galls in agar culture in contrast to those produced in soil infestations (Finetti, 1990). Jatala and Haddad (1993a) found the frequency of root penetration to be the same for juveniles and vermiform immature females in both resistant and susceptible clones, but that resistant clones had cells with less dense cytoplasm and fewer starch granules. Severe necrosis occurred in resistant clones and no nematodes completed their life cycle despite some small syncytia being formed on roots inoculated with vermiform immature females. No hypertrophy or galling was noted. Histopathological studies have also been made in other crops and weeds such as spinach (Caballero and Muñoz, 1987), *Amaranthus hypochondriacus* (L.) Rob. (Santacruz *et al.*, 1986c), *Sisymbrium irio* L. (Ponce de León and Doucet, 1989), *Chenopodium murale* L. and *Malva parviflora* L. (Tovar *et al.*, 1990).

The *Nacobbus*-induced syncytium in *S. arvensis* (a common and important host weed in South America) is located in the distorted vascular cylinder. The cell walls of the syncytium are thickened with cellulose and, occasionally, more than one nucleus per cell occurs (Doucet *et al.*, 1994).

There are only a few reports that compare the histopathology of *N. aberrans* infection with that of other plant parasitic nematodes that induce feeding sites in their hosts (Schuster and Sullivan, 1960; Schuster *et al.*, 1965; Jones and Payne, 1977; Jones, 1981). Also, few reports deal with simultaneous infections of more than one species of nematode (Jarquin *et al.*, 1984; Inserra *et al.*, 1984c; López-Portillo *et al.*, 1984).

The histopathological responses of bean cultivars Nemasnap (resistant to *Meloidogyne incognita* (Kofoid & White, 1919) Chitwood, 1949) and Black Valentine (susceptible) to infection by *M. incognita* and *N. aberrans*, alone or combined, were studied by Jarquin *et al.* (1984). Both nematodes induced hypertrophy and hyperplasia in cv. Black Valentine. Nemasnap was immune to *N. aberrans* but *M. incognita* reproduced on this cultivar, causing hypertrophy but not hyperplasia or galling. Simultaneous infection by *M. incognita* race 1 and *N. aberrans* of tomato resulted in the formation of feeding sites for

both species, the sites being located in either the same or separate vascular bundles; it was also noted that *N. aberrans* affected the development of the giant cells induced by *M. incognita* (López-Portillo *et al.,* 1984).

Histological sections of a simultaneous infection by *N. aberrans* and *H. schachtii* on sugarbeet revealed that the *N. aberrans* syncytium was located in the central part of the root and contained scattered vascular elements, whereas the syncytium of *H. schachtii* lacked such elements and was displaced to the periphery of the root (Inserra *et al.*, 1984c).

Finally, it is important to mention that *N. aberrans* not only induces feeding sites in its hosts but also causes loss of anatomical and physical structures such as the druses (calcium oxalate crystals) in the syncytia formed in *O. tortispina*, structures that are present in the normal, adjacent cells (Schuster *et al.*, 1965).

Physiology: Rojas *et al.* (1993) studied the effect of *N. aberrans* on plant-water relationships (relative water content), photosynthesis rate, stomatal conductance, transpiration and leaf temperature. Infected plants showed a water deficit, which was related to reduction of stomatal conductance and increase of leaf temperature. Photosynthesis was also diminished in infected plants.

Nutrient alterations induced by *N. aberrans* in tomato include a decrease of the N, P, K and Ca contents of the roots and leaves of infected plants, and reductions of Mg, B, Cu, Fe, Mn and Zn in the leaves. Potassium deficiency caused by the nematode was considered the most significant nutritional imbalance in roots and leaves (Cristóbal-Alejo *et al.*, 2001a).

Amino acids (phenylalanine and proline), carbohydrates (galactose) and protein levels increased in a susceptible chilli pepper cultivar after inoculation with *N. aberrans* (Hernández, 1990).

HOSTS

Host range: Nacobbus aberrans has a wide host range, including some important commercial crops, in the Americas, such as potato (parts of South America and Mexico), sugarbeet (Nebraska and the Pacific Northwest of the USA), and tomato (Mexico and the subtropical lands of Argentina and Ecuador). Other hosts include crops such as beans, carrot, chard, egg plant, pepper, squash, tobacco, chilli pepper and Andean tuber crops ('mashua', 'oca', 'olluco') (Costilla and González de Ojeda, 1985; Zamudio *et al.*, 1990; Canto-Sáenz, 1992; Triviño *et al.*, 1998).

Lists of botanical families and host species (weeds included) were produced by Canto-Sáenz (1992) and Brodie *et al.* (1993). These combined lists include 84 cultivated and non-cultivated plant species within 18 families. *Nacobbus aberrans* has a wide range of weed hosts, which form an important infection reservoir within and between crops. In Peru, the most important weed hosts are callamato (*Callandria albis*—Euphorbiaceae) and 'chitincoya' (*Physalis* spp.—Solanaceae), which are common weeds in potato fields (Cornejo-Quiroz, 1977d), and *Chenopodium album* L. (Chenopodiaceae). In Bolivia, the most important weed host is *Spergula arvensis* (Caryophyllaceae) because of its very wide occurrence and the difficulty of eradicating it (Franco *et al.*, 1992). In Argentina, *N. aberrans* was recorded naturally infesting *Sisymbrium irio* (Compositae) by de Ponce de León and Doucet (1989) and *Ch. album* by Doucet (1989). In the USA, *Bassia* (= *Kochia*) *scoparia* (L.) Voss (Chenopodiaceae) is the most important wild host (Schuster and Thorne, 1956; Inserra *et al.*, 1984a). For Mexico, there are several reports of *N. aberrans* on various weed species (Rodríguez, 1974; Tinoco, 1981; Torres *et al.*, 1985, 1994; Cruz *et al.*, 1987; De la Jara *et al.*, 1990), the

most important being: 'verdolaga' (*Portulaca oleracea* L., Portulacaceae) and various species of *Chenopodium*. The commonest weed hosts of *N. aberrans* in all countries of the Americas are *Chenopodium* spp.

Although some Poaceae species are listed as hosts (Aguilar *et al.*, 1978; Franco *et al.*, 1997), it is usually the juveniles and vermiform adults that are found in the roots, not the obese females (Clark, 1967; Quimí, 1979; Cruz *et al.*, 1987; Manzanilla-López, 1997). An updated list of host species (crops and weeds) reported for *N. aberrans* is presented in Table 3.

RACES

Physiological and host races: Intraspecific variation in *N. aberrans* affects the planning of crop rotations and selection of sources of resistance for breeding. Variation between populations of *N. aberrans* has been assessed both morphologically and physiologically (by response to a set of differential plants) to clarify their taxonomic position. The approaches have included morphometrics (Doucet, 1989; Doucet and Di Rienzo, 1990, 1991; Manzanilla-López *et al.*, 1999), scanning electron microscopy (Baldwin and Cap, 1992; Jatala and Haddad, 1993c; Rowe and Manzanilla-López, 1997), electrophoresis (Ramallo, 1991; Doucet and Gardenal, 1992a, b; Jatala *et al.*, 1993; Olvera *et al.*, 1997; Manzanilla-López *et al.*, 1997; Doucet *et al.*, 2002), molecular studies (Ibrahim *et al.*, 1997; Manzanilla-López *et al.*, 1997), cytogenetics (Jatala and Boluarte, 1993; Martínez *et al.*, 1995) and host range tests (Boluarte and Jatala, 1992, 1993; Toledo *et al.*, 1993; Manzanilla-López *et al.*, 1996; Cid del Prado *et al.*, 1997c). However, as Baldwin and Cap (1992) have pointed out, "Validity of species and subspecific groups is not resolved, and there is frustration by those who propose to use identification to predict pathogenicity on particular hosts". It would be convenient if host differences could be matched to morphology to facilitate rapid recognition but, despite some reported morphometrical differences, a scheme of properly characterized races of *N. aberrans* does not yet exist.

For *N. aberrans*, terms such as races, physiological races (Jatala and Boluarte, 1993; Toledo *et al.*, 1993) and pathotypes (Costilla, 1992) have been used to address the infraspecific variation but gene-for-gene relationships have not been rigorously demonstrated.

Thorne and Schuster (1956) were the first to produce evidence of interspecific variation in *Nacobbus* by listing host and non-host crops for *N. batatiformis* (= *N. aberrans*). Later, this list was compared with one for *N. serendipiticus* (= *N. aberrans*) by Clark (1967), the differences resulting in a questioning of the host status of some species (e.g., Poaceae). Before Sher's revision of the genus in 1970, differences in host range were considered important in supporting the validity of species (Thorne and Schuster, 1956; Franklin, 1959; Lordello *et al.*, 1961; Clark, 1967). However, since the synonymization of *Nacobbus* species, the infraspecific variation of *N. aberrans* has been assessed mainly by host range and host response, the differences being used to define races or physiological races (Inserra, *et al.*, 1985; Boluarte and Jatala, 1993; Toledo *et al.*, 1993; Ortuño *et al.*, 1997). Most of the examples are from South America, a region where this species has been subjected to more intensive studies.

Differences in host range: Different cultivars of the same species may react differently to a single population of the nematode (Table 3). A recent study (Gray *et al.*, 1997) showed that cultivars of cruciferous plants, such as kale, mustard, radish and turnip, were immune to populations of *N. aberrans* from the Pacific Northwest

Table 3. Crop and weed species reported as hosts for *Nacobbus aberrans*.

Host species	Country	References
Abelmoschus (=*Hibiscus*) *esculentus* Moench	USA (Texas)	Johnson, 1971
Alcea rosea L.	USA (Texas)	Johnson, 1971
Amaranthus sp.	Andean region (Argentina, Bolivia, Chile and Peru); Mexico	Costilla and González de Ojeda,1985; Toledo *et al.*, 1993
A. hybridus L.	Andean region (Argentina, Bolivia, Chile and Peru); Mexico	De la Jara *et al.*, 1983; Montes-Belmont, 1988; Canto, 1992; Rivera, 1994
A. hypochondriacus L.	Andean region (Argentina, Bolivia, Chile and Peru); Mexico	Santa-Cruz and Marbán-Méndoza, 1986a, b; Costilla and González de Ojeda, 1985; Rivera, 1994
A. quitensis H.B. & K.	Andean region (Argentina, Bolivia, Chile and Peru)	Costilla and González de Ojeda, 1985
A. retroflexus L.	Andean region (Argentina, Bolivia, Chile and Peru)	Costilla and González de Ojeda, 1985
A. spinosus L.	Andean region (Argentina, Bolivia, Chile and Peru)	Costilla and González de Ojeda, 1985
Anoda cristata (L.) Schlecht.	Mexico	De la Jara *et al.*, 1990
Atriplex confertifolia (Torr. and Frém.) S. Wats	USA (Nebraska and Pacific Northwest)	Thorne and Schuster, 1956
Baccharis salicifolia (Ruiz and Pavón) Pers.	Andean region (Argentina, Bolivia, Chile and Peru)	Céspedes *et al.*, 1994
Bassia (=*Kochia*) *scoparia* (L.) Voss	Andean region (Argentina, Bolivia, Chile and Peru); USA (Nebraska, Wyoming and Pacific Northwest)	Thorne and Schuster, 1956; Inserra *et al.*,1984a; Costilla and González de Ojeda, 1985; Gray *et al.*, 1997
Beta vulgaris L.	Andean region (Argentina, Bolivia, Chile[2] and Peru); England[3]; Mexico; USA (Nebraska, Wyoming and Pacific Northwest)	Thorne and Schuster, 1956; Clark, 1967; Costilla and González de Ojeda, 1985; Toledo *et al.*, 1993; Manzanilla-López, 1997; Gray *et al.*, 1997
B. vulgaris L. ssp. *cicla* (L.) Koch	Andean region (Argentina, Bolivia, Chile and Peru); Mexico; USA (Nebraska and Pacific Northwest)	Thorne and Schuster, 1956; Johnson, 1971; Costilla and González de Ojeda, 1985; Cid del Prado, 1993; Toledo *et al.*, 1993.
B. vulgaris macrorhiza L.	USA (Nebraska and Pacific Northwest)	Thorne and Schuster, 1956
Brassica campestris L.	Argentina	Costilla, 1985a; Canto, 1992
B. juncea (L.) Czern. & Cass. (=*B. japonica*)	USA (Texas)	Johnson, 1971
B. napus (L.) Rchb. Napobrassica Group	Andean region (Argentina, Bolivia, Chile and Peru); USA	Thorne and Schuster, 1956; Johnson, 1971; Costilla and González de Ojeda, 1985
B. nigra (L.) Koch	USA (Texas; Nebraska and Pacific Northwest)	Thorne and Schuster, 1956; Johnson, 1971
B. oleracea L. Botrytis Group	USA (Texas; Nebraska and Pacific Northwest)	Thorne and Schuster, 1956; Johnson, 1971
B. oleracea L. Capitata Group	USA (Texas; Nebraska and Pacific Northwest)	Thorne and Schuster, 1956; Johnson, 1971
B. oleracea L. Gemmifera Group	USA (Texas; Nebraska and Pacific Northwest)	Thorne and Schuster, 1956; Johnson, 1971
B. oleracea L. Gongyloides Group	USA (Nebraska and Pacific Northwest)	Thorne and Schuster, 1956

Table 3. (Continued) Crop and weed species reported as hosts for *Nacobbus aberrans*.

