Chapter 22
Breeding for Nematode Resistance: Use of Genomic Information

Bernard Caromel and Christiane Gebhardt

22.1 Introduction

Plant parasitic nematodes are an important threat to cultivated plants, in addition to pathogenic viruses, bacteria, fungi, oomycetes and chewing insects. Sedentary nematodes, belonging to the genera *Meloidogyne* (root-knot nematodes) and *Heterodera* or *Globodera* (cyst nematodes), are the most damaging plant nematodes. These soil borne sedentary nematodes invade the plant's roots, where each animal establishes a feeding site. This is an intricate developmental process, which leads to major changes in root structure and metabolism, for example, the formation of syncytia (Jones and Northcote 1972) or root galls ('knots') containing giant cells (see Chaps. 4 and 5). Damage is caused to the plant by the loss of nutrients diverted to the nematode over several weeks for the completion of its own life cycle. Cyst nematodes can survive for many years in the soil without the appropriate host plant, due to the formation of cysts (the remains of the female nematode's body surrounded by a hardened cuticle), which encapsulate the next generation of juveniles. The juveniles hatch in response to host cues and begin a new life cycle. Chemical control of nematodes is difficult, due to the limited effectiveness of nematicides and their toxicity to other soil organisms. Infested soils cannot be cultivated for long time with susceptible crops. Nematodes are therefore frequently quarantine pathogens.

Harnessing crops with genetic resistance against nematodes is therefore an important component in plant breeding programs. This requires the phenotypic screening of germplasm to identify sources of resistance, the introgression of resistance factors, which are often found in the crop plant's wild relatives, into adapted genetic backgrounds and then the combination of resistance with other agronomic traits such as yield and quality. This is a very time consuming process, particularly for nematode resistance. Resistance to nematodes is assessed by inoculation of test plants with specific pathotypes or by planting in nematode infested soil. After four

B. Caromel (✉)
INRA-UR1052 Génétique et Amélioration des Fruits et Légumes, Domaine St Maurice Allée des Chênes BP 94, 84143 Montfavet Cedex, France
e-mail: bernard.caromel@avignon.inra.fr

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to twelve weeks, the newly formed cysts or galls are observed and eventually quantified. This phenotypic evaluation is time consuming, costly and often ambiguous. Alternative methods for handling nematode resistance in breeding programs are therefore of interest.

Research on the genetic and molecular basis of nematode resistance over the last 20 years, which is reviewed in this chapter, has opened two new options, which can facilitate breeding for resistance. First, the genetic dissection of qualitative and quantitative nematode resistance based on molecular linkage maps has resulted in DNA-based markers, which are closely linked with resistance loci of various origins. Such markers can assist the introgression, combination and maintenance of specific resistance genes in breeding materials, thereby reducing the number of phenotypic tests and increasing the precision of selection. Second, a small number of genes conferring resistance to nematodes have been cloned and characterized at the molecular level. These genes can be transferred to adapted, susceptible cultivars by genetic transformation, thereby avoiding the lengthy cycles of introgression breeding from wild species. The DNA sequence of cloned nematode resistance genes can also be used to develop gene specific markers, the diagnostic value of which is no longer limited by recombination events.

22.2 Mapped Nematode Resistance Genes and QTLs

Since the development of molecular markers, numerous major genes and Quantitative Trait Loci (QTL) involved in nematode resistance have been located on genetic maps from several crop species. The number of resistance genes or QTLs mapped in a particular species reveals both the importance of nematodes as a threat to that species and the research effort dedicated to this species. The highest number of publications concerning the genetics of resistance to nematodes are available for soybean, cereals, and species from the *Prunus* genus and the Solanaceae family (potato, tomato, pepper, etc.).

