

Root-knot Nematodes

Edited by

Roland N. Perry

*Plant Pathology and Microbiology Department, Rothamsted Research,
Harpenden, Hertfordshire, UK and Biology Department,
Ghent University, Ghent, Belgium*

Maurice Moens

*Institute for Agricultural and Fisheries Research,
Merelbeke, Belgium and Department of Crop Protection,
Ghent University, Ghent, Belgium*

and

James L. Starr

*Department of Plant Pathology and Microbiology, Texas A&M University,
College Station, USA*



www.cabi.org

Contents

About the Editors	xix
Contributors	xxi
Preface	xxv
1 Meloidogyne species – a Diverse Group of Novel and Important Plant Parasites	1
<i>Maurice Moens, Roland N. Perry and James L. Starr</i>	
1.1 Introduction	1
1.2 Impact	2
1.3 History of the Genus	2
1.4 Current Trends in Species Identification	2
1.5 Life Cycle	3
1.5.1 Incompatible host reactions	6
1.6 Diversity in Biology	6
1.6.1 Concept of host races	7
1.7 Major and Emerging Species	8
1.7.1 <i>Meloidogyne enterolobii</i> (= <i>Meloidogyne mayaguensis</i>)	9
1.7.2 <i>Meloidogyne paranaensis</i>	9
1.7.3 <i>Meloidogyne fallax</i> and <i>Meloidogyne chitwoodi</i>	10
1.7.4 <i>Meloidogyne minor</i>	11
1.8 Interactions with Other Plant Pathogens	11
1.9 Management and Control	11
1.10 Conclusions and Future Directions	12
1.11 References	13
2 General Morphology	18
<i>Jonathan D. Eisenback and David J. Hunt</i>	
2.1 General Morphology	18
2.1.1 Second-stage juvenile	19
2.1.2 Male	21
2.1.3 Female	21
2.1.4 Egg	22

2.2 Body Wall	23
2.2.1 Cuticle	23
2.2.2 Hypodermis	33
2.2.3 Somatic muscles	34
2.3 Nervous System	37
2.3.1 Cephalic sensory structures	39
2.3.2 Caudal sensory structures	40
2.4 Digestive System	40
2.4.1 Stoma and pharynx	40
2.4.2 Intestine	42
2.4.3 Rectum	42
2.5 Secretory-Excretory System	42
2.6 Reproductive System	43
2.6.1 Second-stage juvenile	43
2.6.2 Male	43
2.6.3 Female	44
2.7 Morphological Methods	44
2.8 Minimum Standards for Describing a New Species	44
2.8.1 The text	45
2.8.2 The figures	47
2.9 References	50
3 Taxonomy, Identification and Principal Species	55
<i>David J. Hunt and Zafar A. Handoo</i>	
3.1 Introduction	55
3.1.1 History	55
3.1.2 Major reference sources	60
3.1.3 Rate of species descriptions	60
3.1.4 Recent advances in characterization	61
3.2 Systematic Position	61
3.3 Subfamily and Genus Diagnosis	61
3.4 List of Species and Synonyms	63
3.5 Identification	67
3.5.1 General techniques	67
3.5.2 Perineal pattern	68
3.5.3 Root staining	68
3.5.4 Scanning electron microscopy	68
3.5.5 Diagnostic characters	68
3.5.6 Root-knot or cyst-forming nematode?	70
3.5.7 Differential host test	70
3.5.8 Gall form	70
3.5.9 Isozyme phenotyping	72
3.5.10 Molecular diagnostics	72
3.6 Principal Species	72
3.6.1 <i>Meloidogyne arenaria</i>	72
3.6.2 <i>Meloidogyne hapla</i>	74
3.6.3 <i>Meloidogyne incognita</i>	74
3.6.4 <i>Meloidogyne javanica</i>	74
3.6.5 <i>Meloidogyne acranea</i>	77
3.6.6 <i>Meloidogyne chitwoodi</i>	79
3.6.7 <i>Meloidogyne enterolobii</i>	80