Host species	Country	References
B. oleracea viridis L.	USA (Nebraska and Pacific Northwest)	Thorne and Schuster, 1956
B. rapa L.	Andean region (Argentina, Bolivia, Chile and Peru); USA (Texas; Nebraska and Pacific Northwest)	Thorne and Schuster, 1956; Johnson, 1971; Costilla and González de Ojeda, 1985
B. rapa L. Pekinensis Group	USA (Texas; Nebraska and Pacific Northwest)	Thorne and Schuster, 1956; Johnson, 1971
Calandria albis Kunth.	Andean region (Argentina, Bolivia, Chile and Peru)	Cornejo Quiroz, 1977b; Jatala, 1991
Capsella bursa-pastoris (L.) Medic.	Andean region (Argentina, Bolivia, Chile and Peru)	Costilla and González de Ojeda, 1985
Capsicum annuum L.	Argentina; Mexico	Brunner, 1967; Rodríguez, 1974; Costilla and González de Ojeda, 1985; Montes-Belmont, 1988; Toledo *et al.*, 1993
C. annuum L. var. *glabriusculum* (Dunal) Heiser & Pickersgill (=*C. baccatum* L.)	Mexico	Castillo and Marbán-Méndoza, 1984
C. frutescens L.	USA (Texas)	Johnson, 1971
C. pendulum Willd.	Mexico	Brunner, 1967
C. pubescens Ruiz & Pav.	Mexico	Brunner, 1967
Cestrum roseum H.B. & K.	Mexico	Cruz *et al.*, 1987; De la Jara *et al.*, 1990
Chenopodium album L.	Andean region (Argentina, Bolivia, Chile and Peru); England[3]; USA (Nebraska, Wyoming and Pacific Northwest)	Thorne and Schuster, 1956; Clark, 1967; Costilla and González de Ojeda, 1985; Doucet, 1989; Jatala, 1991; Gray *et al.*, 1997
Chenopodium ambrosioides L.	Mexico	De la Jara *et al.*, 1990
Ch. murale L.	Mexico	De la Jara *et al.*, 1990
Ch. nuttalliae Saff.	Mexico	De la Jara *et al.*, 1990
Ch. quinoa Willd.	Andean region (Argentina, Bolivia, Chile and Peru)	Cornejo Quiroz, 1977b; Costilla and González de Ojeda, 1985
Cucumis sativus L.	USA (Texas)	Johnson, 1971
Cucurbita maxima Duchesne	Andean region (Argentina, Bolivia, Chile and Peru); USA (Texas)	Johnson, 1971; Costilla and González de Ojeda, 1985
C. pepo L.	Mexico, USA	Thorne and Schuster, 1956; Johnson, 1971; Zamudio *et al.*, 1990; Toledo *et al.*, 1993; Cid del Prado *et al.*, 1995b
Cyphomandra betacea Sendt.	Ecuador	Quimí, 1979
Datura ferox L.	Andean region (Argentina, Bolivia, Chile and Peru)	Costilla and González de Ojeda, 1985
D. stramonium L.	Mexico	De la Jara *et al.*, 1990
Daucus carota L.	Andean region (Argentina, Bolivia, Chile and Peru); Mexico; USA	Thorne and Schuster, 1956; Costilla and González de Ojeda, 1985; Cid del Prado *et al.*, 1995b
Escobaria (=*Mammillaria*) *vivipara* (Nutt.) F. Buxb	USA (Nebraska and Pacific Northwest)	Thorne and Schuster, 1956
Eupatorium azangaröense Sch. Bip.	Andean region (Argentina, Bolivia, Chile and Peru)	Céspedes *et al.*, 1994
Fagopyrum esculentum Moench.	Mexico	Aguilar *et al.*, 1978

Table 3. (Continued) Crop and weed species reported as hosts for *Nacobbus aberrans*.

Host species	Country	References
Gaillardia pulchella Fouger	USA (Nebraska and Pacific Northwest)	Thorne and Schuster, 1956
Ipomoea batatas Lam.	Andean region (Argentina, Bolivia, Chile and Peru)	Costilla and González de Ojeda, 1985
Lactuca sativa L.	England[3]; USA (Nebraska and Pacific Northwest)	Thorne and Schuster, 1956; Clark, 1967
Lycopersicon esculentum Mill.	Mexico; England[3]; Netherlands[3]; Andean region (Argentina, Bolivia, Ecuador, Chile and Peru); USA (Texas; Nebraska and Pacific Northwest)	Thorne and Schuster, 1956; Clark, 1967; De Bruijn and Stemerding, 1968; Johnson, 1971; Quimí, 1979; Costilla and González de Ojeda, 1985; Toledo *et al.*, 1993
L. peruvianum (L.) Mill.	England[3]; USA (Nebraska and Pacific Northwest)	Thorne and Schuster, 1956; Clark, 1967
Malva parviflora L.	Mexico	Cruz *et al.*, 1987; De la Jara *et al.*, 1990
Mamillaria vivipara (Nutt.) Haw.	USA (Nebraska and Pacific Northwest)	Thorne and Schuster, 1956; Canto, 1992
Matthiola sp.	USA (Nebraska and Pacific Northwest)	Thorne and Schuster, 1956
Mirabilis jalapa L.	Mexico	De la Jara *et al.*, 1990
Nicotiana tabacum L.	Andean region (Argentina, Bolivia, Chile and Peru); USA (Texas)	Johnson, 1971; Costilla and González de Ojeda, 1985
Opuntia fragilis Haw.	USA (Nebraska and Pacific Northwest)	Thorne and Schuster, 1956
O. macrorhiza Engelm. (= *tortispina* Nutt.)	USA (Nebraska and Pacific Northwest)	Thorne and Schuster, 1956
Origanum vulgare L.	Chile	Gallo, 1974
Oxalis tuberosa Molina	Andean region (Argentina, Bolivia, Chile and Peru)	Costilla and González de Ojeda, 1985; Jatala, 1991; Céspedes *et al.*, 1994
Phaseolus vulgaris L.	Mexico	Toledo *et al.*, 1993
Physalis spp.	Andean region (Argentina, Bolivia, Chile and Peru), Mexico	Cornejo Quiroz, 1977b; Zamudio *et al.*, 1990; De la Jara *et al.*, 1990; Jatala, 1991
Pisum sativum L.	USA (Nebraska and Pacific Northwest); Mexico	Thorne and Schuster, 1956; Zamudio *et al.*, 1990
Plantago lanceolata L.	Andean region (Argentina, Bolivia, Chile and Peru)	Costilla and González de Ojeda, 1985
Portulaca oleracea L.	Argentina; Mexico; U.S.A. (Wyoming)	Costilla, 1985a; Montes-Belmont, 1988; De la Jara *et al.*, 1990; Toledo *et al.*, 1993; Gray *et al.*, 1997
Raphanus sativus L.	Andean region (Argentina, Bolivia, Chile and Peru); Mexico; USA (Texas, Nebraska and Pacific Northwest)	Thorne and Schuster, 1956; Johnson, 1971; Costilla and González de Ojeda, 1985; Zamudio *et al.*, 1990
Salsola kali L. var *tenuifolia* Tausch	USA (Nebraska, Wyoming and Pacific Northwest); Mexico	Thorne and Schuster, 1956; De la Jara *et al.*, 1990; Gray *et al.*, 1997
Simsia amplexicaulis Pers.	Mexico	De la Jara *et al.*, 1990
Sisymbrium irio L.	Argentina	Ponce de León and Doucet, 1989
Solanum sp.	Andean region (Argentina, Bolivia, Chile, Ecuador and Peru)	Cornejo Quiroz, 1977b; Costilla and González de Ojeda, 1985; Jatala, 1991; Ortuño *et al.*, 1997
S. andigena Juz. and Buk.	Bolivia	Lordello *et al.*, 1961
S. chacoense Bitter	Andean region (Argentina, Bolivia, Chile and Peru)	Costilla and González de Ojeda, 1985

Table 3. (Continued) Crop and weed species reported as hosts for *Nacobbus aberrans*.

Host species	Country	References
S. melongena L.	Andean region (Argentina, Bolivia, Chile, Ecuador and Peru); England[3]; Mexico; USA (Nebraska and Pacific Northwest)	Thorne and Schuster, 1956; Clark, 1967; Quimí, 1979; Costilla and González de Ojeda, 1985; Manzanilla-López, 1997
S. nigrum L.	England[3]; Mexico	Clark, 1967; De la Jara *et al.*, 1990
S. rostratum Dun.	Mexico	De la Jara *et al.*, 1990
S. triquetrum Cav.	USA (Nebraska and Pacific Northwest)	Thorne and Schuster, 1956
S. tuberosum L.	Mexico, Andean region (Argentina[1], Bolivia, Chile and Peru); former Soviet Union[3]	Kirjanova and Lobanova, 1975; Costilla and González de Ojeda, 1985; Jatala, 1991; Toledo *et al.*, 1993; Rivera, 1994
S. tuberosum ssp. *andigena* Juz. & Buk.	Andean region (Argentina[1], Bolivia, Chile and Peru)	Jatala, 1991
Spergula arvensis L.	Andean region (Argentina, Bolivia, Chile and Peru)	Jatala, 1991
Spinacia oleracea L.	USA (Texas; Nebraska and Pacific Northwest); Mexico	Thorne and Schuster, 1956; Johnson, 1971; Rodríguez, 1974
Stellaria media (L.) Vill.	England[3]	Clark, 1967
Tagetes mandonii Sch. Bip.	Andean region (Argentina, Bolivia, Chile and Peru)	Jatala, 1991
Taraxacum officinale L.	Andean region (Argentina, Bolivia, Chile and Peru)	Céspedes *et al.*, 1994
Tragopogon porrifolius L.	USA (Nebraska and Pacific Northwest)	Thorne and Schuster, 1956
Tribulus terrestris L.	USA (Nebraska and Pacific Northwest)	Thorne and Schuster, 1956; Gray *et al.*, 1997
Trifolium sp.	Mexico	De la Jara *et al.*, 1990
Tropaeolum tuberosum Ruíz. et Pav.	Andean region (Argentina, Bolivia, Chile and Peru)	Jatala, 1991
Ullucus tuberosus Caldas	Andean region (Argentina, Bolivia, Chile and Peru)	Cornejo Quiroz, 1977b; Jatala, 1991; Canto, 1992

[1]Some Argentinian populations do not attack potato in subtropical areas.
[2]Although Chile is included along with the Andean countries where *N. aberrans* occurs (CABI and EPPO, 1997), only a few records were found for this country.
[3]Eradicated since recorded.

(USA), although other cultivars of the same plant species had been reported as susceptible by Thorne and Schuster (1956). *Nacobbus aberrans* populations from different geographical areas may share host species yet attack different cultivars within the species (Table 3).

Similar behavior was recorded for South American populations of *N. aberrans* by Gómez-Tovar (1973), who found differences between populations from Peru and Bolivia in host range tests. Barley was not invaded by J2s, in contradiction to Clark (1967), but olluco (*Ullucus tuberosus* Caldas), mashua (*Tropaeolum tuberosum* Ruíz & Pav.) and oca (*Oxalis tuberosa* Molina) were more efficient hosts for Bolivian populations of *N. aberrans* from La Paz and Cochabamba than those from Puno (Peru).

Populations from the same country also may differ in host and cultivar preferences. Gómez-Tovar (1973), Bravo-Baldeón (1977)

and Cornejo-Quiroz (1977d) detected differences between populations from Puno and Mantaro (Peru). The former was more damaging on potato and parasitized quinoa (*Chenopodium quinoa* Willd.) but not the weeds *Erodium cicutarium* (L.) L'Her. or *Brassica campestris* L., whereas the Mantaro population was more damaging on olluco with *E. cicutarium* and *B. campestris* being hosts and quinoa a non-host. When 30 cultivars of quinoa were tested by Blanco (1992), some were highly resistant (Chechueca and UNTA 136) while others were susceptible (Sajama, Blanco de Juli, UNTA 133, etc.).

Populations with similar host ranges (sugarbeet but not potato) to those reported for Nebraska and the Pacific Northwest populations (Table 3) have been reported from the subtropical areas of Argentina (Costilla and González de Ojeda, 1985). However, these populations also damage chilli pepper, a non-host for the Pacific Northwest populations (Inserra *et al.,* 1985). Detailed information on the host range of *N. aberrans* populations from Andean regions is available only for Argentina (Table 3). Potato is the only cultivated host for populations from Tafi del Valle and Las Estancias, while populations from tomato in Lules (Tucumán) and Santa María (Cajamarca) parasitized chilli pepper but not potato (Costilla, 1990). Populations of *N. aberrans* from Ecuador were found on potato and tomato by Jatala (1978) but other Ecuadorian populations may not attack potato and thus behave similarly to some Mexican and Argentinian populations. Quimí (1979) reported that no galls were produced 10 weeks after inoculation on potato (cv. Pentland Crown), although juvenile stages were recovered from roots.

Glasshouse tests (Manzanilla-López, 1997) showed that populations from Bolivia and Peru reproduced on potato and sugarbeet but not on chilli pepper cv. Jalapeño, while two populations from Argentina reproduced on chilli pepper but not on potato cv. Désirée. The fact that the Argentinian populations reproduced on chilli pepper supports their possible relatedness to Mexican populations.

Mexican populations from nearby localities within the same geographical region can have different responses to host species and host cultivars, again supporting the existence of races. Brunner (1967) tested 90 pepper species and cultivars against a population from Chapingo (State of Mexico). All *C. annuum* cultivars were susceptible and only *Capsicum baccatum* L. showed any resistance. In contrast, Sosa-Moss and González (1973) obtained different cultivar responses in terms of height, dry and fresh weight and galling index with a different population from the same locality. Similar observations were made by Hernández (1992) and some populations failed to reproduce on chilli pepper (Toledo, 1989, Zamudio *et al.*, 1990).

Bean (*Phaseolus vulgaris* L.) is an important host for *N. aberrans* in Mexico and differences in host and cultivar response also occur. Silva-Jaramillo (1989 found significant differences in foliage and root weight between ten inoculated cultivars, but not between the uninoculated controls, with a population from Tecamachalco (State of Puebla). The greatest galling was on cvs Canario 107 and 1087, the least on cvs Black Puebla and Puebla 458. Nematode populations from Cuautla (State of Morelos) and Actopan (State of Hidalgo) did not reproduce on cv. Negro Querétaro Toledo (1989), but galling of cvs Bayo and Negro Jamapa was reported (Hernández and Manzanilla-López, 1992) for a population from a neighboring locality (Ixmiquilpan, State of Hidalgo).