22.2.1 Mapped Genes and QTLs for Resistance to Nematodes in Solanaceae

22.2.1.1 Genes and QTLs Acting on Resistance to Potato Cyst Nematodes

Cyst nematodes (*Globodera* sp.) are a major pest of potato (*Solanum tuberosum* ssp. *tuberosum*) in temperate climates. Two species in particular are a threat for potato production: *G. rostochiensis* and *G. pallida*. Several major genes conferring complete resistance to *G. rostochiensis* have been described whereas resistance to *G. pallida* is mainly quantitative due to oligogenic inheritance. The first nematode resistance gene mapped in potato was the *Gro1* gene. The *Gro1* locus on chromo-

some VII originates from the wild potato species *S. spegazzinii* (Barone et al. 1990). This was followed by the mapping of the *H1* gene from *S. tuberosum* ssp. *andigena* on to chromosome V (Gebhardt et al. 1993; Pineda et al. 1993) and of the *GroV1* gene from *S. vernei* to a similar position on the same chromosome arm (Jacobs et al. 1996). *Gro1, H1* and *GroV1* all confer resistance to *G. rostochiensis*. *H1* was first introduced in the potato cultivar 'Maris Piper' in 1966 and many cultivars now carry this gene (Cook 2004; Ross 1986). As these major genes proved efficient and were not been readily overcome by *G. rostochiensis* populations, very little work was done on the genetic dissection of quantitative resistance to *G. rostochiensis*, with the exception of Kreike et al. (1993), and quantitative resistance was not used in breeding schemes. In 2000, half of the potato area in Britain was planted with cultivars resistant to *G. rostochiensis* (Trudgill et al. 2003), most of them carrying the *H1* gene. The *H1* gene is one of few success stories for introgression of durable genetic resistance against a pathogen in the cultivated potato. However, repeated use of cultivars containing *H1* has led to selection for *G. pallida* in many parts of the UK.

Breeding for resistance to *G. pallida* is much more difficult than breeding for resistance to *G. rostochiensis*. The genetic determinism of resistance, originating from five relatives of potato, *S. tuberosum* ssp. *andigena, S. spegazzinii, S. vernei, S. sparsipilum* and *S. tarijense* has been investigated. *Gpa2*, originating from *S. tuberosum* ssp *andigena* is the only major gene for resistance to *G. pallida* and was located to potato chromosome XII (Rouppe van der Voort et al. 1999). This gene, which confers resistance to a very restricted range of *G. pallida* populations, was introgressed in *S. tuberosum* ssp *tuberosum* due to its close vicinity with the *Rx* gene, which confers extreme resistance to *Potato Virus X* (Rouppe van der Voort et al. 1999). Because of its narrow pathotype spectrum, the utility of the *Gpa2* gene in potato growing areas is low. High level and broad spectrum resistances to *G. pallida* in potato are oligogenic and are determined by one major effect QTL and one or few minor effect QTLs. Major effect QTLs have been mapped on the short arm of chromosome IV in *S. tuberosum* ssp. *andigena* ($GpaIV^{s}_{adg}$, Bradshaw et al. 1998; Bryan et al. 2004; Moloney et al. 2010), on the long arm of chromosome XI in *S. tarijense* ($GpaXI^{l}_{tar}$, Tan et al. 2009), and on chromosome V in the three species *S. spegazzinii* (*Gpa*, Kreike et al. 1994, *GpaM1*, Caromel et al. 2003), *S. vernei* (*Gpa5*, Bryan et al. 2002; Rouppe van der Voort et al. 2000, *Grp1*, Rouppe van der Voort et al. 1998) and *S. sparsipilum* ($GpaV_{spl}$, Caromel et al. 2005). *Grp1* also provides resistance to *G. rostochiensis*. Minor effect QTLs acting on *G. pallida* resistance mapped on chromosomes IV, VI, VIII and XII in *S. spegazzinii* (Caromel et al. 2003; Kreike et al. 1994), on chromosome XI in *S. sparsipilum* (Caromel et al. 2005), and in *S. andigena* (Bryan et al. 2004) and on chromosome IX in *S. vernei* (Bryan et al. 2002; Rouppe van der Voort et al. 2000) and/or *S. tarijense* (Tan et al. 2009). Epistatic interactions between major effect and minor effect QTLs have been detected in *S. tarijense* and *S. sparsipilum*. In *S. sparsipilum*, the joint presence of resistance alleles at both QTLs boosts the resistance reaction which takes the form of a strong necrosis around the head of the nematode (Caromel et al. 2005).