3.6.8 <i>Meloidogyne ethiopica</i>	80
3.6.9 <i>Meloidogyne exigua</i>	80
3.6.10 <i>Meloidogyne fallax</i>	84
3.6.11 <i>Meloidogyne graminicola</i>	84
3.6.12 <i>Meloidogyne paranaensis</i>	84
3.7 Conclusions and Future Directions	88
3.8 Acknowledgements	88
3.9 References	88
4 Biochemical and Molecular Identification	98
<i>Vivian C. Blok and Thomas O. Powers</i>	
4.1 Introduction	98
4.2 Biochemical Methods	100
4.2.1 Isozymes	100
4.2.2 Antibodies	102
4.3 DNA-based Methods	103
4.3.1 DNA extraction	103
4.3.2 Restriction fragment length polymorphisms (RFLPs)	104
4.3.3 Satellite DNA probes and PCR	104
4.3.4 Ribosomal DNA PCR	105
4.3.5 Mitochondrial DNA	106
4.3.6 Sequence characterized amplified regions (SCARs)	108
4.3.7 Random amplified polymorphic DNA (RAPD)	109
4.3.8 Other PCR targets	110
4.3.9 Real-time PCR	110
4.3.10 Microarrays	110
4.4 Conclusions and Future Directions	111
4.5 Acknowledgements	112
4.6 References	112
5 Molecular Taxonomy and Phylogeny	119
<i>Byron J. Adams, Adler R. Dillman and Camille Finlinson</i>	
5.1 Introduction	119
5.2 The History of Reconstructing <i>Meloidogyne</i> Phylogenetic History	119
5.3 Molecular Phylogenetics: Genetic Markers and Evolutionary Relationships	120
5.3.1 Nuclear ribosomal DNA sequences	120
5.3.1.1 18S (small ribosomal subunit)	121
5.3.1.2 28S (large ribosomal subunit)	122
5.3.1.3 ITS (internally transcribed spacer region)	123
5.3.2 Orthologous nuclear genes	125
5.3.2.1 Dystrophin	125
5.3.2.2 Major sperm protein (msp)	125
5.3.2.3 Elongation factor 1-alpha (EF1- α)	125
5.3.2.4 RNA polymerase 2	126
5.3.3 Mitochondrial DNA	126
5.3.4 Phylogenomics	127
5.4 A <i>Meloidogyne</i> Supertree Analysis	127
5.5 Conclusions and Future Directions	130
5.6 References	135

6 Hatch and Host Location	139
<i>Rosane H.C. Curtis, A. Forest Robinson and Roland N. Perry</i>	
6.1 Introduction	139
6.2 Hatching	139
6.2.1 General hatching response	140
6.2.2 Hatching mechanism	140
6.2.3 Dependence on root exudates	142
6.2.4 Egg numbers and embryogenesis	143
6.3 Movement Through Soil	144
6.3.1 How root-knot juveniles move	144
6.3.2 Factors influencing rate of movement	144
6.3.3 Plant-independent factors influencing the direction of nematode movement	145
6.4 Host Location	147
6.4.1 General considerations	147
6.4.2 Heat	147
6.4.3 Soil gases	147
6.4.4 Uniquely plant-specific compounds	148
6.5 Nematode Changes and Responses at the Root–Soil Interface	149
6.5.1 Chemical communication at the root–soil interface	149
6.5.2 Perturbing chemosensory perception	152
6.5.3 Surface cuticle changes in response to environmental signals	153
6.6 Conclusions and Future Directions	155
6.7 References	155
7 Invasion, Feeding and Development	163
<i>Pierre Abad, Philippe Castagnone-Sereno, Marie-Noëlle Rosso, Janice de Almeida Engler and Bruno Favory</i>	
7.1 Introduction	163
7.2 Root-knot Nematode Life Cycle	164
7.3 Nematode Parasitism	165
7.4 Compatible Interactions with Resistant Plants: the Case of Virulent Root-knot Nematodes	167
7.5 (A)virulence Determinants and Pathogenicity Factors: Root-knot Nematode Effectors with Dual Function?	169
7.6 Tools for Molecular and Functional Analysis of Root-knot Nematode Parasitism	169
7.7 Giant Cell Development	170
7.8 Cytoskeleton Organization and Cell Cycle Progression During Giant Cell Ontogenesis	172
7.9 Extensive Cell Wall Modifications to Build Up Giant Cells	173
7.10 Suppression of Plant Defence Associated with Giant Cell Development	174
7.11 Major Reprogramming of Plant Metabolism and Transport	174
7.12 Comparison between <i>Meloidogyne</i> Parasitism and Symbiotic Rhizobia in <i>Medicago</i>	175
7.13 Conclusions and Future Directions	176
7.14 Acknowledgements	176
7.15 References	176