Tomato is the most important commercial crop host for *N. aberrans* in Mexico and

probably the most important vehicle for its dissemination from infested nurseries to different parts of the country. *Nacobbus* has been reported almost everywhere that tomatoes are grown but, according to Toledo (1989), a population from Melchor Ocampo does not reproduce on this crop. However, other populations also claimed as not reproducing on tomato, e.g., from Saltillo, State of Coahuila (Camargo, pers. comm.), have reproduced on tomato under glasshouse conditions (Manzanilla-López, unpublished).

Potato has not been recorded as a natural or important host for *N. aberrans* in Mexico, although *N. aberrans* males have occasionally been found in important potato cropping areas such as Huamantla (State of Tlaxcala; Cid del Prado, pers. obs.). Gall production on potato varies according to cultivar and nematode population (Toledo, 1989; Cid del Prado, 1993; Cid del Prado *et al.* 1996b, 1997c). Thus, the host range differences reported for Mexican populations are often contradictory and the scheme proposed by Toledo *et al.* (1993) for Mexican races of *N. aberrans* needs to be confirmed by additional experimentation.

Race schemes: Race classification is considered necessary, particularly in places where this species is a serious pest, so the search for differential hosts and non-hosts has been continuous (Inserra *et al.*, 1985; Costilla, 1985a, 1990, 1992; Boluarte and Jatala, 1992, 1993; Cid del Prado, 1993; Toledo *et al.*, 1993; Canto-Sáenz *et al.*, 1996; Costilla, 1996; Cid del Prado *et al.*, 1996b, 1997c; Ortuño *et al.*, 1997). Although the results are not conclusive, these schemes have proved useful in separating *N. aberrans* populations within confined geographical areas, but are not adequate for differentiating populations from a wider geographical region. The basic host race scheme proposed for *N. aberrans* by Inserra *et al.* (1985) has been the most generally accepted. This scheme included three races: sugarbeet, potato and chilli pepper.

It may now be appropriate to revise this classification as new information has appeared since it was proposed. Some comments can be made on the allocation to races of populations of *N. aberrans* from the Americas. The first (sugarbeet) and second (potato) races include sugarbeet as an important host and it appears to be the commonest host for North and South American populations (Table 3). Exceptions, however, do occur: the Texas (USA) population does not attack sugarbeet (Johnson, 1971) and it is not known whether it attacks potato (Table 3); the population from Melchor Ocampo (Mexico) is claimed not to reproduce on either sugarbeet or potato (Toledo *et al.*, 1993). The host range data available for the Mexican populations (Table 3) support their inclusion in the chilli pepper race as proposed by Inserra *et al.* (1985), even though some Mexican populations reproduce on sugarbeet as well as potato.

A condition intermediate between the sugarbeet and chilli pepper races apparently occurs in some populations from Bolivia and Peru, the nematodes reproducing on sugarbeet and potato but not on chilli pepper (Manzanilla-López, 1997). Although not pointed out in the race scheme of Inserra *et al.* (1985), it seems that at least some of the potato race populations fail to reproduce on chilli pepper.

Some Mexican populations also reproduce on beans, but the host response varies. Hernández (2001) found that infection of a highly susceptible cultivar occurred at a minimum inoculum of 100 juveniles/plant but these results have been difficult to reproduce. More studies are needed before a "bean race" can definitely be established but, in the meantime, it is convenient to place populations infecting

beans in a separate group, and to refer to what have previously been called races as groups until better ways of describing races are defined.

Thus, for practical purposes and on the basis of the most valuable crops damaged by these various *N. aberrans* populations, it may be appropriate to separate *N. aberrans* populations into three slightly different groups:

1. *The sugarbeet group*, to include populations infecting sugarbeet and tomato but not potato. Populations of this type are found in the lowlands of Argentina, Nebraska and the Pacific Northwest (USA), and probably Ecuador.

2. *The potato group*, which damages potato and also infects sugarbeet and tomato but not chilli pepper. Populations of this type are present in the highland Andean regions of Argentina, Bolivia, Chile, Peru and Mexico.

3. *The bean group*, to include populations that attack beans and chilli pepper but are not able to infect potato or sugarbeet. Such populations are reported in Mexico.

Many of the physiological races so far recorded can be assigned to one or other of these three groups. For example, the chilli pepper race, which infects pepper and sugarbeet in the lowlands of Argentina but not potato, belongs to group 1 (sugarbeet). The sugarbeet race, which infects sugarbeet in Nebraska and the Pacific Northwest, but not potato or chilli pepper, also belongs to the sugarbeet group. The Mexican race designated as Na-1 (Toledo *et al.,* 1993), which does not infect bean but does infect chilli pepper, potato and sugarbeet, belongs to the potato group. The Mexican race Na-2 (Toledo *et al.,* 1993), which infects bean and also potato, sugarbeet and chilli pepper, also belongs to the potato group, whereas race Na-3, which infects bean but not potato or sugarbeet, belongs to the bean group. More host range information is required before the three races proposed (on the basis of their parasitic habit on potato) by Ortuño *et al.* (1997) can be allocated to a group or groups.

In order to validate, alter or extend this or any other race scheme, it is necessary to standardize the conditions for the host range test, such as source of inoculum (e.g., infested soil, galls), temperature and duration of the bioassay (Instituto Boliviano de Tecnología Agropecuaria, 1994). The cultivars of potato, chilli pepper, kochia, sugarbeet, bean or other hosts (e.g., crucifers) to be used must also be specified and, if possible, several nematode populations covering most of the known geographical distribution of the species in each country should be used. The use of molecular tools should be strongly encouraged as they have the potential for quick and reliable diagnosis of local races. Testing the potential of *N. aberrans* populations to infect potato is very important, especially for regulatory purposes, because populations that infect potato can spread rapidly on and in the tubers.

Populations change over time so, as long as *N. aberrans* continues to spread to different geographical areas and adapts to local host crops, it is likely that new races will be recorded. Thus, race groups or schemes are not permanent, but merely temporary, practical frameworks of local value in planning appropriate crop rotations and management strategies. Nevertheless, it is essential that stringent conditions for defining races of *N. aberrans* be agreed upon by researchers. If this is not done there is a risk that schemes of ever greater complexity will be proposed, but which still fail to solve the basic problems.

DAMAGE AND EPIDEMIOLOGY

Yield losses: In Bolivia and Peru, *N. aberrans* can cause yield losses of more than 60% on potato (Otazú *et al.*, 1985; Franco *et al.*, 1992, 1993; Ortuño *et al.*, 1994; Canto-Sáenz *et al.*, 1996) and, in the USA, *N. aberrans* is considered to be among the six most important species of plant parasitic nematodes affecting sugarbeet, capable of causing 27 to 75% reduction in plant weight under glasshouse conditions and 10-20% in the field (Inserra, 1983; Inserra *et al.*, 1984a, c, 1996). In Mexico, Silva-Jaramillo (1989) estimated that *N. aberrans* caused yield losses on bean in the Valsequillo Valley (Puebla) of 18 to 36%. It is also a serious problem in tomato production, yield losses being estimated at up to 50 or 60% (Zamudio, 1983, 1987; Cristóbal *et al.*, 2000), but statistics and estimates of losses in tomato, chilli pepper and bean are lacking for most regions of Mexico. However, an initial inoculum of 30 ± 5 nematodes per 200 g of soil can reduce amaranth yield by 10-14% (Santa-Cruz and Marbán-Méndoza, 1986b).

To the direct yield losses must be added indirect costs such as the establishment of control measures, the degradation of land quality, cost of quarantine procedures and the loss of nematode-free land for seed production (Main *et al.*, 1999). Specific figures are needed to establish a basis for economic and effective control as appropriate decision making at all levels depends on quantitative estimates of loss (Smith *et al.*, 1984).

Understanding the relationship between damage intensity and crop losses allows us to predict yield loss from appropriate pest indices (Smith *et al.*, 1984). For *N. aberrans*, a number of studies of incidence and severity have been made (Otazú *et al.*, 1985; Ramos *et al.*, 1993, 1998; Cristóbal-Alejo, 2001), yield losses being estimated mainly by using nematicides to remove nematode-related constraints on yield (Equihua, 1977; Equihua and Téliz, 1977; Zamudio, 1983, 1987; Otazú *et al.*, 1985; Silva-Jaramillo, 1989; Cid del Prado *et al.*, 1997b; Ramos *et al.*, 1998; Cristóbal-Alejo, 2001). A combination of work on population dynamics (Franco *et al.*, 1992; Cid del Prado *et al.*, 1996b, 1997a; Manzanilla-López *et al.*, 1998a) with epidemiological studies on the progress and development of disease (Cristóbal-Alejo, 2001; Otazú *et al.*, 1985) has begun to provide the basics for models to predict disease levels and to select the most appropriate management strategies.

A major objective of epidemiology is to study plant diseases and their population dynamics in natural environments (Aust and Kranz, 1988). Assessment of yield losses would be impossible without a means to quantify the dynamics of epidemics (Teng and Johnson, 1988). Epidemiological field studies can be holistic (studying the effects of as many variables as possible) or meristic (studying only a few variables). Some of the early studies of the ecology and control of *N. aberrans* explored as many aspects as possible in relation to host, parasite and environment (Clark, 1967; Prasad and Webster, 1967; Costilla, 1985a; Inserra *et al.*, 1985). Others focused on more specific factors, such as those affecting incidence, prevalence, dissemination, and the effects of weeds and cultural practices (Otazú *et al.*, 1985; Ramos *et al.*, 1998).

Incidence: Disease 'incidence' describes the proportion of infected individuals within a host population, while disease 'severity' describes the proportion of host tissue showing symptoms (Teng and Johnson, 1988). Evaluation of disease according to its severity or incidence depends largely on the type of disease and the objective of the evaluation. Surveys of

pest incidence have been carried out very widely, but usually fail to estimate losses accurately because they depend heavily on the skill and experience of the surveyor (Chiarappa, 1981).

The distribution of *N. aberrans* in terms of incidence (presence or absence) and severity of damage (root galling and yield losses) was studied by Siles *et al.* (1996). The frequency of infestation and severity of root galling of potato plants was related to cropping system. Frequent potato cropping led to high incidence, which was patchy or homogeneous and accompanied by severe plant damage, and the presence of common weed host plants or volunteer potato plants led to homogeneous incidence with much plant damage. Yield and tuber infection were both strongly correlated with root galling at flowering (Siles *et al.*, 1996).

Dissemination: The importance of clean seed tubers in the dissemination of *N. aberrans* was evaluated by Otazú *et al.* (1985). Seed tubers (cv. Imilla Blanca) from moderately infested or nematode-free soils were sown either under field conditions in uninfested and infested soils or in the glasshouse in pots containing infested and sterilized soil. Clean tubers sown in infested soil in the field resulted in a similar amount of galling (380 galls/plant) as when infected tubers were sown (375 galls/plant) in the same field. Clean tubers grown in infested soil under greenhouse conditions and infected tubers sown in infested soil produced plants with similar numbers of galls. Infected seed tubers are an important means for dissemination of *N. aberrans* but they are of no significance for gall development or yield in already infested soil.

Weeds: The effects of the weeds *S. arvensis* and *Calandrinia* sp. in maintaining soil infestations in different cropping systems were evaluated by inspecting 5% of the area of fields sown with potato, 'tarwi' (*Lupinus mutabilis* Sweet) and oat (*Avena sativa* L.), and recording weed populations/m^2. Fields sown according to local rotation (Otazú *et al.*, 1985) with oats, tarwi, barley-*Vicia*, oat-*Vicia*, potato, or fallow were also assessed for the presence of both the nematode and weeds. Rotations were not effective as a control measure unless weeds were under control. *Spergula arvensis* was considered to be the principal alternative weed host for *N. aberrans*.

The progress of disease: When disease increases in a population of host plants, an epidemic is in progress and, theoretically, its course is subject to epidemiological analysis (Smith *et al.*, 1984). Knowledge of the sequence and timing of events can be employed to determine the critical periods during the course of an epidemic. The simplest such function is a linear regression equation based on the index at one point in time, but more complicated models can be used.

Otazú *et al.* (1985) determined the progress curve of *N. aberrans* infection on potato during the growing season. The number of galls per plant increased considerably when tuber production started, a phenological stage that is critical in determining crop yield. The epidemiology of the relationship between *N. aberrans* and tomato cv. Río Grande was studied by Cristóbal-Alejo (2001) and Cristóbal-Alejo *et al.* (2000) under three different management strategies: integrated control (IC), which included fertilization and application of the nematicide ethoprop and chicken manure; technical control (TC) based on local practices; and an absolute control (AC), with no application of chicken manure or nematicide. The numbers of galls were used as estimators of disease severity. Galls/plant and females/g of root were used to define the area under a disease progress curve (DPC), and the rate of

apparent infection was determined by the b^{-1} parameter of the Weibull model (Pennypacker *et al.*, 1980; Thal *et al.*, 1984). Population densities fluctuated in soil and roots, with at least three generations of the nematode occurring through the crop cycle. Numbers of galls increased 70 and 90 days after transplanting, corresponding to the late stages of the first and second generations of the nematode. The *N. aberrans* epidemic was adequately described by the Weibull model during the first 50 days of crop development ($r^2 \leq 0.94$), having rates (b^{-1}) in the ranges 0.025-0.050, 0.077-0.096, and 0.080-0.084 for the IC, TC, and AC treatments, respectively. IC had the fewest galls (15 252 galls/plant), while TC and AC had 28 308 and 32 628 galls/plant, respectively. The IC produced 40.9 and 48.6% increments in plant height, and 36.9 and 53.1% increments in dry weight of foliage over the TC and AC treatments, respectively. The commercial yield of the IC bettered that of TC and AC by 33.9% and 82.0%, respectively, and the yield losses due to *N. aberrans* were estimated at 11.7, 29.4 and 83.1% in the IC, TC, and AC, respectively.

