

Occurrence and Pathogenicity of Root-Knot Nematodes (*Meloidogyne* species) in South African Vineyards¹

J.T. Loubser

Viticultural and Oenological Research Institute, Private Bag X5026, 7600 Stellenbosch, Republic of South Africa

Date submitted for publication: July 1988

Date accepted for publication: August 1988

Keywords: Root-knot nematodes, *Meloidogyne*, grapevine.

The occurrence of root-knot nematodes (*Meloidogyne* species) in viticultural regions of South Africa was determined. *Meloidogyne javanica* constituted 73,2% of all species identified while *M. arenaria* (17,0%), *M. incognita* (7,1%) and *M. hapla* (2,7%) were also found. The relative frequency of species in the various regions differed widely, with *M. incognita* more prominent in the warm inland regions. Experiments on different rootstock cultivars showed that all four species were able to infest susceptible rootstocks while none of them could infest cultivars known to be resistant to root-knot nematodes. *Meloidogyne incognita* and *M. javanica*, however, were found to be more pathogenic than the other two species. *Meloidogyne incognita* also showed a higher pathogenicity at 33°C than *M. javanica*, while results demonstrated a breakdown of rootstock resistance at this temperature. It could not be verified by short-term pot trials that a sandy soil type enhance the degree of root-knot nematode infestation.

The majority (95%) of root-knot nematode populations found on agricultural crops belongs to only four species, viz. *Meloidogyne incognita* (47%), *M. javanica* (40%), *M. arenaria* (7%) and *M. hapla* (6%) (Taylor, Sasser & Nelson, 1982). Surveys on the occurrence of these and other species on grapevines, done before the redescription of the genera by Chitwood (1949), are of little value, while only a few surveys have been done since.

The root-knot nematode species on grapevines were best studied in Australia. The distribution and relative importance of the four major species in the different viticultural regions have been reported by several researchers (Seinhorst & Sauer, 1956; Sauer, 1962; 1967; 1977; Meagher, 1969; Stirling, 1976; Stirling & Crami, 1984). *Meloidogyne javanica* was the dominant species.

The occurrence of *Meloidogyne* species on vineyards in the USA was documented by Lider (1954; 1960), Raski, Hart & Kasimatis (1965), Raski, Schmitt & Hemstreet (1973), Siddiqui, Sher & French (1973) and Hafez, Raski & Kheir (1981). *Meloidogyne incognita*, *M. javanica* and *M. arenaria* is widespread and *M. incognita* is the most common species in California.

According to Boubals (1954; 1979) and Dalmasso & Cuany (1976), *M. incognita* and *M. hapla* were found in French vineyards but the relative importance of these species was not mentioned. Results from other countries are limited. Conzales (1970) reported that *M. incognita* was found in Chile while Darekar, Patil & Patil (1985) conducted experiments in India to control the "dominant" species, *M. incognita*.

In South Africa Smith (1977) found root-knot nematodes in 77% of all vineyards sampled but did not identify the species. Coetzee (1968) reported that the four major species occurred in the Western Cape and identified *M. javanica* on grapevines.

With regard to the relative importance of the four major species on grapevines, little research has been done. It is often reported in literature that a certain species is dominant in a specific region, but this does not necessarily reflect its virulence. Furthermore, several reports have shown that populations of the same species from different regions may differ in pathogenicity towards grapevines and other hosts (Dalmasso & Cuany, 1976; Dropkin, 1980; Cain, McKenry & Tarallo, 1984). Chitamber & Raski (1984) reported that *M. incognita*, *M. javanica* and *M. arenaria* infest grapevine cultivars to various degrees in glasshouse experiments. However, the differences in pathogenicity recorded in this experiment were shown to vary between cultivars, with time and with temperature. Predicting pathogenicity of these species under field conditions, using these results, is therefore not possible.

In two climatically different regions of South Africa *M. incognita* and *M. javanica* populations on grapevines showed a similar cyclic annual fluctuation (Loubser & Meyer, 1987b). *Meloidogyne incognita* populations, however, reached higher levels of infestation than that of *M. javanica* on the same rootstock. It is known that several climatic factors have a direct or indirect influence on the biological activities of *Meloidogyne* species (De Guiran & Ritter, 1979; Ferris & Van Gundy, 1979; Freckman & Caswell, 1985; Van Gundy, 1985). Temperature and soil type, two of the major factors involved, differed substantially between the two vineyards studied by Loubser & Meyer (1987b). Together with species differences, these factors may influence infestation severity in the different regions.