8 Reproduction, Physiology and Biochemistry	182
<i>David J. Chitwood and Roland N. Perry</i>	
8.1 Introduction	182
8.2 Reproduction and Moultng	182
8.2.1 Reproduction mechanisms and cytogenetics	182
8.2.1.1 Mode of reproduction	183
8.2.1.2 Sex ratios	183
8.2.1.3 Chromosome complement	183
8.2.1.4 Evolution of <i>Meloidogyne</i> species	186
8.2.1.5 Origin and evolution of parthenogenesis	186
8.2.2 Moultng	187
8.3 Physiology	188
8.3.1 Respiration	188
8.3.2 Effects of osmotic and ionic stress	188
8.3.3 Secretory- excretory products	189
8.4 Biochemistry	189
8.4.1 Enzymes	189
8.4.2 Other proteins	190
8.4.3 Amino acids and sugars	190
8.4.4 Neuropeptides	191
8.4.5 Complex carbohydrates and lipids	191
8.4.6 Steroids	191
8.5 Sensory Perception and Neurotransmission	192
8.5.1 Sensory perception	192
8.5.2 Neurotransmission	193
8.6 Conclusions and Future Directions	193
8.7 References	194
9 Survival Mechanisms	201
<i>Adrian A.F. Evans and Roland N. Perry</i>	
9.1 Introduction	201
9.2 Dormancy, Diapause and Quiescence	202
9.3 Embryonation and the Egg Mass Environment	202
9.3.1 The egg mass	202
9.3.2 The effect of soil moisture	203
9.3.3 The effect of soil aeration	204
9.3.4 Other roles for the egg mass	204
9.3.5 The egg mass and dormancy	205
9.4 Temperature Effects on Development of Eggs and Infective Stages	206
9.4.1 Temperature as an isolated factor	207
9.4.2 Low temperature survival	208
9.4.3 The influence of soil type and moisture content on temperature effects	209
9.4.4 A case study investigating factors affecting infectivity of <i>Meloidogyne javanica</i> J2	211
9.4.5 Overwintering of adult stages	212
9.4.6 Diapause in <i>Meloidogyne naasi</i>	212
9.4.7 A critique of de Guiran's use of 'diapause' as an explanation of late-emerging J2	213

9.5 The Effect of Osmotic Stress on Infective Stages in Soil	213
9.6 Survival Mechanisms Deployed: Life History Strategies in <i>Meloidogyne</i> Species	214
9.6.1 <i>Meloidogyne javanica</i>	215
9.6.2 <i>Meloidogyne arenaria</i>	216
9.6.3 <i>Meloidogyne incognita</i>	217
9.6.4 <i>Meloidogyne hapla</i>	217
9.7 Conclusions and Future Directions	218
9.8 References	219
10 Interactions with Other Pathogens	223
<i>Rosa H. Manzanilla-López and James L. Starr</i>	
10.1 Introduction	223
10.2 Interactions with Microbial Pathogens	226
10.2.1 Vascular wilt pathogens	226
10.2.2 Root-rot pathogens	228
10.2.3 More recently described disease complexes	230
10.3 Interactions with Other Plant-parasitic Nematodes	230
10.3.1 Interactions and parasitic habits	231
10.3.2 Sequential infections	234
10.3.3 Additive interaction	235
10.3.4 Competition	235
10.3.5 Interactions between <i>Meloidogyne</i> species	236
10.3.6 Effect on host	237
10.4 Basis for Interactions	238
10.5 Conclusions and Future Directions	239
10.6 References	240
11 Population Dynamics and Damage Levels	246
<i>Nicola Greco and Mauro Di Vito</i>	
11.1 Introduction	246
11.2 Patterns of Population Dynamics	246
11.3 Factors Affecting Population Dynamics	248
11.3.1 The nematode species	248
11.3.2 Crop and cropping system	249
11.3.3 The season	250
11.3.4 The soil	251
11.4 Modelling Population Dynamics	251
11.5 Damage Levels	253
11.6 Pattern of Nematode Damage to Crop Plants	254
11.7 Factors Affecting Nematode Damage	256
11.7.1 Nematode species and population level	256
11.7.2 Soil and environmental conditions	256
11.7.3 Crop and cropping system	259
11.8 Modelling Damage Levels	259
11.9 Implementing Experiments to Assess Nematode Dynamics and Crop Damage	260
11.9.1 Preparation and type of inoculum	261
11.9.2 Glasshouse experiments	263
11.9.3 Field experiments	263
11.9.4 Microplots	263
11.9.5 Maintenance of experiments	264
11.9.6 Fitting the models to data	266