POTATO—A CASE STUDY (IMPACT OF *N. ABERRANS* ON POTATO PRODUCTION IN BOLIVIA)

Of the traditional Andean crops (*Solanum* spp., *U. tuberosus*, *O. tuberosa*, *T. tuberosum*, *L. mutabilis*, *Ch. quinoa*, etc.), potato is the most important because of its great diversity and large consumption per capita. Potatoes are grown on small farms in different ecological niches between 1500 and 4500 meters above sea level (masl). However, as a result of biotic and abiotic constraints, the national average yield in Bolivia of *c.* 5 t/ha is one of the lowest in the world (Franco *et al.*, 1992; Zeballos, 1997). Among the biotic problems, plant parasitic nematodes such as *Globodera* spp. and *N. aberrans* have strong negative effects on yields (Franco, 1994). These effects depend on the population densities of the nematodes, soil and environmental conditions, and the plant's ability to withstand damage.

Nacobbus aberrans affects potato yields because no large potato tubers are produced as nematode infestation levels increase (Caero, 1984; Otazú *et al.*, 1985; Franco, 1994). Once this nematode is introduced into a previously uninfested field/area through the use of infected potato seed tubers, it is almost impossible to eliminate because of its wide host range (see section on host range).

During the 1990s, a priority in Bolivia was to develop a management strategy to reduce the risk of dissemination and the yield losses caused by high population densities of *N. aberrans*. The production of potato seed was threatened by the scarcity of land free of the nematode (Franco *et al.*, 1992; Ramos *et al.*, 1998). This was the first extensive long-term study carried out in South America using standardized methodologies for sampling and extraction. During this study, the incidence, distribution, severity of damage and yield losses caused by *Globodera* spp. and *N. aberrans* were recorded, and the economic impact at the departmental level in Bolivia was calculated. The results of this program are summarized in the following sections.

Incidence: Several studies had shown that *N. aberrans* was widely distributed in all departments in the Andean region of Bolivia, causing important yield losses (Franco *et al.*, 1998/1999). Information on the incidence and severity of damage to potatoes by *N. aberrans* in six departments of Bolivia (Chuquisaca, Cochabamba, La Paz, Oruro, Potosí and Tarija) was summarized by Franco *et al.* (1998/1999). The numbers of field samples used to assess *N. aberrans* incidence and severity per com-

munity were standardized. The percentage incidence of *N. aberrans* (number of affected plants/total number of sampled plants × 100) was estimated from the total number of fields sampled (Fernández, 1991; Flores, 1996; Lanza, 1996). *Nacobbus aberrans* was found either alone or with *Globodera* spp. in most of the potato fields sampled in Bolivia, its incidence being highest in Oruro (100%), followed by Potosí (85%), Tarija (77%), Cochabamba (76%), and Chuquisaca (71%). The two nematodes showed clear patterns of distribution according to altitude. Although *N. aberrans* and *Globodera* spp. were mostly found between 3001 and 4000 m a.s.l (35.4 and 31.4% of all infestations, respectively), *N. aberrans* was present in a higher proportion of fields than *Globodera* spp. The number of fields free of nematodes increased below 3000 m a.s.l, a tendency especially obvious below 2000 m a.s.l.

Severity: Nematode damage, i.e. any deleterious effect on the host causing loss of value (Bos and Parlevliet, 1995), has not been assessed in a standard way by different authors. Some authors have estimated the severity of *Nacobbus* damage by the number of galls per root system of potato plants at the flowering stage (Rivera, 1994; Ali, 1995; Siles *et al.*, 1996) or in a bioassay (Lanza, 1996; Alconz, 1997; Tola, 1997). Others have considered the numbers of nematodes in 100 g of soil (Lanza, 1996; Alconz, 1997) and estimated potato yield losses in relation to nematode population density under both indoor and outdoor conditions (Montalvo *et al.*, 1992; Villca, 1993; Rivera, 1994; Siles *et al.*, 1996). Despite these variations, a standard scale relating soil population densities and the numbers of root galls was developed and applied to all data on the incidence and severity of damage caused by *N. aberrans*, in order to estimate expected potato production losses (Table 4). The severity of disease caused by *N. aberrans* per community was estimated as follows: % severity = n1*1 + … n4*4 *100/A*4, where: n1 = number of plots with grade 1 of severity … n4 = plots with grade 4 of severity, A = total number of plots (Rivera, 1994; Ramos *et al.*, 1998). The severity of infestation in potato fields in different departments was mainly incipient (49.4%) or medium (22.5%).

Table 4. An index scale for assessing *Nacobbus aberrans* infection levels (galls/root system).

Degree	Number of galls	Soil infestation
0	0	Free
1	1-10	Incipient
2	11-30	Medium
3	31-75	High
4	>75	Very high

Yield losses: Crop losses due to *N. aberrans* were estimated from the scale relating percentage yield loss to soil population level (Table 5) and the average potato yields per department (Table 6). Once the information on yield losses was collated, this was related to potato market prices in the *N. aberrans* affected areas in order to estimate departmental and national economic gross losses due to the presence of *N. aberrans* (Table 6). Losses were initially estimated on the basis of yield reductions

Table 5. Yield losses of potatoes grown in soil infested with different densities of *Nacobbus aberrans* in Bolivia (Ramos *et al.*, 1998).

Severity of infection	Number of individuals per 100 g of soil	Yield loss (%)
Free	0	0
Incipient	1-15	33
Medium	16-30	68
High	31-70	77
Very high	>70	88

Table 6. Area of potatoes grown, average yield and estimated losses due to *Nacobbus aberrans* in the six most important departments for potato production in Bolivia (Ramos *et al.*, 1998).

Department	Area (ha)	Mean yield (kg/ha)	Annual loss ($US)
La Paz	37,800	5076	9,095,754
Potosí	30,750	5051	11,939,069
Cochabamba	25,850	6759	15,390,372
Chuquisaca	19,780	5752	7,406,340
Oruro	9,650	3787	3,952,798
Tarija	7,500	6942	3,990,786
Total	131,330		51,775,119

found in indoor and outdoor experiments at different soil population densities. These losses were then extrapolated to the total infested area in each department. Application of ware potato selling prices to the information on yield losses for each department showed that monetary losses varied from 733 $US/ha (medium infestation level) to 1739 $US/ha (very high infestation level). The area with only incipient infestations is about twice that with medium infestations, but the overall economic losses are similar for the two categories (37.9 and 36.7%, respectively). The gross losses in $US (Table 6) are greatest in the departments of Cochabamba and Potosí and smallest in Tarija and Oruro. The total annual losses caused by *N. aberrans* to the national potato crop in Bolivia (taking into account the departments of minor importance—Santa Cruz, Beni and Pando) were estimated at $US 53,385,000.

MANAGEMENT

Although 'control' and 'management' are often used interchangeably, they do not mean the same thing. Control refers to activities that destroy a pest or disease at a fixed time and place, which may lead to a marked reduction in host damage so that yield and quality of the harvested product are not severely reduced (Berger, 1988). Management is a comprehensive and integrated approach towards the pest and the agroecosystem, through the concerted application of several tactics of control over a prolonged period. The goal of management is not eradication but manipulation of population densities to reduce their number below the economic threshold (Ferris and Noling, 1987).

Formerly, integrated management schemes for pests and diseases shared the basic principles of: (1) exclusion through quarantine, (2) eradication, and (3) protection by physical, chemical, biological, genetic and cultural methods. The use of some or all of them depends on the pest and the extent of the problem. The present trend, however, is towards the use of control options under specific circumstances determined by biomonitoring and economic thresholds. Thus, the basic elements in a management program are sampling, diagnosis, prediction, and management tactics.

Diagnostics: Above ground symptoms and the galls on the root system are not considered specific, the identification of the nematode itself being the best diagnostic method available. Early detection in soil samples from endemic areas is difficult as the species is not easily detected and/or populations are underestimated, with potentially serious consequences for subsequent susceptible crops. Although modification of sieving and

centrifugation extraction methods can give reasonable results, the development of a reliable diagnostic method to detect *N. aberrans* in soil samples is an important priority. According to Franco *et al.* (1992), the best method is a bioassay consisting of a potato plant grown in moist soil and maintained in a closed transparent container kept at 25°C in darkness for 3 days, which produces galling that can be assessed after 30 or 35 days. The same method can be used to assay potato tubers for infestation by growing them in sterilized soil in the same type of container. The time taken to carry out these bioassays is considerable, so the development of a quicker, reliable method for diagnosis in soil samples is important for the implementation of appropriate management practices.

The economic threshold and tolerance limit: The economic threshold can be defined as the population density of a pest at which the damage equals control costs (Ferris and Noling, 1987). The economic threshold density may oscillate with the amount of stress the plants are under and with their age, more vigorous plants being able to support more nematodes (Bird, 1970; Wallace, 1970). Although progress has been made in applying knowledge of nematode population dynamics to the determination of economic threshold values (Seinhorst, 1965; Oostenbrink, 1966), this remains one of the major challenges in population management. Despite lack of a formal study to establish the economic threshold of *N. aberrans*, several reports have noted the potential danger that even low levels of infestation represent to crop yield.

Inserra *et al.* (1984a, b) reported the effect of the initial nematode population density (Pi) of *N. aberrans* on the growth of sugarbeet cv. Tasco AH14 and kochia in glasshouse tests. Tolerance thresholds, according to the equation $y = m + (1-m)z^{P-T}$, where y = relative yield, m = relative minimum yield, z < 1, P = initial nematode density, z^T = 1.05, and T = tolerance limit (Seinhorst, 1965), were found for total fresh weight, top weight, and storage root weight, at values of Pi of 0.77, 0.54 and 0.19 J2/cm^3 soil, respectively. The maximum rate of nematode population increase was 32× and occurred at Pi = 0.25 J2/cm^3 soil, whereas the greatest final nematode population density (Pf, consisting of eggs and J2), occurred at Pi = 4 J2/cm^3 soil. Pf/Pi was negatively correlated with Pi. In this experiment, no growth suppression of kochia was observed at any Pi. Kochia appeared to be a less favorable host and more tolerant of *N. aberrans* than sugarbeet.

Otazú *et al.* (1985) noted that when soils had a low to medium infestation, nematicides were more effective, but that higher dosages were required at higher infestation levels, thus increasing cost. Cid del Prado *et al.* (1996a) reported that control treatments did not increase tomato yield significantly when *N. aberrans* occurred at 1.5 nematodes/g of soil and 331 nematodes/g of root. However, increased yield has been obtained on tomato at Pi levels of *N. aberrans* ranging from 0.02-0.06 nematodes/g soil (Zamudio, 1987; Gómez, 1992).

Nacobbus aberrans affects potato yield at only 1-10 galls/plant and the effects worsen as infestation increases. The effects on yield are greater than with *Globodera* spp. so keeping soils free of infestation is crucial.

Management strategies may include keeping nematode densities low while the crop is young and intolerant by using crop rotation, cultural manipulations, and changes in planting time. A cropping system should be designed so that one crop does not produce a population of nematodes larger than the economic threshold density of the succeeding crop in the system.

Control strategies. Effective pest management requires the establishment of a crop loss profile (Chiarappa, 1981). This implies

an understanding of the damage/loss relationship, estimation of probable yield loss and damage based on estimates of pest incidence, and forecasts of how much of this loss can be avoided by appropriate control methods of known cost. Treating on the basis of an assessment generally brings significant economic saving over that of treating routinely. New conditions (e.g., new techniques, new chemicals, changed market prices for a given commodity) can affect the relationship between actual and potential crop losses and yields.

Management approaches for *N. aberrans* aim to produce a package acceptable to farmers. However, if the value of the crop per hectare is low, it may be difficult to find measures that are economic. The belief that losses can be reduced is based on the assumption that the cost of achieving this objective is relatively low, but this has to be demonstrated for each particular case. Therefore, economic analysis has been made of several of the integrated pest management packages that have produced significant yield improvements in *N. aberrans* affected crops (Zamudio, 1987; Silva-Jaramillo, 1989; Gómez, 1992; Cid del Prado *et al.*, 1997b; Yáñez-Juárez, 1997; Ramos *et al.*, 1998). Examples of and references for most of the control strategies used with *Nacobbus* are given below.

Antagonistic crops: The incorporation of dry powdered flowers of *Chrysanthemum cinerariaefolium* (Trev.) Vis. in pots of naturally infested soil drastically reduced the galling caused by *N. aberrans* when compared with the control (Franco *et al.*, 1992). Marigold (*Tagetes erecta* L.) sown in rotation or associated with tomato plants reduced the nematode population (by 70 to 98%) in soil and roots, but incorporation of residues into the soil before planting did not significantly affect the population, the antagonistic effect being linked to disposition and number of marigold plants relative to the tomato plants (Gómez *et al.*, 1991; Gómez, 1992; Zavaleta-Mejía and Ochoa, 1992). Marbán-Méndoza *et al.* (1989) evaluated the control of *M. incognita* and *N. aberrans* with two legumes: *Concanavalia* (*Canavalia*) *ensiformis* (L.) DC and *Mucuna deeringiana* Small. A reduction in galling was observed with *M. deeringiana*, giving the better control. The reduction in severity of symptoms was attributed to the presence of the lectin concanavalin A in the soil.

The nematicidal activity of aqueous and petroleum ether extracts from leaves of *Melia azedarach* L. (Meliaceae) and *Ruta chalepensis* L. (Rutaceae) was investigated on juveniles of *N. aberrans* by Mareggiani *et al.* (1994). Significant differences were found between extract treatments and the control ($P \leq 0.05$) based on counts of inactive juveniles at 24 and 48h intervals.