Many new sources of resistances to potato cyst nematodes have recently been discovered in the Potato Commonwealth Collection (Castelli et al. 2003). The genetic determinism of these new sources has not been published to date.

Potato cyst nematodes also attack tomato. The *Hero* gene, introgressed from the wild tomato species *Solanum pimpinellifolium*, confers a high level of resistance to all pathotypes of *G. rostochiensis* and partial resistance to *G. pallida*. This gene was mapped on the short arm of tomato chromosome T4 (Ganal et al. 1995). This genomic area is collinear with the potato chromosome IV region where the $GpaIV^{s}_{adg}$ QTL has been mapped (Bradshaw et al. 1998; Bryan et al. 2004; Moloney et al. 2010).

22.2.1.2 Genes and QTLs Acting on Resistance to Root-Knot Nematodes

The root-knot nematode species most frequently encountered on Solanaceous crops are *Meloidogyne incognita, M. arenaria* and *M. javanica* in Mediterranean, tropical and equatorial climates, and *M. hapla, M. fallax* and *M. chitwoodi* in temperate climates. Resistance to root-knot nematodes originates from the wild relatives, *S. arcanum* and *S. peruvianum* (both formerly belonging to the *Lycopersicon peruvianum* complex) for tomato (Ammati et al. 1985; Veremis et al. 1999; Veremis and Roberts 1996a, b, c, 2000), and *S. bulbocastanum* and *S. sparsipilum* for potato (Brown et al. 1996; Kouassi et al. 2006). In pepper, resistance originates from the most cultivated species *Capsicum annuum* as well as from related species (Djian-Caporalino et al. 2006). Six *Me* genes from *C. annuum* clustered in a 28 cM region on pepper chromosome 9 (Djian-Caporalino et al. 2007). The three *Mi* genes mapped in tomato are located on chromosome 6 (Mi-1 and Mi-9; Ammiraju et al. 2003; Klein-Lankhorst et al. 1991; Messeguer et al. 1991) and on chromosome 12 (*Mi-3*; Yaghoobi et al. 1995). In potato, resistance genes to *M. fallax* ($MfaXII^{s}_{spl}$; Kouassi et al. 2006) and to *M. chitwoodi* (*Rmc1*; Brown et al. 1996) are located on chromosomes XII and XI respectively. Interestingly, the genomic regions to which nematode resistance genes have been mapped on potato chromosome XII, tomato chromosome T12 and pepper chromosome P9 are collinear (Djian-Caporalino et al. 2007). Thus, the majority of genes conferring resistance to root-knot nematodes in Solanaceous crops could have descended from a common ancestor.

All currently available tomato cultivars resistant to root-knot nematodes (*M. incognita, M. arenaria* and *M. javanica*) possess the *Mi-1* gene from *S. peruvianum*. However, the resistance conferred by *Mi-1* is broken at temperatures above 28°C (Williamson 1998). The *Mi-9* gene from *S. arcanum*, located in the same genomic region as *Mi-1*, has the same spectrum of action than *Mi-1* but is temperature-insensitive. The repeated use of *Mi-1* in tomato breeding has selected *Meloidogyne* sp. populations, which are able to develop on plants carrying this resistance gene (Castagnone-Sereno et al. 2001; Jacquet et al. 2005; Kaloshian et al. 1996; Tzortzakakis et al. 2005). Other *Mi* resistance genes are difficult to introgress into cultivars due to the sexual barrier between the wild and the cultivated species (Williamson 1998). Of the other *Mi* genes, *Mi-3* is particularly interesting because it is effective at high

temperature against *M. incognita* strains virulent on *Mi-1* (Yaghoobi et al. 1995). Interspecific crosses followed by embryo rescue methods have recently allowed the introgression of *Mi-3* resistance into a *S. lycopersicum* genetic background (Moretti et al. 2002).