11.10 Yield Loss Assessment	268
11.11 Importance of Information on Nematode Damage Levels and Dynamics in Management Strategies	268
11.12 Conclusions and Future Directions	269
11.13 Acknowledgements	269
11.14 References	269
12 Sampling Root-knot Nematodes	275
<i>Larry W. Duncan and Mark S. Phillips</i>	
12.1 Introduction	275
12.2 Nematode Spatial Patterns	276
12.3 Characterizing Sample Accuracy and Reliability	278
12.4 Sample Processing	281
12.5 Extracting Nematodes from Soil	281
12.6 Extracting Nematodes from Plant Material	282
12.7 Root Gall Indices	282
12.8 Other Plant Symptoms	283
12.9 Research to Optimize Sampling Programmes for Root-knot Nematodes	283
12.10 Examples of Results from Sampling Programmes	285
12.10.1 Surveys	285
12.10.2 Field experimentation	285
12.11 Conclusions and Future Directions	293
12.12 References	295
13 Mechanisms and Genetics of Resistance	301
<i>Valerie M. Williamson and Philip A. Roberts</i>	
13.1 Introduction	301
13.2 Sources and Inheritance of Root-knot Nematode Resistance	302
13.3 Mechanisms of Resistance to Pathogens in Plants	307
13.4 Structure and Function of the Nematode Resistance Gene <i>Mi-1</i>	308
13.5 What is Known About Other Nematode R-Genes	310
13.6 Nematode Virulence and Durability of Resistance	311
13.7 Management of Resistance and Virulence in the Field	315
13.8 Conclusions and Future Directions	317
13.9 References	319
14 Development of Resistant Varieties	326
<i>James L. Starr and Chris F. Mercer</i>	
14.1 Introduction – the Plus Side of Resistance	326
14.2 Introduction – a Look at the Other Side	326
14.3 Successful Use of Resistance – Room for Wider Deployment	327
14.4 Planning a Resistance-breeding Programme	328
14.4.1 Identification of the root-knot nematode species present	329
14.4.2 Establishing pure cultures	329
14.4.3 Nematode variability	329
14.4.4 Screening methods	329
14.4.5 Sources of resistance	330
14.4.6 Mass selection	331
14.4.7 Recurrent selection	331
14.5 Screening Methods, Including Marker-assisted Selection	331
14.6 Quality of Candidate Resistant Material	333

14.7	Engineered Resistance	334
14.8	Conclusions and Future Directions	335
14.9	References	335
15	Plant Biotechnology and Control	338
<i>Howard J. Atkinson, Peter E. Urwin and Richard S. Hussey</i>		
15.1	Introduction	338
15.2	Proteinase Inhibitors	339
15.3	Cry Proteins of <i>Bacillus thuringiensis</i> as Biopesticides	340
15.3.1	Cry proteins	340
15.3.2	Activity of Cry proteins against nematodes	340
15.3.3	Activity of Cry6A against <i>Meloidogyne incognita</i>	341
15.3.4	Resistance to Cry proteins in nematodes	341
15.4	<i>In planta</i> RNAi to Target Plant-parasitic Nematodes	342
15.5	Repellents	345
15.6	The <i>Mi-1</i> -mediated Resistance Response	346
15.7	Efficacy and Durability	347
15.7.1	Efficacy	347
15.7.2	Durability	348
15.8	Promoters for Transgenic Control of <i>Meloidogyne</i>	349
15.9	Biosafety	349
15.9.1	Food	349
15.9.2	Environment	350
15.10	Developing World Needs	352
15.10.1	The need for biotechnology to control <i>Meloidogyne</i> in the developing world	352
15.10.2	Appropriate technology	353
15.11	Conclusions and Future Directions	353
15.11.1	Proteinase inhibitors	353
15.11.2	Cry proteins	354
15.11.3	RNAi	354
15.11.4	Commercial prospects of deployment of transgenic resistance to <i>Meloidogyne</i>	354
15.11.5	Prospects of uptake in support of food security	355
15.11.6	Rate of uptake possible	355
15.12	References	356
16	The Complete Sequence of the Genomes of <i>Meloidogyne incognita</i> and <i>Meloidogyne hapla</i>	363
<i>Pierre Abad and Charles H. Opperman</i>		
16.1	Introduction	363
16.2	<i>Meloidogyne incognita</i> Genome	364
16.2.1	A genome constituted by pairs of homologous but divergent segments	365
16.2.2	The gene content of a plant-parasitic nematode	367
16.2.3	Identifying plant parasitism genes	368
16.2.4	A nematode adapted to a privileged plant host environment	370
16.2.5	Does the <i>Caenorhabditis elegans</i> genome reflect nematode lifestyle diversity?	370
16.2.6	Exploration of new anti-parasitic drug targets	372