Biological control: Attempts to control *N. aberrans* by biological agents, such as *Paecilomyces lilacinus*, started in the 1980s in South America. Mareggiani and Gallardo (1983) demonstrated *in vitro* that *P. lilacinus* parasitized the eggs and females of *N. aberrans*. Its effectiveness in controlling the nematode under field conditions was later evaluated on the tomato cultivar Platense Sais (12 g/plant of fungal inoculated rice) and compared with the nematicide fenamifos (Nemacur 10G, 3 kg a.i./ha). A 53% reduction in the number of galls occurred with the nematicide but only 26.5% with the fungus. The reproductive ratio (Pf/Pi) was lower in the nematicide (0.43) and fungus (1.4) treatments than in the control (2.17). Some 71.4% of egg masses were infected at the end of the experiment, a level which may allow the fungus to become persistent in soil under favorable conditions (Mareggiani *et al.*, 1985). Eguiguren-Carrión (1995) evaluated, under glasshouse conditions, the efficacy of different doses of rice colonized by

P. lilacinus to reduce the population of *N. aberrans* on tomato cv. Jefferson.

In *in vitro* assays, *Beauveria brongniartii* (Saccardo) Petch parasitizes all stages of *N. aberrans*, except when they are molting. Balderrama *et al.* (1993) investigated the pathogenicity of *Beauveria* under glasshouse conditions using different animal manures (bovine, ovine and chicken) previously inoculated with the fungus produced on rice or barley and incorporated into the soil at rates equivalent to 7 t/ha. Treatments included inoculated and non-inoculated manures incorporated either before or at sowing. No significant differences were found between the treatments, but less hatching occurred in eggs from the ovine manure treatments.

The trapping capacity of *Arthrobotrys conoides* Drechsler (strain Montecillo, Mexico) against the J2 of *N. aberrans* was evaluated *in vitro* at 25°C by Méndoza *et al.* (1994). The fungus showed a high trapping capacity (more than 90%), destroying or partially destroying most of the J2s. Flores-Camacho *et al.* (2001) reported that a Mexican isolate of *Verticillium chlamydosporium* Goddard (= *Pochonia chlamydosporia* (Goddard) Zare, Evans & Gams) parasitized a high proportion of *N. aberrans* eggs (60%) and showed good root colonization. Also, J3s and J4s have been found naturally parasitized by *Catenaria* Sorokin, 1889 in soil samples from Mexico (Flores-Camacho *et al.*, 1999).

Gardezi *et al.* (1995, 1998, 1999) showed that mycorrhizal (*Glomus* sp.) tomato plants grew better and had significantly fewer galls/plant.

Soil from the Chinampa agricultural system in the Valley of Mexico suppresses damage caused by plant-parasitic nematodes. Zuckerman *et al.* (1989) evaluated the influences of the Chinampa and Chapingo (Mexico) soils on plant growth and root galling caused by *N. aberrans* and *M. incognita* on tomato (*L. esculentum* cv. Ace) and bean (*P. vulgaris* var. Flor de Mayo) in glasshouse and growth chamber trials. The glasshouse trial with *N. aberrans* showed less root galling ($P < 0.05$) of both tomato and bean plants in non-sterile Chinampa and sterilized Chapingo soil. The results of the growth chamber experiment supported those obtained in the glasshouse. The Chapingo soil, both sterile and non-sterilized, showed no nematode suppression. Sterilization of the Chinampa soil resulted in a loss of the suppressive effect, indicating that one or more biotic factors were responsible for the low incidence of nematode damage.

Chemicals: Several studies have been made of the use of nematicides to reduce or control populations of *N. aberrans*. Considerable differences between treated and non-treated chilli pepper plants were evident in the yield, numbers of fruits and average stem diameter when 200 l/ha of D-D were applied (Caballero, 1970). Several nematicides were tested for control of *N. aberrans* in chilli pepper cv. V-2 Mulato by Equihua (1977) in a naturally infested sandy soil. Differences between treatments were very significant. Vorlex and Telone protected the plants during early development but their effects were reduced later, whereas Vydate provided longer lasting control. A negative correlation was found between yield and galling percentage. The economic analysis was positive for most treatments, particularly during early harvests when market value was higher.

Reduced galling and 10, 14 and 15% increases in seed production of 'alegría' (*Amaranthus hypochondriacus* Rob.) cvs White, Brown and Black, respectively, were reported by Santa Cruz and Marbán-Méndoza (1986a, b) when aldicarb was used at 2.5 kg a.i./ha. Under glasshouse conditions aldicarb (4.7 and 9.4 ppm) had the best therapeutic effect in reducing root

galling caused by *N. aberrans* on tomato cv. AC-VF-55 (Franco and Marbán-Méndoza, 1983). Application of phenamiphos at 3.0 kg a.i./ha increased yield in more than half of 49 tomato cultivars and reduced the gall index in most of them. The best responses were in cultivars ACE 55 F, Floradade, Río Grande, Peto Early TM, Manalucie, and UC-82-A, and in experimental lines 1-18-1-1 and 1-4-2-1 and the accession BG-LY-47. Some cultivars showed phytotoxic effects from the nematicide but the improvements in production were considered very profitable (Zamudio, 1987). Phenamiphos, carbofuran and aldicarb (2.5 kg a.i./ha) increased yields by 18 to 38% in bean cvs Negro Puebla and Canario 107, but treatments were not profitable (Silva-Jaramillo, 1989).

In South America, chemical control has been tried using organophosphates and carbamates at various application rates under different conditions of temperature, soil type and crop (Cornejo-Quiroz, 1977a; Jatala, 1985). The importance of potato seed tubers in *N. aberrans* dissemination to non-infested areas has prompted the testing of nematicides and other methods of control. Costilla *et al.* (1981) evaluated the efficiency of different chemical compounds for control of J3 and J4 resting stages of *N. aberrans* in infected potato tubers, under glasshouse and field conditions. Treatments (a.i./ha) included: carbofuran 75% (300, 400, 600 g), oxamyl 24% (216 g), malathion 3.6% (45 g), carbofuran 30 TS (375 g). New tubers obtained from the treated plots were sown in sterilized soil 90 days after chemical treatment and potato plants checked for nematode infection. Carbofuran 30 TS produced 90% of healthy plants, while other treatments allowed more extensive nematode development and root galling. Franco *et al.* (1992, 1993) and Franco and Main (2001) reported that immersion of propagative material in various chemical compounds (e.g., nematicides and insecticides) prevented spread of the nematodes (e.g., on infected potato tubers), Carbodan (carbofuran), Chlorox and hot water being among the better treatments for tubers.

Other nematicide tests have focused on reducing root galling and increasing potato yield. Otazú *et al.* (1985) tested different nematicides (aldicarb, phenamiphos, carbofuran, oxamyl, CGA-12223) in locations with different levels of *Nacobbus*. None of the nematicides reduced the galling at normal rates but high dosages of aldicarb (5 kg a.i./ha) reduced the number of galls (114/plant) in comparison to the control (552/plant).

Several commercial formulations (Furadan 5G, Curater 10G, Carbodan 5G) of carbofuran were assessed by Montecinos and Franco (1993) for control of *N. aberrans* on the cvs Waych'a (*S. tuberosum andigena*) and Alpha (*S. tuberosum tuberosum*) in heavily infested soils. No significant difference in nematode multiplication (Pf/Pi) was found between treatments. However, Carbodan at 3 kg a.i./ha was the most effective at reducing galling and increasing yield (Franco *et al.*, 1992; Instituto Boliviano de Tecnología Agropecuaria, 1994).

The effects of aldicarb, herbicides and fungicides on the incidence of *Rhizoctonia* disease and weeds and on the severity of *N. aberrans* damage to sugarbeet were studied in Wyoming, USA, by Beaupré *et al.* (1990). No effect on yield due to *Nacobbus* infection could be detected despite a high population of weed hosts and at least three years of continuous sugarbeet before the experiment. Temik 15G reduced galling by 50% and was more effective when combined with Rovral 4F. No interaction between the two pathogens under study could be detected, possibly due to the low levels of *N. aberrans* or because they do not interact.

Kerr (1991) found no differences of yield between chemical treatments (aldicarb, furadan, 1,3-dichloropropene or carbofuran + aldicarb) to control *H. schachtii* and *N. aberrans* in Nebraska.

Sowing dates: Caballero and Muñoz (1987) sowed spinach on four different dates to identify when development of cvs Viroflay, Híbrido 7 and Califlay would be least affected by *N. aberrans* in Mexico. The greatest number of nematode eggs (1854/ml soil) was found when spinach was sown in October and the least in May (98/ml). These results were related to the local weather conditions, the number of eggs being reduced when sowing occurred during the season of high precipitation.

Iriarte *et al.* (1999) evaluated different sowing dates for potato in Bolivia. Potato yield and net income were greater when planting was from June to September (27.1-30.1 t/ha). The lowest yields (17.5-23.0 t/ha) were obtained from plantings made from October to January, due to heavy infestations of *N. aberrans*, heavy precipitation (75-86 mm) and frost (in January).

Crop rotation: The rotation of crops is one of the oldest and most important approaches to the control of nematodes that feed on the roots of annual crops (Nusbaum and Ferris, 1973). Although many of the early rotation schemes were developed empirically, field experiments are now needed to aid the selection of suitable alternative crops and the length of rotations between main crops for the desired degree of control. Crop rotation is a major management strategy for the suppression of *N. aberrans* populations in potato fields in South America and also in sugarbeet fields in Nebraska, USA.

Nacobbus aberrans has a wide range of hosts, making it difficult to select appropriate crop rotations, although crucifers, some graminaceous plants and most legumes are considered resistant. According to Jatala (1985), populations decline rapidly in the absence of a suitable host, with a minimum of three years rotation considered advisable (IBTA, 1994). *Lupinus mutabilis* (tarwi) not only reduces root infestation and galling by *Nacobbus*, but also the number of cyst nematode females (Cornejo-Quiroz, 1977b). A comparative study of the effect on nematode reproduction rate of annual cropping of tarwi, horse-bean, barley, oat and a susceptible potato cultivar showed that the rate was highest with potato (Franco *et al.*, 1992). Two semiperennials (*Vicia villosa* Roth. and *C. cinerariaefolium*) also gave reproduction rates of *Nacobbus* that were significantly lower than on a susceptible potato cultivar (Franco *et al.*, 1992).

Montalvo *et al.* (1994) followed a four-year rotation scheme, using a combination of susceptible (cv. Waych'a) and partially resistant (cv. Gendarme) potato cultivars, tarwi, oat and fallow. The reproduction rate of *N. aberrans* was reduced to less than unity in rotations that included tarwi, oats or fallow.

The economic benefits of crop rotation on potato yield were also shown by Ortuño *et al.* (1994). Potato cultivars were sown in plots that had followed different rotation schemes. Losses were greater under potato monoculture, and aldicarb helped to reduce the losses.

The host range of *N. aberrans* makes it difficult to find suitable crops to grow in Andean regions up to 4500 masl. *Hordeum vulgare* L., triticosecale, *Bromus unioloides* (Willd.) Raspail and *Distichus humilis* Phil. were identified as potential trap crops. Barley (cvs Lucha and IBTA-80) and triticale (cv. Renacer) were evaluated as candidates for a rotation scheme (Franco *et al.*, 1997). Main *et al.* (1999) tested a range of cultivars of various crops as potential trap crops for *N. aberrans* and found that 60% of the quinoas, 10% of the 'papalisas' and 93% of

the 'isaños' did not develop root galls, despite being reported as hosts for *N. aberrans* (Gonzáles, 1985; Jatala, 1991; Castiblanco, 1992). In general, the oats and ocas behaved as non-hosts but some 46% of the oat cultivars, 100% of the quinoas and 8% of the isaños allowed invasion but not reproduction of the nematode, thus being considered suitable as trap plants. The ocas Bol4038 and Bol4346 and the isaño Bol4051 reduced galling markedly (1.0, 4.0 and 2.0 galls/bioassay, respectively) in comparison to potato and fallow (40.4 and 19.8 galls/bioassay, respectively). The reduced multiplication of the nematode was attributed to death of J2s after penetration, but for isaño it was attributed to root toxicity.

At present, rotation in Bolivian potato fields is based on a four-year cropping system, comprising resistant cultivars of potato, barley trap crops, lupin or horsebean incorporated in the soil after early harvest, followed in the fourth year by a tolerant or susceptible potato cultivar (Franco *et al.*, 1996). This meets some of the requirements of a successful rotation: (a) to restrict development and reproduction of the nematode to levels that allow the subsequent crop to become established and complete early growth without serious damage; (b) at least to pay the expense of working the land; (c) to enrich the land or at least not impoverish it; (d) to make such vigorous, dense growth as to choke out susceptible weed hosts; and (e) to preserve competitive, antagonistic, and predacious nematodes and other organisms at population densities effective in buffering the pathogenic species (Nusbaum and Ferris, 1973).

In Nebraska, USA, rotation of sugarbeet with a non-host crop such as cereals and alfalfa (*Medicago sativa* L.) reduces nematode populations in the soil; however, coordinated use of herbicides to control weed hosts such as kochia and lambsquarter is essential (Inserra *et al.*, 1985).

The non-hosts maize, vetch and beans were recommended for use in rotations against *N. aberrans* in Argentina (Costilla, 1992), and maize was similarly recommended in Mexico (Manzanilla-López *et al.*, 1996).

Fertilization: The deficiency or oversupply of nutrients may have a positive or negative effect on nematode populations. Schuster *et al.* (1966) noted that fertilization decreased the severity of *N. batatiformis* (= *N. aberrans*). Aparicio *et al.* (1989) exposed J2s of *N. aberrans* to different dosages (1000, 1500 and 2000 ppm) of ammonium sulphate and urea under laboratory conditions. High mortality occurred 24h after exposure, ammonium sulphate being the more toxic. Márquez and Montes (1991) increased tomato yields by applying 60 kg of N per ha along with Curater 100%.