22.2.2 Mapped Genes and QTLs for Resistance to Nematodes in Soybean

22.2.2.1 Genes and QTLs Acting on Resistance to Soybean Cyst Nematodes

The soybean cyst nematode (SCN), *Heterodera glycines* (HG), is the most damaging pest of soybean (*Glycine max*). *H. glycines* populations are classified into HG groups, depending on their multiplication rates on soybean indicator lines (Niblack et al. 2002). Hundreds of soybean cultivars carry some resistance to SCN, but none are highly resistant to all HG groups. The genetic bases of the resistance are narrow. Two accessions, Peking and PI88788, are in the pedigree of most resistant cultivars bred in the United States (Concibido et al. 2004; Klink and Matthews 2009). As a review on mapping of SCN resistance has recently been published (Concibido et al. 2004), this report will outline only the major characteristics of soybean resistance to SCN.

The genetic architecture of the analysed SCN resistance sources is mainly polygenic, involving dominant and recessive additive QTLs and epistatic interactions between QTLs and/or genetic background. Several mapping studies have been published over the last fifteen years localizing additive or epistatic SCN resistance QTLs on 19 of the 20 soybean linkage groups (Concibido et al. 2004; Wu et al. 2009a). Two loci are particularly noticeable: the *rhg1* locus on linkage group G and the *Rhg4* locus on linkage group A2. Resistance conferred by *rhg1* is recessive and resistance at this locus was found in six soybean accessions. Resistance conferred by *Rhg4* is dominant and resistance at this locus was found in at least three soybean accessions. Epistatic interactions between both loci and between *rhg1* and another QTL contribute significantly to resistance (Meksem et al. 2001a; Wu et al. 2009a). Resistance QTLs originating from the wild ancestor of domesticated soybean, *G. soja*, mapped to different locations than the QTL originating from *G. max*. Introgression of QTLs of *G. soja* would probably improve the genetic diversity of resistance QTLs in soybean germplasm (Kabelka et al. 2005; Wang et al. 2001; Winter et al. 2007).

22.2.2.2 QTLs Acting on Resistance to Root-Knot Nematodes

Resistance to root-knot nematodes (RKN) in soybean is quantitative. Major effect QTLs conferring resistance to *M. incognita* are located on linkage groups O and M, and minor effect QTLs have been mapped on linkage groups G and C2 (Fourie et al. 2008; Ha et al. 2007a; Li et al. 2001; Shearin et al. 2009; Tamulonis et al. 1997a). The effect of the major QTL on linkage group O is reduced on race 2 of *M. incog-*

nita (Fourie et al. 2008). In contrast to the quite broad spectrum of the majority of RKN resistance genes in tomato (Williamson 1998), soybean resistance QTLs to *M. arenaria* and *M. javanica* mapped on different chromosomes to the QTLs acting on resistance to *M. incognita* (Tamulonis et al. 1997b, c).

22.2.2.3 QTLs Acting on Resistance to the Reniform Nematode

The reniform nematode (*Rotylenchulus reniformis*) attacks many species of cultivated plants including cotton and soybean. In cultivated soybean (*G. max*), resistance to the reniform nematode is quantitative. Three QTLs on linkage groups B1, L and G are involved in resistance to *R. reniformis* (Ha et al. 2007b). The QTLs on linkage groups B1 and G act in an epistatic manner.

22.2.3 Mapped Genes and QTLs for Resistance to Nematodes in Cotton

Despite the high commercial value of cotton, papers reporting mapped genes or QTLs acting on nematode resistance in cotton have only been published recently. The root-knot nematode *M. incognita* and the reniform nematode *R. reniformis* are the most damaging nematodes in cotton. A review by Starr et al. (2007) summarises the knowledge on nematode management in this species.