16.3	<i>Meloidogyne hapla</i> Genome	372
16.3.1	General characterization of the genome	372
16.3.2	Estimation of gene numbers	373
16.3.3	Gene families	373
16.3.4	Genome organization	373
16.3.5	Pathway conservation with free-living nematodes	374
16.4	Conclusions and Future Directions	375
16.5	Acknowledgements	376
16.6	References	376
17	Biological Control Using Microbial Pathogens, Endophytes and Antagonists	380
<i>Johannes Hallmann, Keith G. Davies and Richard Sikora</i>		
17.1	Introduction	380
17.2	Bacterial Pathogens and Antagonists	381
17.2.1	Endoparasitic bacteria	381
17.2.1.1	<i>Pasteuria penetrans</i>	382
17.2.1.2	Mass production, <i>in vivo</i> and <i>in vitro</i> culturing methods	382
17.2.1.3	Quantification, nematode suppression and the problem of host specificity	383
17.2.1.4	Mechanism of endospore attachment	384
17.2.1.5	Potential for root-knot control	385
17.2.2	Rhizosphere bacteria	385
17.2.3	Endophytic bacteria	387
17.2.4	Other bacteria	387
17.3	Fungal Pathogens and Antagonists	389
17.3.1	Nematophagous fungi	389
17.3.1.1	Predacious fungi	392
17.3.2	Saprophagous fungi	393
17.3.3	Endophytic fungi	394
17.4	Commercialization and Future Directions	395
17.4.1	Commercial products	395
17.4.2	The development of a commercial product	398
17.4.3	Potential markets	398
17.4.4	Enhancement strategies	399
17.4.5	Transgenic approaches	400
17.4.6	Future prospects	400
17.5	References	401
18	Current and Future Management Strategies in Intensive Crop Production Systems	412
<i>Andrew P. Nyczepir and Stephen H. Thomas</i>		
18.1	Introduction	412
18.2	Current Control Practices	413
18.2.1	Chemical control	413
18.2.1.1	Fumigant nematicides	414
18.2.1.2	Non-fumigant nematicides	415
18.2.1.3	Other compounds	416
18.2.2	Cultural control	416
18.2.2.1	Crop and fallow rotation	417

18.2.2.2	Trap crops, cover crops and soil amendments	418
18.2.2.3	Exploitation of phenology	420
18.2.2.4	Sanitation	420
18.2.2.5	Steam heat and solarization	421
18.2.3	Biological control and host plant resistance	422
18.3	Current Management Practices	423
18.3.1	Significance of diagnostic sampling and government regulation	424
18.3.2	Implementation of management strategies	425
18.4	Future Opportunities and Challenges	428
18.4.1	Emerging control options	429
18.4.1.1	Chemical control	429
18.4.1.2	Cultural control	430
18.4.1.3	Technological advances	431
18.4.2	Emerging management options	432
18.4.2.1	Natural resource availability	432
18.4.2.2	Knowledge gaps	432
18.4.2.3	Alternatives to methyl bromide	434
18.5	Conclusions and Future Directions	435
18.6	References	435
19	Current and Future Management Strategies in Resource-poor Farming	444
<i>Danny L. Coyne, Hendrika H. Fourie and Maurice Moens</i>		
19.1	Introduction and Definitions	444
19.2	Options	446
19.3	Correct Diagnosis	446
19.4	Prevention	447
19.4.1	Healthy planting material	447
19.4.2	Seed and seedling supply	448
19.4.3	Heat treatment	448
19.4.4	Tissue culture	450
19.4.5	Quarantine	450
19.5	Cultural Control	451
19.5.1	Removal of infected material	451
19.5.2	Planting date	451
19.5.3	Flooding	451
19.5.4	Mulching and soil amendments	452
19.5.5	Physical methods	453
19.6	Cropping Systems	453
19.6.1	Rotation	453
19.6.2	Fallow	455
19.6.3	Cover crops (improved fallow)	455
19.6.4	Antagonistic or trap crops	456
19.7	Resistance	458
19.8	Biological Control	459
19.9	Chemical Control	459
19.9.1	Past and current nematicide use	460
19.9.2	Bionematicides	461
19.9.2.1	Avermectins	462
19.9.2.2	Neem products	462
19.9.2.3	Glucosinolates in <i>Brassica</i> spp.	463

19.9.2.4	Polythienyls in <i>Tagetes</i> spp.	463
19.9.2.5	Ricin in <i>Ricinus communis</i>	464
19.9.2.6	Velvet bean compounds	464
19.9.2.7	Monocrotaline in <i>Crotalaria</i> spp.	464
19.9.2.8	Glucoside in cassava	464
19.9.2.9	Other sources of phytochemicals with nematicidal properties	464
19.10	Conclusions and Future Directions	465
19.11	References	466
Gene Index		477
Nematode Genus and Species Index		479
General Index		483

The colour plate section can be found following p. 262.