The effect of N, P and K dosages on the multiplication rate (MR) of *N. aberrans* and yields of potato cvs Waych'a and Alpha were assessed over two crop cycles (Montecinos *et al.*, 1993). Increasing N levels (80 kg/ha) decreased the MR. However, the absence of N, combined with 60 and 120 kg/ha of P and 60 kg/ha of K, increased the MR, more so in Alpha than in Way'cha.

Genetic control: Screening and breeding for resistance to *N. aberrans* has focused mainly on potato, chilli peppers, beans and tomato. In South America, the search for sources of resistance in potato started during the 1970s and resistance to *N. aberrans* has been reported by several authors (Alarcón, 1977; Cornejo-Quiroz, 1977c; Jatala, 1985; Franco *et al.*, 1992; IBTA, 1994). However, temperature can influence the expression of resistance (Vanderplank, 1975; Mullin *et al.*, 1991). Alarcón and Jatala (1977) reported resistance of cv. Huaca Lajra to different populations of the nematode in plants grown at lower temper-

atures (10 to 22°C), but galling occurred with populations from Huancayo when plants were grown in Lima, a location with a higher temperature regime (18 to 30°C). Studies have been undertaken in Bolivia to increase the genetic basis of resistance for *N. aberrans* through the use of resistance from wild and cultivated sources combined with resistance to potato late blight (*Phytophthora infestans* (Mont.) de Bary.) and freezing tolerance. From 597 clones evaluated, 63 were initially selected as resistant (Franco *et al.*, 1992; Instituto Boliviano de Tecnología Agropecuaria, 1994).

In Mexico, Brunner de Magar (1967) evaluated 90 varieties of chilli peppers (*Capsicum* spp., varieties and lines) in a search for resistance. None was immune but the Peruvian variety Amarillo Tacna (*Capsicum pendulum* = *C. baccatum*) was considered resistant. Castillo and Marbán-Méndoza (1984) recorded superior root and above-ground growth in *C. baccatum* compared to *C. annuum* when both were parasitized, but listed *C. baccatum* as susceptible-tolerant rather than resistant, since the nematode reproduced without any evident effect on host development.

Few studies have been conducted to select resistant and/or tolerant bean cultivars, the first study being made by Silva-Jaramillo during the 1980s followed by those of Arciga (1995) and Hernández (2001). The latter author evaluated ten bean cultivars against two Mexican populations of *N. aberrans*. All cultivars were resistant to the Puebla population; cvs Bayo Macentral, Amarillo Calpan, Negro San Luis and Río Grande were resistant to the Zacatecas population.

Zamudio (1987) evaluated 60 varieties (wild, creole and commercial) of tomato (*Lycopersicon* spp.) under glasshouse conditions and 81 in the field in a search for resistance. None was immune and varieties tested in the glasshouse showed a positive correlation between the weight of root system and the quantity of galls and eggs. Some of the varieties tested in glasshouse conditions showed greater tolerance in the field and yield was not correlated with gall index.

In Argentina, Mareggiani and Pelicano de Casaurang (1983) found that cultivated tomatoes were susceptible to *N. aberrans*, including those carrying the Mi gene (cvs Rossol and Planeuco). Accessions with a degree of nematode resistance were identified in the species *L. esculentum*, *L. pimpinellifolium* (Jusl.) Mill. and *L. cheesmanii* Riley. Cap *et al.* (1993) used glasshouse pot tests to screen accessions of *Lycopersicon* spp. carrying the heat stable resistance gene Mi-2 (effective against root knot nematode *M. incognita*). Based on the number of eggs per g of root tissue, some accessions were considered moderately to highly resistant to a population of *N. aberrans* from Argentina. Variability observed in some of the accessions was considered as possible segregation for resistance. Other accessions of *L. cheesmani*, *L. chmielewskii* Rick, Kesicki, Fobes & Holle, *L. esculentum* var. *cerasiformis* Alef., *L. hirsutum* Dunal, *L. parviflorum* Rick, Kesicki, Fobes & Holle, *L. peruvianum* (L.) Mill., *L. pennelli* (Correll) D'Arcy, *L. pimpinellifolium* and three inter-specific hybrids of *L. peruvianum* with *L. esculentum*, were not resistant to two populations of *N. aberrans* in glasshouse tests by Veremis *et al.* (1997). Further screening of *Lycopersicon* for resistance was recommended on the basis of the large germplasm resource in wild relatives of tomato.

Mulching, organic amendments and solarization: Montes-Belmont (1972) studied the effects of organic matter decomposition and antagonists on control of *N. aberrans* under glasshouse conditions. Tomato plants (cv. Homestead-24) in pots, containing 10 g/kg of *Mentha piperita* L. green manure, *Crotalaria* sp. green manure, pineapple green manure, corn straw, barley

straw or dry residues of tomato, were inoculated with 1,250 nematodes/kg. The green manures had no significant effects, but a significant decrease of juveniles occurred in the second week with corn residues and by the fourth week with barley residues. Chemical analyses showed that high levels of nitrogen were associated with the corn straw and low levels of potassium with the barley.

Franco *et al.* (2001) and Franco (2002) studied the effects of *Brassica oleracea* var. *capitata* and *Ricinus communis* L. green manures on host (*L. esculentum*) nutrition and *N. aberrans* control. Different quantities of cabbage and *Ricinus* residues were incorporated into soil before or at transplanting, under greenhouse (*B. oleracea*, *R. communis*) or field (*B. oleracea*) conditions. Galling was reduced by up to 70% when larger quantities (32.5 and 52 t/ha) of cabbage were incorporated one week before or at transplanting, but there was also some phytoxicity. The manures had overall positive effects on plant height, foliage and root dry weights, and N, K, Ca, Mg and micronutrients levels. Yield was increased by up to 62%.

The combined effects of solarization and mulching (black plastic sheets) with fertilizer, chicken manure and dung (1,360 and 1,285 kg/ha, respectively) on bean yield and control of *N. aberrans* were evaluated by Silva-Jaramillo (1989). The highest yields were produced by cv. Negro Puebla with mulching-chicken manure and mulching-dung treatments, but the overall effect was attributed to improving availability of nutrients and water, rather than a solarization effect on the nematode, since final populations did not decrease in comparison to the control. Incorporation of 10 t/ha of chicken manure or dung did not control *N. aberrans* on beans and much galling persisted, yield increases being attributed to the fertilizing effect of these materials (Silva-Jaramillo, 1989). Franco *et al.* (1992) found that incorporation of chicken manure (10 t/ha) increased yield of potato tubers, but there was no effect on the reproduction rate of *N. aberrans* compared with other treatments such as dung and compost. Nevertheless, chicken manure (7 t/ha) incorporated at sowing did not allow high levels of reproduction of the nematode (IBTA, 1994). According to Canto-Sáenz *et al.* (1996), the use of manure increased yields by 70-84% and reduced the numbers of *Nacobbus* by 85%.

Yáñez-Juárez *et al.* (2001) combined several management strategies with solarization, using a double sheet of clear plastic or a single sheet of black plastic to control *N. aberrans*, *Phytophthora capsici*, wilting and virosis in two Mexican locations (Montecillos and Tecamachalco). Population levels of *N. aberrans*, *P. capsici*, soil fungi and bacteria were quantified through the study. The highest temperature was registered under a double sheet of clear plastic in the top 5 cm of soil (42.3°C), followed by black plastic (36.5°C) and the control (29.3°C). Reductions in initial inoculum of 69% for *N. aberrans* and 86.3% for *P. capsici* were found after solarization. In Montecillos, temperatures were lower than in Tecamachalco, but *N. aberrans* and *P. capsici* inocula were still reduced (76.4 and 90.3%, respectively). Effects on inocula were quantified through bioassays on tomato cv. Rio Grande using soil samples taken before the experiment began and on a monthly basis afterwards. Galling was evaluated 40 days after transplanting. Pre-solarization bioassays in Tecamachalco showed values of infestation ranging from 25.8-42.8 galls/plant. Only the solarization treatment reduced nematode inoculum significantly (54-69%). The initial inoculum in Montecillos (5.8-14.3 galls/plant) was reduced after solarization to 1.7-5.5 galls/plant

(11.7 galls/plant in the control). Monthly sampling showed a reduction of *Nacobbus* inoculum varying between 39 and 76%. The greatest improvements in yield occurred when addition of chicken manure was combined with plant residues of chilli pepper and marigold in the ratio 3:1 plus mulching with black plastic (292%) and when chicken manure was combined with just marigold residues and mulching with black plastic (420%), the latter having the highest marginal return (3,934%) in comparison to local traditional production (156%). However, higher yield and quality of fruits were not directly related to reduction of *N. aberrans* and *P. capsici* inocula or wilting and virosis but rather to nutrient availability, which allowed better development of the plants and greater tolerance of the pathogens.

Integrated management: Despite the variety of control strategies now available, only in a few cases has a regional Integrated Pest Management (IPM) program been implemented successfully for *N. aberrans*. Some studies have been inconclusive and have not been transferred to, or evaluated by, farmers, particularly where research resources are scarce or the importance of the nematode has only recently been recognized. Once the nematodes are introduced to land their eradication is impossible and populations can only be managed through an IPM program. The costs of adopting some of the available control methods are not always compensated for by the increase in value of the crops in the rotation. Note, however, that when calculating costs and benefits, the indirect costs and benefits, such as the long-term preservation of soil fertility and the agroecosystem, should also be included in the budget of the system. Better knowledge and understanding of agroecosystems should lead to better use of IPM strategies.

Integrated pest management programs vary according to crop. The general strategies recommended for potato production include: use of quality seed, use of organic amendments (i.e., animal manure), use of resistant and/or tolerant potato cultivars, early ploughing, removal of potato volunteers and weeds in fallow fields, chemical control, a four-year crop rotation scheme, and burning of infected roots after potato harvest (Canto-Sáenz *et al.*, 1996; Franco *et al.*, 1996). Monitoring farmers' fields using management programs of this type has shown high potato yields and low nematode population densities in the soil. Along with research on IPM programs, training and education (technology transfer and its evaluation by the farmers) are important (Franco *et al.*, 1992). Van Gundy (1972) pointed out that, regardless of how successful crop rotation is and can be, it may not survive the technological revolution in agriculture unless grower attitudes can be changed. The ecosystem approach to pest management presents great challenges and opportunities for the future. A stage is being reached where quantification of information on population dynamics and epidemiology of *Nacobbus* is possible. In Mexico, a series of studies covering population dynamics, host range, control strategies and epidemiology has been conducted, under both glasshouse and field conditions. Cid del Prado *et al.* (1997b), in a field study of tomato, evaluated a combination of treatments that included tomato and *Tagetes* sp. in a 1:1 ratio, four applications of oxamyl (Vydate L, 260 ml a.i./ha), incorporation of chicken manure, and dazomet (Basamid, 940 g a.i./ha). Significant differences were found between treatments and controls: dazomet gave the highest yield. However, plants grown with *Tagetes* or treated with oxamyl had fewer galls than those treated with dazomet. Based on these and other

results (Zamudio, 1987; Silva-Jaramillo, 1989; Zamudio *et al.*, 1990; Gómez, 1992; Cid del Prado *et al.*, 1996a; Yáñez-Juárez, 1997; Cristóbal *et al.*, 2000; Cristóbal, 2001), an IPM strategy has been developed for tomato and includes the disinfection of the soil in the nursery stage, fertilization, use of nematicides, incorporation of chicken manure (10 t/ha), and removal of tomato plants (including roots) after harvest.

Pest exclusion programs, seed certification and quarantine: Nacobbus aberrans is a pest that warrants special quarantine effort. It can severely reduce yields of major food crops, but is not present in many parts of the world where it has potential to reduce crop yields. Currently, the following countries impose quarantine restrictions against *N. aberrans*: Argentina, Brazil, Bulgaria, Colombia, European Union and other related countries (Austria, Belgium, Denmark, Finland, France, Germany, Greece, Guadeloupe, Ireland, Italy, Luxembourg, Martinique, Monaco, Netherlands, Portugal, Reunion, San Marino, Spain, Sweden, United Kingdom, and Vatican City), Hungary, Iceland, Indonesia, Japan, Morocco, Norway, Paraguay, Republic of Korea, Thailand, Tunisia, USA (California), Uruguay, and Former Republics of Yugoslavia (Bosnia and Herzegovina, Macedonia, Slovenia) (Source: Export Certification Project-Excerpt; http://excerpt.ceris.purdue.edu, 8/2/01).

All *N. aberrans* races, as other plant parasitic nematodes, can be disseminated in infested soil or in infected or contaminated propagative plant material regardless of whether it is in soil or bare-rooted. As *N. aberrans* causes severe losses to potatoes and other crops in the Andean region of South America, and may be disseminated on tubers with other potato pests such as *Globodera* spp., many countries impose regulatory restrictions on the importation of potato tubers.

The potato race is easily disseminated because active J2s are able to invade tubers where, under favorable environmental conditions, they molt to inactive J3s, J4s and vermiform females. These life-stages are a source of inoculum when infected tubers are planted in clean soil (Jatala and de Scurrah, 1975). In small tubers, males and females with egg masses are observed rarely (Costilla, 1985b). Usually there are no galls, lesions or other infection symptoms on the tubers but nematodes can survive in the tuber for at least 10 months (Costilla, 1985b). Infected tubers are a major means of short and long distance nematode dissemination and have allowed the nematode to reach geographical areas far distant from the Andean regions, such as Finland and Russia (Kirjanova and Lobanova, 1975). The wide distribution of *N. aberrans* in the temperate uplands of the Andean regions of Bolivia and Peru has been favored by the exchange and use of infected tubers since the pre-Colombian era.

The production of certified seed-potatoes free of *N. aberrans* and other nematode pests should be encouraged by local governments in South America to limit its spread within and between the countries of that continent. In South America, Argentina, Bolivia and Chile have adopted seed certification programs for the production of potato tubers free of *N. aberrans* and cyst nematodes (Franco, 1994; Costilla, 1997; Franco *et al.*, 1998). The efficacy of this policy has been questioned because of the wide distribution of the potato race of the false root-knot nematode in Bolivia (Franco, 1994; Franco *et al.*, 1998). However, the beneficial effects of such a policy should not be underestimated, because the use of certified seed-potatoes free of nematodes avoids augmentation of initial nematode densities in infested potato fields under a regime of long rotations, and avoids the introduction of the nematode to potato-growing areas that are still free of this pest.