In the present study a survey was done in the different South African viticultural regions to identify the root-knot nematode species associated with grapevines. The pathogenicity of the species found at Vaalharts and

The assistance of Dr K.P.N. Kleynhans of the Plant Protection Research Institute, Pretoria, in identifying the nematode species, and the technical assistance of Miss E. C. du Toit, are gratefully acknowledged.

1. Part of a thesis submitted to the University of Stellenbosch for the Ph.D. (Agric.) degree.

Bien Donn , and other major species, was investigated. Furthermore, the effect of soil type and temperature was studied in order to explain differences in infestation severity and population numbers between regions as were found by Loubser & Meyer (1987b).

MATERIALS AND METHODS

1. Occurrence of *Meloidogyne* species

Grapevine roots and soil samples were collected from major grapevine regions of South Africa (Fig. 1). A total of 121 samples were examined: 80 soil samples from randomly selected farms and 41 root samples from grapevine nurseries. Each soil sample was mixed in a 3:1 (v/v) ratio of soil and sterile peat moss and two plastic planting bags (200 x 100 mm) filled with this mixture. A nematode-free tomato seedling (var. Money-maker) was planted in each bag and grown in a glasshouse at approximately 25 C. After two months the plants were removed and galled roots collected.

The *M. incognita* and *M. javanica* populations from Vaalharts and Bien Donn  respectively, studied by Loubser & Meyer (1987b), were both included.

2. Pathogenicity of *Meloidogyne* species

Eight rootstock cultivars of variable susceptibility to root-knot nematodes (Loubser & Meyer, 1987a) were used to determine the pathogenicity of the four species. An inoculum of approximately 2 000 larvae, suspended in sterile water, was pipetted into holes (ca. 25 mm deep) around the stems of each rootstock one month after their being planted in a sterile sand-peat moss mixture. Replication was tenfold. Plants were grown under natural light conditions at temperatures ranging between 19 C and 29 C.

After 65 days the plants were lifted and the number of galls and egg sacs per 5 g roots counted. The number of eggs extracted from the same root mass (Hussey & Barker, 1973), gave an indication of reproduction.