22.2.3.1 Genes and QTLs Acting on Resistance to Root-Knot Nematodes

Resistance to *M. incognita* in cotton (*Gossypium hirsutum*) originates mostly from a small number of unrelated *G. hirsutum* sources. The first source of resistance was the upland cotton accession Auburn 623 RNR. Resistance from this accession is oligogenic, with a major effect QTL always detected on chromosome 11 and minor effect QTLs on chromosomes 14 or 7 (Shen et al. 2006; Ynturi et al. 2006). In a second, unrelated resistance source, the Acala accession NeemX, the resistance is conferred by a major recessive gene *rkn1* (Wang et al. 2006; Wang and Roberts 2006). The effect of *rkn1* is enhanced by an epistatic interaction with a linked locus, in an interspecific cross involving G. *barbadense* (Wang et al. 2008). Thus, for all resistance sources identified to date, high resistance levels to *M. incognita* in cotton require a genetic factor located on chromosome 11 (Niu et al. 2007).

22.2.3.2 QTLs Acting on Resistance to the Reniform Nematode

In cotton, no resistance to the reniform nematode, *R. reniformis*, was found in the tetraploid cultivated species *G. hirsutum*. Resistance was therefore introgressed

from the wild diploid species *G. longicalyx* and *G. aridum*. The resistance gene from *G. aridum* mapped to a region on chromosome 21 that is duplicated on chromosome 11 (Romano et al. 2009), where a resistance gene from *G. longicalyx* has also been mapped (Dighe et al. 2009). Interestingly, this region of cotton chromosome 11 also carries RKN resistance genes and QTLs (Niu et al. 2007; Shen et al. 2006; Wang et al. 2006; Ynturi et al. 2006).

22.2.4 Mapped Genes and QTLs for Resistance to Nematodes in Grasses

Several cyst nematodes attack cereals around the world, including *Heterodera avenae, H. filipjevi* and *H. latipons*. A review on the importance of damage caused by nematodes in temperate and Mediterranean climates has recently been published (Nicol and Rivoal 2007). A lot of breeding effort has been put into producing wheat and barley cultivars resistant to *H. avenae*. *H. avenae* is the most widely distributed cereal cyst nematode (CCN) under temperate and Mediterranean climates. It causes severe yield losses in wheat and barley. Several pathotypes of *H. avenae* have been described (Andersen and Andersen 1982).

22.2.4.1 Genes and QTLs Acting on Resistance to Cyst Nematodes

Several genes (*Cre* genes) and QTLs acting on resistance to *H. avenae* have been mapped in wheat. Two of these (*Cre1* and *Cre8*) originate from hexaploid wheat (Safari et al. 2005). The others originate from related *Aegilops* species and were introgressed via chromosome addition or substitution lines (Barloy et al. 2007; Delibes et al. 1993; Eastwood et al. 1994; Jahier et al. 2001; Ogbonnaya et al. 2001a; Romero et al. 1998). Even though these genes have been mapped as major dominant genes, they express partial resistance to *H. avenae*. Moreover, the effectiveness of these genes depends on the nematode pathotype. Thus, against Australian pathothypes, *Cre3* is the most efficient gene in reducing the number of cysts, followed by *Cre1* and then *Cre8* (Ogbonnaya et al. 2001a; Safari et al. 2005), whereas *Cre3* exhibits a lower resistance than *Cre1* against a Spanish pathotype (Montes et al. 2008). *Cre1* and *Cre3* map to homeologous loci (de Majnik et al. 2003).

In barley, most genes conferring resistance to *H. avenae* mapped to the *Ha2* locus on chromosome 2H (Kretschmer et al. 1997), which is collinear to the *Cre1/Cre3* locus in wheat. A single additional resistance locus (*Ha4*) has been mapped on another barley chromosome (Barr et al. 1998) allowing pyramiding of *Ha2* and *Ha4* in the same cultivar.