In countries where false root-knot nematode is present, protocols for the production of certified seed-potatoes free of *N. aberrans* can be established by research agencies in cooperation with farmers. Production sites and seed stocks should be sampled and found negative for *N. aberrans*. Before harvest, these fields should be checked for the presence of galls on potato roots. If galls are found, further microscopic examination must determine if they are caused by *Nacobbus* or *Meloidogyne* species. Sanitation practices should be followed strictly in these production fields in order to avoid introduction of nematodes with contaminated tools, irrigation and run-off water, or plant hosts.

Standard nematological extraction procedures can be used to extract *N. aberrans* from soil and roots. Active vermiform stages of the false root-knot nematode can be extracted from potato tubers by incubating 2 mm thick peels of potato in a film of water in jars, Petri dishes, or Baermann funnels for 24 to 72 hours.

The number of soil samples needed per hectare varies as a function of nematode distribution and density, but for assay purposes 20 or more cores (~2 cm in diameter by 20 cm deep) per hectare has been recommended (Barker, 1978). Because an effective seed certification program requires zero tolerance, bulking soil cores and sub-sampling them after mixing them well also should be considered. This allows more cores to be taken per unit area, which will increase accuracy without increasing the costs for sample processing and nematode diagnosis. Detection of nematodes in potato tubers for regulatory purposes is difficult, because at low population densities few tubers will show symptoms. Furthermore, according to the binomial probability of distribution, if 5% of the potato tubers are infected in a lot of 1,000 tubers, analysis of 50 and 100 tubers would be required for a 95 or 99% probability of detecting the nematode, respectively. If only 1% of the potato tubers are infected in a potato tuber lot of the same size, the numbers of tubers to be analyzed increase to 300 and 500 for 95% and 99% chances of detection (McSorley and Littell, 1993). Samples of such size would be impractical for any regulatory agency. The best approach is to import tubers only from areas where fields are not infested with *N. aberrans* or from countries where the nematode is not present.

Although infected tubers represent an important means by which *N. aberrans* may be introduced into non-infested regions, it should be emphasized, especially with the emergence of multinational regional trading blocks in which food crops are marketed over long distances via air transport, that more attention needs to be given to the other hosts which may serve as avenues for the dissemination of this pest. *Nacobbus aberrans* has many hosts that produce fleshy roots or tubers, such as: *B. vulgaris* (table beet and sugarbeet), *Brassica napobrassica* Mill. (rutabaga), *Brassica rapa* L. (turnip), *Daucus carota* L. (carrot), *Raphanus sativus* L. (radish), *O. tuberosa* (oca), *T. tuberosum* (mashuar, isaño or anu), and *U. tuberosus* (olluco) (Canto-Sáenz 1992). For example, as a result of trade agreements during the past decade between the USA and countries where *N. aberrans* is found, many vegetable hosts of this nematode, including five fleshy root hosts, are marketed commercially between countries in the trading block with minimal regulatory inspection. In the next decades, many regional trading blocks will probably merge and expand and it is likely that a unified trading block will emerge that will include most countries in North, Central and South America. If the trends of the past decade are indicative of the future, this will increase the risk of dissemination

of *N. aberrans* because more food crop hosts will be commercially exchanged between countries in these large trading blocks. The nematode can also be spread with non-hosts (e.g., ornamentals) grown in infested soil, and increased plant trade will increase the risks of dissemination.

Even though many countries consider *N. aberrans* a quarantine pest, this does not ensure its exclusion. The federal regulatory inspectors at most ports of entry, including those in the USA, rely primarily on visual symptoms or signs such as galls and cysts to indicate the presence of quarantine nematodes. These regulatory introduction centers are not equipped to sample, extract, and identify nematodes or other pests that do not cause visible symptoms and cannot be seen without the aid of a hand lens. Additional personnel are needed who are trained in nematode identification. Research that would provide more information on ornamental plant hosts of *N. aberrans* would also strengthen efforts by regulatory agencies to exclude this nematode. Many ornamental nurseries are multinational and increasing numbers of plants are being marketed internationally. However, there is limited knowledge of plants hosts that should be targeted for more careful inspection by regulatory agencies.

The costs and benefits of excluding this pest can be illustrated for potatoes in the USA, where both *N. dorsalis* and *N. aberrans* occur but populations of these species are not known to parasitize potatoes. If races of *N. aberrans* that parasitize potatoes were introduced and became established on potatoes in the USA, and losses averaged only 1%, potato growers would lose $30 million annually. Similar benefits could be calculated for European potato growers but, in addition, European sugarbeet growers benefit from the efforts to prevent the introduction of *N. aberrans* from South and North America, where races of the nematode parasitize sugarbeet. The introduction of this nematode could have a very negative impact because European countries produce about 85% of their sugar from beet, which represents approximately one third of the total worldwide sugar production from cane and beet. With the expansion of multinational trade agreements, regulatory agencies need to continue to shift their thinking from pest exclusion policies that are geopolitically based to a more co-operative multinational approach that is based on pest biology and ecology.

NACOBBUS DORSALIS

Nacobbus dorsalis is of minor economic importance and has been found only in California (USA) on the type host *E. cicutarium* and on *Salvia* sp. (Sher, 1970). There are no reports of *N. dorsalis* infestations on cultivated plants. Steele (1984) attributed an infestation of the false root-knot nematode on sugarbeet in California to *N. dorsalis*. However, this identification has not been confirmed. In spite of the negligible economic importance of this species, some countries, such as Brazil and Uruguay, impose quarantine restrictions against *N. dorsalis* (Source: Export Certification Project-Excerpt; http://excerpt.ceris.purdue.edu, 4/27/99).

DISCUSSION AND FUTURE PERSPECTIVES

The main objective of the present review was to summarize our knowledge of different aspects of *N. aberrans* and *N. dorsalis*. *Nacobbus aberrans* remains a challenging problem in nematology because it is of major economic importance in agriculture. Research has progressed steadily on burrowing (*Radopholus similis* Cobb), cyst (*Globodera* spp., *Heterodera* spp., etc.), root lesion (*Pratylenchus* spp.), and root-knot

nematodes (*Meloidogyne* spp.), and the basic knowledge so gained has already been used in novel areas such as molecular taxonomy, genetic engineering, monoclonal antibody technology, semiochemical studies and plantibody technology, but other groups, including *N. aberrans*, have not had the same attention.

In the more prosperous North American countries, such as the USA, the majority of studies on *Nacobbus* were conducted during the expansion of the sugarbeet industry in the central and western states in the 1960s and 1970s. Limited work was carried out on *N. aberrans* in the 1980s and 1990s due to the reduction of the cultivation of sugarbeet in the USA, where, today, *N. aberrans* damage occurs mainly in the state of Nebraska (Inserra *et al.*, 1996). In Mexico and the Andean region of Latin America, research on *N. aberrans* has been subject to fluctuations without any strong commitment by the potato and bean industries. Outside the Americas, *N. aberrans* is considered a potential threat for Europe, Asia and Africa. Perhaps most of the danger of that threat resides in the acknowledgement by most nematologists of how little we know about *Nacobbus*, how much work is still needed, and how difficult control of this species could be once established. As a result, *N. aberrans* has been placed under international quarantine regulation. However, exclusion is no longer an alternative in places where land has already been infested. Research into fast and reliable diagnostic methods (perhaps molecular-based) is required to help avoid further dissemination and reduce crop losses.

Nacobbus aberrans has some similarities to root-knot nematodes but the assumption that it could be controlled and managed in a similar way to root-knot nematodes is an easy, but false, conclusion. With typical pratylenchid behavior, it does not commit itself to continuous development once it has invaded the roots as a second stage juvenile. This is in total contrast to what occurs with the J2 of root-knot nematodes. Instead, it retains the ability to leave the roots, repeatedly arresting its development until conditions are suitable and the young adult stage is attained. On the other hand, once the young female is established and has induced a syncytial feeding site, its development in the root will continue unless brought to an end by unfavorable environmental or biological conditions. This aspect of its behavior is comparable with that of heteroderids in general. *Nacobbus aberrans* shares some of the best ecological and evolutionary strategies developed by both the migratory and sedentary endoparasites. It is likely that such a complicated cycle has evolved in response to the harsh conditions that this species faces in the semi-arid and mountainous regions where it occurs. The best long-term prospects for its management probably lie in finding and exploiting plant resistance, while immediate benefit would probably result from the use of soil fumigants on crops where the gross margin is sufficient to support the costs involved.

Despite similarities, it is the biological peculiarity of *N. aberrans* that prevents many generalizations with other root-knot or pratylenchid nematodes. Aspects such as the dormancy of the different stages in this species and its impact on the life cycle and survival strategies need to be studied further. Other life cycle strategies are shared with other genera having obese females (e.g., *Rotylenchulus* spp.), such as the retention of unshed old cuticles, and the importance of this type of convergence needs to be addressed. Whether the nematode is amphimictic or parthenogenetic remains to be solved, although the available evidence supports amphimixis.

Nacobbus aberrans is capable of overcoming the hypersensitive response by the host.

This is an important feature, as it may be related to changes in oesophageal secretions and cuticular coating of the juveniles that elicit a different response from the host tissues as the nematode develops. Partial characterization of the hypersensitive response has been achieved for other plant parasitic nematodes (Robinson *et al.*, 1988) and has led to research on host-parasite relationships with the ultimate aim that new biotechnologies could interfere with, or block, important processes. In *Nacobbus*, however, this is another area yet to be explored. A further example of the chemical interaction of *N. aberrans* with its host is the production of proteinaceous (external) secretions through the oral cavity, anus, vulva and cuticle (i.e., through pores) (Manzanilla-López *et al.*, 1998b). Secretions coating the cuticle could be involved in the host response to the presence of the nematode. As in *Meloidogyne* (Orion *et al.*, 1987), it is likely that *Nacobbus* secretions have a lytic effect. In the case of the gelatinous matrix, this would produce the extensive cavities or galleries that are observed inside the galls. These help to retain eggs in the interior of the root tissue, thus providing additional protection in comparison to eggs that are laid outside the root or have been forced to the exterior of the gall by the pressure exerted by the expanding gelatinous matrix. However, where and how the gelatinous matrix is produced remains unsolved for *Nacobbus* (Geraert, 1994).

Estimation of egg population densities in soil deserves special consideration as eggs are critical in studies of population dynamics and need to be detected in soil for quarantine and diagnostic purposes. Preliminary immunoassays showed the potential of this technology for the development of a quantitative immunoassay for *N. aberrans* (Evans *et al.*, 1997). Despite the progress made so far on the study of the resting stages, further research is needed.

Research on *N. aberrans* has focused mainly on practical (i.e., control and management) and taxonomic aspects. The topic of discussion that has dominated research around this species is, however, the systematics of the genus and the so-called physiological races. Most taxonomic work on *N. aberrans* is based on traditional studies of morphology and morphometrics with few studies using SEM, biochemistry or molecular techniques.

Descriptions of the first two species of *Nacobbus* (*N. dorsalis* and *N. aberrans*) were based on morphological features and some biological attributes. Subsequently, such differences between putative species, i.e., *N. batatiformis*, *N. serendipiticus* and *N. serendipiticus bolivianus*, were emphasized. The amount of morphological variation was not fully appreciated in the type populations, due to the small numbers of specimens on which the descriptions were based. The revision of the genus by Sher (1970) demonstrated not only the poor knowledge of the morphological variation that prevailed in the genus but also the lack of information about the internal and external anatomy. Although Sher extended the morphometric data available for *N. aberrans* and *N. dorsalis*, the morphology and range of variation therein remained incompletely understood.

The statement made by Jatala and Golden (1977), that ". . . all known species found in South America at present are considered to be of the *N. aberrans* complex," promoted the assessment of variation in populations. Since then, it has been frequently claimed that *N. aberrans* is a complex of species or aggregates, an aggregate being a number of species (binomials) which are in classical taxonomy terms morphologically closely related and difficult to discriminate.

Nacobbus aberrans is a non-homogeneous species and discrimination of individuals into easily recognizable and internally

homogeneous groups has not been possible. Different groups occur in populations from North and South America, represented by a few individuals mixed with the dominant group. To sort out such heterogeneity, it would be advisable to evaluate the variation produced from a single egg mass and to define whether different groups are part of the variation found in a particular population or whether they reflect the variability of this species.

Acquisition of morphological distinctness is not always correlated with reproductive isolation and difficulties may result from evolutionary intermediacy. Parasite populations, however, are often slightly different on different hosts. Morphological differences can be produced by non-genetic modification resulting from the different physiological environment of the different hosts, but differences can also be indicative of a subspecific or even species rank.

Discussion of the taxonomic status of *N. aberrans* is difficult. The possibility of splitting *N. aberrans* into several species or subspecies has been suggested but researchers have restrained themselves from making formal propositions on this subject. Two different approaches, related to supraspecific and infraspecific categories, have been used to deal with the variation in this species, and the term 'species complex' is usually applied indiscriminately to *N. aberrans* variation. If *N. aberrans* is considered as a species complex, we will be dealing with supraspecific variation and sibling species: reproductively isolated species without (or with very slight) morphological differences. The second approach deals with infraspecific categories, such as subspecies, which are biologically equivalent to races.

Does *N. aberrans* include sibling species? Indications that a complex of sibling species exists in nature may come from biological variation in populations, but reproductive isolation can reinforce recognition despite the lack of distinguishing morphological characters (White, 1981). Food preference (host specificity), habitat preference (Mayr, 1969), breeding season, and tolerance/resistance to other ecological factors may help to discriminate the aggregates in what seems to be a single species. Many aspects of ecology and life history are species-specific. The phenotype of animal populations of the same species often varies according to locality, season or habitat and differences between phenons may thus reflect either a species difference or intraspecific variation. Therefore, a complete understanding of intraspecific variation is necessary before deciding if a phenon belongs to a different species or not. These are all arguments to support a thorough understanding of individual and geographic variation in *N. aberrans* before deciding whether to split it into new species, the information available still being very incomplete.