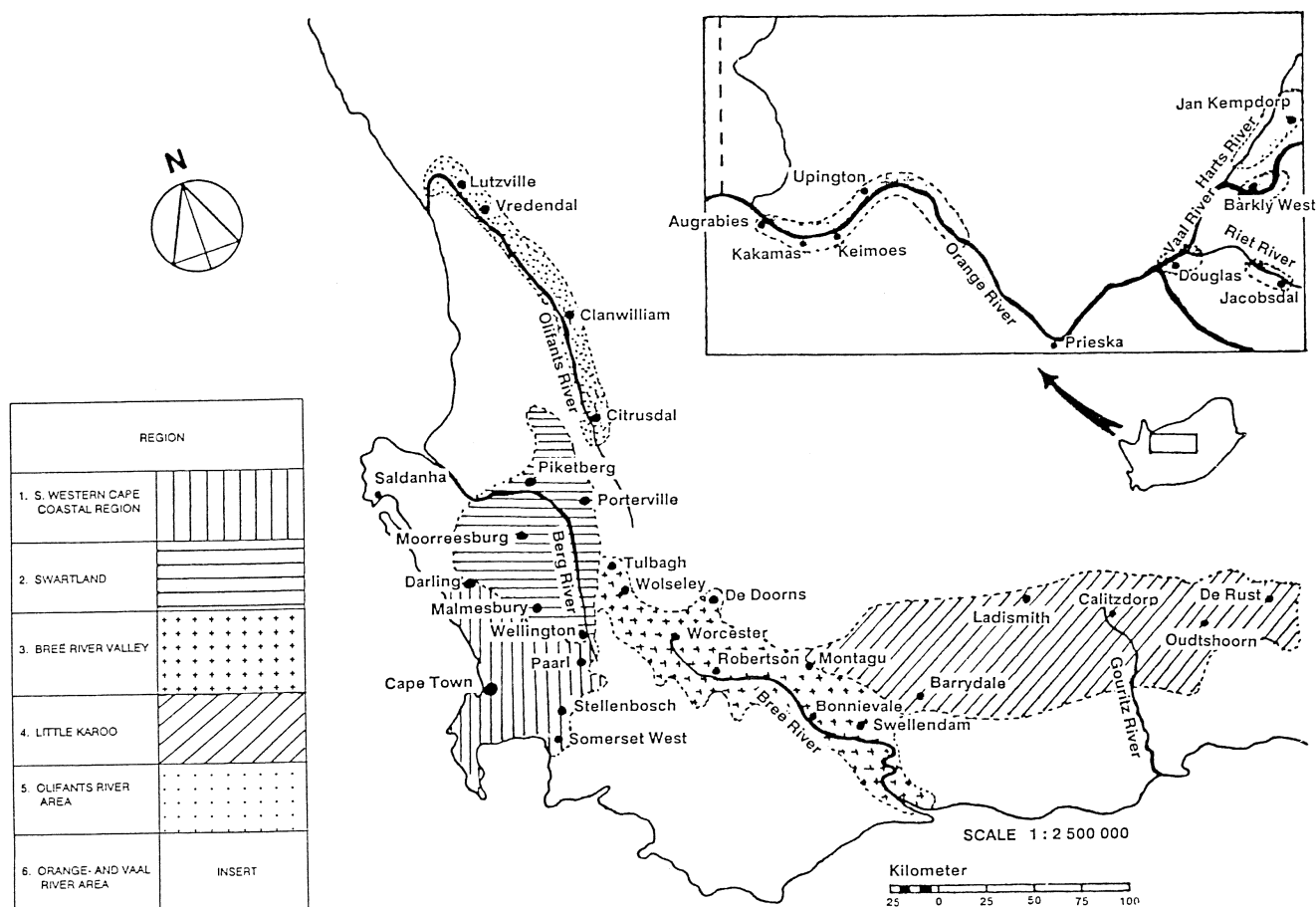


FIG. 1

Major grapevine growing regions of South Africa.

Infested tomato roots, as well as the grapevine roots collected from nurseries, were microscopically dissected for adult males and females which were then identified using the techniques described by Taylor & Netscher (1974), Hartman & Sasser (1985) and Eisenback *et al.* (1981). The four species used in further experiments were additionally subjected to the North Carolina differential host test (Taylor & Sasser, 1978) to verify the identifications and to determine the races

3. Effect of soil type and temperature on the pathogenicity of *M. javanica* and *M. incognita*

3.1 Soil type

Two-bud cuttings of 140 Ruggeri (*Vitis Berlandieri* x *Vitis rupestris*) classified as susceptible by Loubser & Meyer (1987a), were rooted in a sterile potting mixture and subsequently planted in the different soil types (Table 1) in plastic bags (200 x100 mm). The two soil

types used were collected from the experimental sites at Vaalharts and Bien Donn  which were studied by Loubser & Meyer (1987b). Both soils were steam sterilised four weeks before use.

TABLE 1

Characteristics of Bien Donn  and Vaalharts soils used in pot trials with *M. javanica*.

| Soil Type | Sand (%) | | | Silt (%) | Clay (%) | pH (KCl) | R (ohm) |
|-------------------------|----------|--------|--------|----------|----------|----------|---------|
| | Fine | Medium | Coarse | | | | |
| Sandy-loam (Bien Donn ) | 24,4 | 30,1 | 11,1 | 18,3 | 16,1 | 4,2 | 3933 |
| Loamy-sand (Vaalharts) | 73,2 | 16,5 | 0,9 | 1,0 | 8,4 | 5,6 | 1900 |

Eighteen plants in each soil type were inoculated with *M. javanica* larvae as described above. Plants were kept in a glasshouse at 25 C. Six plants were evaluated after 33, 63 and 98 days respectively with regard to new root mass (expressed as a percentage of the total root mass), number of galls and egg sacs per 5 g of new roots and number of eggs per egg sac.

3.2 Temperature

Three rootstock cultivars, viz. Jacquez (*Vitis aestivalis* x *Vitis cinerea* x *Vitis vinifera*), 143 B Mgt (*Vitis vinifera* x *Vitis riparia*) and 99 Richter (*V. Berlandieri* x *V. rupestris*) were employed in this experiment because they were designated susceptible (Jacquez) and moderately resistant (143 B Mgt and 99 Richter) by Loubser & Meyer (1987a). Forty plants of each were planted in a sterile potting mix in plastic bags and grown in a glasshouse at 25 C for two months. Twenty plants per rootstock were subsequently inoculated with approximately 2 000 larvae each of *M. javanica* or *M. incognita* as described before. Ten plants of each treatment were grown at 23 C while the other ten were grown at 33 C. Plants were kept under similar light conditions.

Evaluation was done after a pre-determined biological time lapse according to the number of heat units as described by Tyler (1933). Five plants of each treatment were lifted after 44 days and the rest after 78 days. The number of galls and egg sacs per 5 g of roots as well as the number of eggs per egg sac were recorded as before.

All grapevine plants used in the experiments were regularly watered with a standard nutrient solution. An analysis of variance was done on the data.

RESULTS AND DISCUSSION

1. Occurrence of *Meloidogyne* species

Root-knot nematodes were present in 31 of the 41 root samples (76%) and 69 of the 80 soil samples (86%). Results of the species distribution in the different regions are shown in Table 2.

Meloidogyne javanica constituted 73,2% of all populations while *M. arenaria*, *M. incognita* and *M. hapla* represented 17,0%, 7,1% and 2,7% respectively. This relative frequency differs from the worldwide distribution reported by Taylor *et al.* (1982), although the dominance of *M. javanica* agrees with observations in

the warmer regions of Australia (Stirling & Ciri mi, 1984).

Between regions there was a marked difference in species distribution. Only *M. javanica* was found in the Olifants River area (Region 5). Region 6, which includes five separate areas, is the warmest viticultural region of South Africa. Here the relative frequency of species more closely resembled that of Taylor *et al.* (1982), but *M. javanica* was still dominant. The occurrence of *M. hapla* in region 6 was unexpected since it is generally considered a cold region species (Taylor *et al.*, 1982) and was also found in the cooler districts of Australia (Stirling & Ciri mi, 1984).

The four species used in further experiments were identified by the North Carolina differential host test (Taylor & Sasser, 1978) as *M. incognita* (race 4), *M. javanica*, *M. arenaria* (race 2) and *M. hapla*.

2. Pathogenicity of *Meloidogyne* species

Infestation of grapevine rootstocks by the four species is shown in Table 3. *Meloidogyne javanica* and *M. incognita* were significantly more pathogenic than *M. arenaria* and *M. hapla*.

Chitambar & Raski (1984) showed that *M. incognita* became more pathogenic with time and according to their results this species was the most aggressive after 90 days, followed by *M. javanica* and *M. arenaria*. From their results, however, it can also be deduced that *M. arenaria* was the most pathogenic species if evaluations were made after 45 days at 36 C. This stresses the importance of a sufficient time lapse before final evaluations are made. The present findings were recorded after 65 days which were regarded as sufficient for the development of two generations according to the data supplied by Ferris & Hunt (1979).

Rootstock resistance as designated by Loubser & Meyer (1987a) applies only if the average infestation for all four species is considered. The high, albeit not significant, infestation of 140 Ruggeri, 110 Richter and 143 B Mgt by *M. arenaria* in comparison with other species, is noteworthy. Evaluating these rootstocks for resistance by using *M. incognita*, or evaluating any rootstock by using the *M. hapla* population utilised in this experiment, would have led to a different resistance classification.

Although the present study was conducted at ambient temperatures, the fact that *M. hapla* appears to be the least pathogenic species may be indicative of a too high average temperature for this species. It must also be emphasized that the above results were obtained with a specific nematode population of each species. According to Dalmasso & Cuany (1976), *M. hapla* populations from different regions in France varied in their pathogenicity to grapevine. Netscher & Taylor (1979) also found that certain *Meloidogyne* populations were able to break down the resistance of certain host plants, thus increasing its host range. The present findings, therefore, illustrated differences between the populations tested and further trials should be conducted to verify the recorded differences between species.