Data on reproductive isolation on which to base decisions on the species or subspecies levels is unavailable. Hence, we have to rely on a deep and careful analysis of intraspecific variation for each population studied along the entire geographic range of *N. aberrans* to find out if there are sibling species. However, several combined approaches, such as morphological, physiological (host range), biochemical and molecular, can be used to find if patterns in variation can be recognized among populations.

The use of a more general scheme for races needs to be discussed and agreed. The host range test should be standardized and potential differential hosts should include Cruciferae species as they apparently are hosts for some of the North and South American populations that also reproduce on sugarbeet but not on potato.

It is not yet possible to define precisely the geographical origin of *N. aberrans*, although some authors have suggested the Andean region of South America (Jatala,

1991). As for many other plant pathogens, its current distribution does not necessarily reflect its true origins. This is further complicated because the main hosts for this species (e.g., tomato, chilli pepper, potato and bean) are native to the Americas and both Mexico and Peru were important centers of domestication in pre-Colombian times. *Nacobbus* has a vicariant distribution which might be explained by the isolation of South America from North America during the Tertiary Period and, interestingly, a similar vicariant distribution (Simmonds, 1976) is shown by the Chenopodiaceae species *Ch. quinoa* (Andes), *Ch. nuttalliae* (Mexico) and *Ch. pallidicaule* (Andes), the first two being hosts of *N. aberrans*. All three species are native American crops developed by Indian agriculturalists in pre-Colombian times. Therefore, with the introduction to the Americas of sugarbeet from Europe, an alternative host was provided for populations adapted to the Chenopodiaceae and that may have defined the sugarbeet race. The search for sources of resistance must be continued in wild and creole varieties of the Solanaceae in countries where *Nacobbus* occurs.

The morphometric approach has not split the species *N. aberrans* and comparison of populations from different geographical origins is indispensable to the identification of subtle variation in morphological characters. Regarding a population as sufficiently similar to be included under *N. aberrans*, *sensu lato* depends upon the experience of the taxonomist and the criteria for his or her species concept. Morphological discontinuities will be significant for the traditional taxonomist, whereas discontinuities in reproductive behavior (amphimixis, parthenogenesis) will be important for the experimentalist (Heywood, 1963). The situation is further complicated in *N. aberrans* as information on sexuality is incomplete and no attempts have been made to cross different isolates (or populations) of the parasite and define the genetics of pathogenicity.

Despite the fact that more information has been provided from studies such as scanning electron microscopy, electrophoresis, host range differences and some molecular work, the revision made by Sher (1970) has not been rejected and it seems very likely that it will continue unchanged until information on *Nacobbus* can be expanded and carefully analyzed. The need to use new molecular tools (Powers *et al.*, 1997) to study *Nacobbus* is becoming increasingly pressing.

Nacobbus aberrans is problematical on two fronts: the taxonomical and the practical. Both require a deep knowledge of the biology and ecology of the nematode and host-parasite interactions. To proceed further in developing control or management strategies requires the definition of criteria as to how these studies should be conducted in the future, in order to standardize protocols and allow comparison of results and avoid duplication. Such agreement would be very important to Latin American countries. As Thomason and Caswell (1987) have pointed out, pest management is applied ecology. There are many areas to explore and study in *N. aberrans*. Referring just to population ecology studies, Norton (1978) said: "it may take 20-50 years to learn enough about any one pathogen or disease to be confident of prediction success. It is an extremely complex undertaking, but that does not mean that we should not try." The time is ripe for an integrated, multidisciplinary, international study of *N. aberrans* for the benefit of agriculture and science.

APPENDIX: SOME USEFUL TECHNIQUES

Sampling: The objective of sampling is to provide a sample of soil from which to assess the presence and/or density of spe-

cies in a specific area. The information gained allows us to monitor the effectiveness of management practices, such as use of resistant cultivars. Several control strategies do not require a regular sampling strategy or degree of precision to be chosen but, for decisions on nematicide use, sampling is critical (Duncan, 1991). Sampling to quantify *N. aberrans* densities has been by standard procedures (Barker and Campbell, 1981; SON/ASTM, 1978). However, recommended sampling procedures differ in terms of number and size of cores to make up the sample. Specific recommendations for sampling for *N. aberrans* have not so far been provided.

Extraction procedures for soil, roots and potato tubers: Appropriate extraction procedures are essential for accurate estimation of seasonal fluctuations of nematode populations in soil. The selection of technique must be made according to the life cycle of the species under study, the motility or non-motility of the life stages, the date of sampling and other factors such as soil type. Despite various extraction procedures having been used by different authors (Table 7), information regarding extraction efficiency for *N. aberrans* is scant and limited largely to abstracts, with essential details of the procedures unpublished or unavailable (Costilla, 1972, 1985b; Arcos *et al.* 1990a, b; Franco *et al.*, 1992; Ramos *et al.*, 1998).

Franco *et al.* (1992) tested several extraction methods to quantify *N. aberrans* in soil samples and concluded that sieving and centrifugation gave the best results. Some modifications may include repeated sedimentation and sieving procedures through 325 and 500 mesh/inch sieves (Manzanilla-López, 1997). Arcos *et al.* (1990a, b), however, recovered a greater proportion of J2s using a tray method than by using sugar-flotation, but details of the procedure were not given. Sieving and centrifugation-flotation is a particularly suitable procedure for estimating the different stages in soil during crop development and throughout the nematode life cycle because it allows extraction of both motile and non-motile vermiform stages.

Maceration of root samples followed by sieving and centrifugation-flotation recovers vermiform stages from roots. However,

Table 7. Methods for extraction of *Nacobbus aberrans* from soil samples (modified from Ramos *et al.*, 1998).

Method	Author	Reference
Baermann funnel	Baermann, 1917	Caero, 1984
Centrifugation-flotation (sugar)	Caveness and Jensen, 1955	Blanco, 1992; Rivera *et al.*, 1993; Miranda *et al.*, 1994; Rivera, 1994; Alí, 1995; Flores, 1996; Lanza, 1996; Alconz, 1997
Decanting, flotation and centrifugation	Costilla, 1985b	Torrico, 1988; Fernández, 1991
Decanting and sieving	Cobb, 1918	Caero, 1984
Flotation-centrifugation	Gooris and D'Herde, 1972	Montecinos, 1991
Flotation, flocculation and sieving using sugar and Separan®[1]	Byrd, Nusbaum and Barker, 1966	Caero, 1984
"Pocillo" (coffee pot)	Canto-Saenz, 1986, cited by Ortuño, 1990	Ortuño, 1990
Trays	Whitehead and Hemming, 1965	Caero, 1984

[1]Separan is no longer available in the market but good results can be obtained by adding aluminium sulphate (15 µl/200 ml) to 200 g of soil (Manzanilla-López, unpublished).

greater numbers of young females, males and J2s were recovered from roots processed in a mist chamber than with the former method (Manzanilla-López, 1997). The increase in J2 recovery could be due either to their motility or to hatching from eggs retained in the root tissue. Males and young females are motile stages capable of moving to the surface of the root where they are washed off by the mist droplets. Other authors (Arcos *et al.*, 1990a), however, recovered more females by blending root pieces than from using a mistifier method. The J3 and J4 (which are less motile stages) are extracted in greater numbers from roots by means of the maceration-sieving-centrifugation technique than the mist chamber. Costilla (1985b) obtained similar results with potato tubers. A summary of techniques used to extract stages from roots is given in Table 8.

Detection of *N. aberrans* in potato tubers and other tuber crops is very important for regulatory and seed certification purposes. Numbers and sizes of samples to be processed depend on the severity of the nematode infestation as shown in the section on quarantine measures. Potatoes and other tuber crops grown to produce certified seed tubers should not be planted in areas of known *N. aberrans* infestation. All nematode life stages can be extracted from potato tubers by maceration-filtration (Costilla, 1972; Hooper, 1986). This technique involves the maceration in water of sections of peeled tuber skin (0.5 mm thick) in a blender. The resulting suspension is poured through a series of sieves of decreasing aperture. The tuber skin debris are separated from the suspension and caught on 250 or 150 µm-aperture sieves. Dislodged nematodes and small debris are caught on smaller aperture sieves (45 µm). However, the nematode suspension recovered from the small aperture sieve contains starch particles that make the suspension turbid and unfit for microscopical examination. Heating the starch-nematode suspension almost to boiling point solubilizes the starch and decreases the turbidity (Costilla, 1985b). Nematodes in the starchy suspension can also be made more visible by adding 15 ppm (15 mg/l) phloxine B aqueous solution (1 part of nematode suspension to 4 parts of stain solution) and by heating again almost to boiling point. Heating facilitates staining of moribund or dead nematodes (Costilla, 1985b). The

Table 8. Methods for extraction of *Nacobbus aberrans* from root samples (modified from Ramos *et al.*, 1998).

Method	Author	Reference
Blender*	Costilla, 1985b	Ibarra *et al.*, 1992; Rivera *et al.*, 1993; Miranda *et al.*, 1994; Rivera, 1994; Alí, 1995; Durán *et al.*, 1995; Lanza, 1996
Blending and centrifugation (sugar)	Taylor and Loegering, 1953; Costilla, 1985b	Ortuño, 1990; Blanco, 1992
Clearing and staining of plant tissues	Byrd, Kirkpatrick and Barker, 1983	Manzanilla-López, 1997
Maceration-centrifugal-flotation	Coolen and D'Herde, 1972	Manzanilla-López, 1997
Root-incubation	Hooper, 1986	Manzanilla-López, 1997
Staining of root tissues	Hooper, 1986	Caero, 1984, Manzanilla-López, 1997
Mist chamber	Hooper, 1986	Manzanilla-López, 1997

*Can also be used for skins of tubers.

stained nematode suspension can be examined directly in Petri dishes with the aid of a stereo or compound microscope. Adding small drops of detergent to the suspension facilitates microscopical examination of un-stained nematodes.

Bioassays: Nacobbus aberrans occurs in soil not only as eggs (in egg masses) as in root-knot nematodes, but also as juveniles (J2, J3, J4) and young adults. Two methods can be used to estimate the population density of root knot nematodes in infested soil. Either the different stages are extracted from soil directly, or a host plant is grown in the soil to assess the number that invade the roots, but neither method includes all the individuals potentially able to attack the roots (Franklin *et al.*, 1971). Detection and quantification of *N. aberrans* in soil samples can be extremely difficult. Estimates of population density from root invasion are affected by the need for resting stages in soil to be re-activated in order to invade roots and produce galls. This re-activation is best achieved in bioassays that provide appropriate conditions of humidity, temperature and a host (Franco *et al.*, 1992). Bioassays are also used to estimate nematode populations because they are less affected by motility of life stages and date of sampling (Barker *et al.*, 1969). *Nacobbus aberrans* activity is stimulated when soil samples are subjected to a cold or dry regime (CIP, 1992, 1995). Soil pretreatment with low temperature (5°C 3 days), water (20°C 3 days), or potato root exudate accelerates gall formation (Franco *et al.*, 1992). Soaking the egg masses in water (5°C 5 days) followed by incubation in water increases the hatching of J2s (Manzanilla-López, 1997). Veremis *et al.* (1997) noted that chilling combined with drought increased J2 infectivity.

Scales of severity of attack: Values for degrees of root infection have been given according to galling percentage, number of galls on roots taken from the field, or numbers of galls produced in bioassays. Some authors refer to severity not by using numbers of galls but by the numbers of infective stages present in 100 g of soil. Visual estimation of damage has practical implications as it is less time-consuming than processing individual samples of soil or roots. Therefore, the use of scales is a common method to assess *N. aberrans* severity and damage. A combination of such scales was produced by Ramos *et al.* (1998) in an attempt to standardize the assessment of infestations (Table 4). However, scales are qualitative rather than quantitative, and may be confusing as they vary according to author. It would be better if they could be replaced by a quantitative approach.

Scales have been used also to estimate soil infestations of *N. aberrans* by considering the number of galls produced on bait plants in a bioassay. Bioassay figures for *N. aberrans* densities are very similar to estimates made by soil extraction (Ramos *et al.*, 1998), but other quantitative methods, such as the use of immunoassays, produce more accurate and faster results and have already been tested with some *Nacobbus* populations and different stages of development of the nematode (Evans *et al.*, 1997; Manzanilla-López, 1997). The ability of *Nacobbus aberrans* to multiply in Petri dishes containing excised roots (e.g., potato or tomato) grown in culture medium can be used to shorten the time for screening and selection of resistant individual plants in resistance breeding programmes (González *et al.*, 1991).

ACKNOWLEDGMENTS

The authors thank Dr. Nancy Coile for providing Latin names and authorities for plant taxa, Dr. David Hunt for similar assistance with nematode taxa and much additional help, M. C. Gladis Castillo Ponce for

permission to use her illustrations of the histopathology of *Nacobbus aberrans* on chilli pepper, CONACYT (Mexico) for generous financial assistance and the British Council for their support of the intensive period of literature searching. Rothamsted receives grant-aided support from the Biotechnology and Biological Sciences Research Council of the United Kingdom. Thanks are also due to numerous additional colleagues who have provided useful information. Finally, and with great sadness, we would like to acknowledge the invaluable contributions made to the compilation of the review by our co-author Miguel Costilla. His intimate knowledge of the problems caused by *Nacobbus* was acquired through many years of working with the nematode and the farmers who suffered from its effects. We, like they and many others, will miss him greatly, and we dedicate this review to his memory.

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Received: *2.XI.2002*

Recibido:

Accepted for publication: *13.I.2003*

Aceptado para publicacion:

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