No explanation was found for the larger *M. incognita* populations recorded by Loubser & Meyer (1987b) in the Vaalharts plot compared to *M. javanica* at Bien Donn . On the contrary, the latter species showed

TABLE 2Occurrence of *Meloidogyne* species in the grapevine growing regions of South Africa.

| Region ¹ | Number of samples collected/infested | Number of populations ² | | | | Total |
|-----------------------------------|--------------------------------------|------------------------------------|--------------------|---------------------|-----------------|-------|
| | | <i>M. javanica</i> | <i>M. arenaria</i> | <i>M. incognita</i> | <i>M. hapla</i> | |
| 1. S. Western Cape Coastal Region | 29/25 | 23 (88%) | 3 (12%) | 0 (-) | 0 (-) | 26 |
| 2. Swartland | 15/13 | 10 (63%) | 4 (25%) | 1 (6%) | 1 (6%) | 16 |
| 3. Breë River Valley | 34/27 | 22 (67%) | 9 (27%) | 1 (3%) | 1 (3%) | 33 |
| 4. Little Karoo | 16/9 | 7 (78%) | 2 (22%) | 0 (-) | 0 (-) | 9 |
| 5. Olifants River Area | 13/12 | 12 (100%) | 0 (-) | 0 (-) | 0 (-) | 12 |
| 6. Orange and Vaal River Area | 14/14 | 8 (50%) | 1 (6%) | 6 (38%) | 1 (6%) | 16 |
| Total | 121/100 | 82 (73,2%) | 19 (17,0%) | 8 (7,1%) | 3 (2,7%) | 112 |

1. See Fig. 1 for location of regions in South Africa.

2. The percentage each species constitutes of the total number of populations, is shown in brackets.

TABLE 3Pathogenicity of *Meloidogyne* species to different grapevine rootstocks.

| Rootstock | Measure-ment | Infestation ¹ | | | | Average for rootstocks |
|--|--------------|--------------------------|---------------------|-----------------|--------------------|------------------------|
| | | <i>M. javanica</i> | <i>M. incognita</i> | <i>M. hapla</i> | <i>M. arenaria</i> | |
| US 3-6 | G | 46,8 a | 116,0 b | 10,2 c | 13,0 ac | 46,5 |
| | S | 29,2 | 53,0 | 2,6 | 1,0 | 21,5 |
| | E | 482,4 a | 566,0 a | 39,4 b | 21,0 b | 277,2 |
| Jacquez | G | 73,2 a | 40,4 ac | 10,2 bc | 3,2 b | 31,8 |
| | S | 25,2 | 9,2 | 1,2 | 1,6 | 9,3 |
| | E | 180,6 | 238,0 | 73,8 | 26,4 | 129,7 |
| 140 Ruggeri | G | 12,2 | 1,0 | 3,0 | 17,8 | 8,5 |
| | S | 6,6 | 0,8 | 3,0 | 6,4 | 4,2 |
| | E | 45,6 | 23,6 | 9,6 | 205,6 | 71,1 |
| 110 Richter | G | 2,2 | 3,0 | 1,0 | 26,2 | 8,1 |
| | S | 0,8 | 1,8 | 0 | 13,4 | 4,0 |
| | E | 4,4 | 5,3 | 3,0 | 113,0 | 31,4 |
| 143 B Mgt | G | 0,8 | 0,4 | 0 | 8,8 | 2,5 |
| | S | 0,8 | 0,4 | 0 | 4,0 | 1,3 |
| | E | 26,4 | 5,0 | 3,6 | 111,2 | 36,3 |
| 101-14 Mgt | G | 1,2 | 0 | 0,8 | 1,0 | 0,8 |
| | S | 0,6 | 0 | 0 | 0,6 | 0,3 |
| | E | 7,4 | 2,0 | 2,4 | 3,7 | 3,9 |
| Ramsey | - | 0 | 0 | 0 | 0 | 0 |
| 99 Richter | - | 0 | 0 | 0 | 0 | 0 |
| Average for species (infested rootstocks only) | G | 22,7 a | 26,8 a | 4,2 b | 11,7 b | |
| | S | 10,5 a | 10,9 a | 0,7 b | 4,5 b | |
| | E | 124,5 a | 140,0 a | 22,0 b | 80,2 b | |

1. Measurements which differ significantly ($P \leq 0,05$) between species are marked with different letters

G: Average number of galls per 5 g of roots

S: Average number of egg sacs per 5 g of roots

E: Average number of eggs ($\times 10^2$) per 5 g of roots

higher (albeit not significant) galling and reproduction on Jacquez (the rootstock involved in both studies) than *M. incognita* (Table 3). Soil and climatic conditions were, therefore, suspected to have played a major role.

3. Effect of soil type and temperature on the pathogenicity of *M. javanica* and *M. incognita*

3.1 Soil type

Root growth of 140 Ruggeri did not differ significantly between soil types. No significant differences in infestation (galling) between soil types were recorded (Table 4), suggesting that soils with a clay content of 16,1% and 8,4% (Table 1) do not differ in their suitability for root-knot nematode infestation. Observations made by several researchers show that root-knot nematode infestation is higher in sandy soils (Sauer, 1962; Ferris & McKenry, 1974; Stirling, 1976; Smith, 1977). The seemingly contradictory results of the present study can possibly be ascribed to differences between glasshouse and field conditions. On the other hand, if all texture parameters (Table 1) are considered, both the soils can be designated as sandy types. The present results supply no explanation for the differences measured at Vaalharts and Bien Donné by Loubser & Meyer (1987b).

3.2 Temperature

No infestation by *M. javanica* was recorded on 99 Richter and it was therefore not included in Table 5. Root mass did not differ significantly between treatments for the other two rootstocks and for further discussions it was assumed that root growth had no effect on the degree of infestation. The number of galls and egg sacs of *M. javanica* increased with time and temperature on both rootstocks, although not significantly in all cases (Table 5). This increasing infestation with time can be ascribed to normal population increase with increasing degree days (Tyler, 1933). Furthermore, pathogenicity as measured by the degree of galling, also appeared to increase with increasing temperature. This was more evident on the moderately resistant rootstock 143 B Mgt where the number of eggs increased significantly (and galling apparently also) between treatments B and C, irrespective of the number of degree days which remained the same. The reason for this was seen as a breakdown in resistance at the higher temperature. Chitambar & Raski (1984) also found that the grapevine rootstock cultivars Harmony and Couderc 1613 lost their resistance at 36°C. Similar observations were made on other hosts (Holzman, 1965; Dropkin, 1969; Araujo *et al.*, 1982).

Similar to *M. javanica*, *M. incognita* infestation in-

TABLE 4

Effect of soil type on root growth of 140 Ruggeri and infestation by *Meloidogyne javanica*

| Soil Type | New root mass (%) | | | Galls per 5 g of new roots | | | Egg sacs per 5 g new roots | | | Eggs per egg sac | | |
|-------------------------|-------------------|---------|---------|----------------------------|---------|---------|----------------------------|---------|---------|------------------|---------|---------|
| | 33 days | 63 days | 98 days | 33 days | 63 days | 98 days | 33 days | 63 days | 98 days | 33 days | 63 days | 98 days |
| Sandy-loam (Bien Donné) | 33 | 43 | 57 | 14 | 80 | 68 | 2 | 53 | 49 | 398 | 801 | 840 |
| Loamy-sand (Vaalharts) | 14 | 18 | 37 | 33 | 31 | 72 | 8 | 14 | 52 | 363 | 753 | 810 |

No significant differences ($P \leq 0,05$) were found between soils

TABLE 5

Effect of temperature on root growth and infestation of grapevine rootstocks by *Meloidogyne javanica*

| Treatment | Jacquez | | | | 143 B Mgt | | | |
|---|-------------------------------|----------------------|-----------------------|-------------------|-------------------------------|----------------------|-----------------------|-------------------|
| | Root mass ¹ (g) | Galling ² | Egg sacs ³ | Eggs ⁴ | Root mass ¹ (g) | Galling ² | Egg sacs ³ | Eggs ⁴ |
| A. 23°C/44 days (572DD ₁₀) | 5,4 a | 16,2 a | 5,2 a | 460 a | 4,2 a | 1,2 a | 0 a | 0 a |
| B. 23°C/78 days (1014DD ₁₀) | 5,4 a | 62,6 ab | 22,2 a | 560 a | 3,6 a | 2,0 a | 2,0 a | 75 a |
| C. 33°C/44 days (1012DD ₁₀) | 4,4 a | 41,2 ab | 14,6 a | 464 a | 3,5 a | 66,6 ab | 16,6 a | 396 b |
| D. 33°C/78 days (1794DD ₁₀) | 3,2 a | 613,2 b | 613,2 b | 855 b | 3,2 a | 230,6 b | 220,6 b | 825 b |

Treatments which differ significantly ($P \leq 0,05$) are marked vertically with different letters

1. Root mass is the average mass of all new roots
2. Galling is expressed by the number of galls visible per 5 g of new roots under 20 x magnification
3. Egg sacs are expressed by the number visible per 5 g new roots under 20 x magnification
4. Eggs are the average number calculated per egg sac

DD₁₀: Physiological time expressed as degree-days above a predetermined threshold of 10°C

creased both with time and temperature on all rootstock cultivars (Table 6). In this case the resistant rootstock 99 Richter as well as 143 B Mgt became infested to a high degree at 33°C, indicating a breakdown of resistance at the higher temperature. The rate of reproduction (number of eggs) increased substantially between treatments B and C for these two rootstocks. The increase was significant only on 99 Richter.

two soils used did not differ enough with regard to clay content to have influenced nematode infestation of grapevines. On the other hand, root distribution, moisture and temperature fluctuations in the pots must have differed from those in the field and nematode activities were probably not affected to the same degree.

Temperature was important in nematode development and severity of galling and resistance breakdown

TABLE 6

Effect of temperature on root growth and infestation of grapevine rootstocks by *Meloidogyne incognita*

| Treatment | Jacquez | | | | 143 B Mgt | | | | 99 Richter | | | |
|--|-------------------------------|----------------------|-----------------------|-------------------|-------------------------------|----------------------|-----------------------|-------------------|-------------------------------|----------------------|-----------------------|-------------------|
| | Root mass ¹ (g) | Galling ² | Egg sacs ³ | Eggs ⁴ | Root mass ¹ (g) | Galling ² | Egg sacs ³ | Eggs ⁴ | Root mass ¹ (g) | Galling ² | Egg sacs ³ | Eggs ⁴ |
| A. 23°C/44 days (572DD ₁₀) | 5,6 a | 21,4 a | 10,2 a | 675 a | 4,8 a | 2,2 a | 1,4 a | 107 a | 5,4 a | 0 a | 0 a | 0 a |
| B. 23°C/78 days (1014DD ₁₀) | 5,2 a | 96,8 a | 103,4 a | 657 a | 5,2 a | 24,4 a | 17,6 a | 334 ab | 5,9 a | 0 a | 0 a | 0 a |
| C. 33°C/44 days (1012DD ₁₀) | 4,8 a | 29,8 a | 11,2 a | 542 a | 4,6 a | 26,8 a | 17,8 a | 506 ab | 5,0 a | 24,4 a | 18,6 a | 473 b |
| D. 33°C/78 days (1794DD ₁₀) | 4,1 a | 753,6 b | 753,6 b | 980 a | 4,4 a | 530,2 b | 518,2 b | 621 b | 4,6 a | 218,8 b | 283,2 b | 721 b |

Treatments which differ significantly ($P \leq 0,05$) are marked vertically with different letters

1. Root mass is the average mass of all new roots
2. Galling is expressed by the number of galls visible per 5 g of new roots under 20 x magnification
3. Egg sacs are expressed by the number visible per 5 g new roots under 20 x magnification
4. Eggs are the average number calculated per egg sac

DD₁₀: Physiological time expressed as degree-days above a predetermined threshold of 10°C

The higher degree of galling recorded for the *M. incognita* population, proved it was more pathogenic to grapevines at 33°C than *M. javanica*. These two species were isolated from the two populations investigated at Vaalharts (Region 6) and Bien Donné (Region 1) by Loubser & Meyer (1987b). The present results, therefore, indicated that the population differences recorded in the mentioned study can be ascribed to a higher pathogenicity of *M. incognita*. According to the present results on the effect of temperature, population differences in that study can also be explained by the higher number of heat units in the warmer region. Furthermore, the breakdown of resistance at the higher soil temperature recorded in this study, may provide further explanation for the differences in infestation and soil populations recorded in the above-mentioned two regions.

CONCLUSIONS

Root-knot nematodes were found in most vineyards in the major viticultural regions of South Africa. The most common species was *M. javanica* while the other three major species were all present, although not in the same relative frequency as was found in other countries. Results showed that species differed in their pathogenicity to grapevine rootstocks, with *M. incognita* the most pathogenic, followed by *M. javanica*. All species were, however, able to infest susceptible cultivars but not one was capable of infesting the resistant rootstock, Ramsey.

Observations that sandy soils are more favourable for root-knot nematode infestation, could not be verified in the present pot trial. This may indicate that the

occurred at a high temperature. The results of this study have supplied evidence to explain the differences in population numbers between *M. incognita* and *M. javanica* recorded in a previous field experiment.

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