No resistance to nematodes has been found in the widely cultivated rice species *Oryza sativa*, but accessions of the cultivated African rice species, *O. glaberrima*, have been described as resistant to cyst and root-knot nematodes (Plowright et al. 1999). *H. sacchari* is a cyst nematode which attacks sugarcane and rice. Lorieux

et al. (2003) mapped a major gene (*Hsa-1*^{Og}) on chromosome 11, which confers resistance to *H. sacchari* in a *O. sativa* x *O. glaberrima* interspecific progeny. The resistance gene, originating from *O. glaberrima* has been introgressed into the *O. sativa* genetic background.

22.2.4.2 Genes and QTLs Acting on Resistance to Root-Knot Nematodes

The cereal root-knot nematode, *Meloidogyne naasi*, can reduce yield of wheat and barley. It is widely distributed in temperate climates. No resistance has been found in cultivated species (Person-Dedryver and Jahier 1985). Resistance has been introgressed into wheat from the wild relative *Aegilops variabilis* (Yu et al. 1995). Wheat translocation lines carry the resistance gene *Rkn-mn1* on chromosome 3BL, and molecular markers flanking and cosegregating with *Rkn-mn1* have been designed (Barloy et al. 2000).

In rice, *Meloidogyne graminicola* is the most damaging root-knot nematode. A high level of resistance to *M. graminicola* has been found in the cultivated African rice species, *O. glaberrima* (Plowright et al. 1999), and partial resistance has been found in some *O. sativa* cultivars. No resistance gene from *O. glaberrima* has been mapped to date. Six low effect QTLs ($R^2 < 11\%$), that confer tolerance to *M. graminicola*, have been mapped on rice chromosomes 1, 2, 6, 7, 9, 11 (Shrestha et al. 2007). Plants carrying these QTLs support *M. graminicola* reproduction without significant loss of yield. The QTL on chromosome 11 is not collinear to the *Hsa-1*^{Og} from *O. glaberrima*, conferring resistance to *H. sacchari*.

22.2.4.3 QTLs Acting on Resistance to Root-Lesion Nematodes

Resistance to the root-lesion nematodes *Pratylenchus thornei* and *P. neglectus* is a quantitative trait in wheat. QTLs acting on resistance have been mapped on the six wheat chromosomes 1B, 2B, 3B, 4D, 6D and 7A (Schmidt et al. 2005; Toktay et al. 2006; Williams et al. 2002; Zwart et al. 2005, 2006). QTLs located on chromosomes 2B, 6D and 7A have been reported to confer resistance to both root-lesion nematode species *P. thornei* and *P. neglectus*.

22.2.5 Mapped Genes for Resistance to Root-Knot Nematodes in Prunus Species

Several nematode genera attack *Prunus* species, the most damaging of these belong to the *Meloidogyne* genus. Several genes acting on resistance to one or more RKN species have been mapped in several *Prunus* species, including Myrobolan plum (*P. cerasifera*), Japanese plum (*P. salicina*), peach (*P. persica*) and almonds (*P. dulcis*).

RKN resistance genes originating from plum (*Ma* and *Rjap*) mapped to a collinear region of LG7 (Claverie et al. 2004a; Lecouls et al. 1999; Yamamoto and Hayashi 2002). They confer resistance to *M. incognita, M. javanica, M. arenaria*, and *M. floridensis*. In almond, the *RMja* gene, conferring resistance to *M. javanica* and *M. arenaria* but not to *M. incognita* nor to *M. floridensis*, also mapped to LG7, in a collinear position to the plum resistance genes (Van Ghelder et al. 2010).

RKN resistance genes originating from peach (*RMiaNem* and *RMia557*) mapped to linkage group 2 (Claverie et al. 2004a; Gillen and Bliss 2005; Lu et al. 1999). These genes confer resistance only to *M. incognita* and *M. arenaria* and to some isolates of *M. javanica* (Claverie et al. 2004a; Esmenjaud et al. 2009). Resistance to RKN in apricot appears to be polygenic (Esmenjaud et al. 2009).

Most *Prunus* species (peach, almond, apricot, and plum) are sexually compatible, and fruit-producing cultivars are grafted on rootstocks. Thus, RKN resistance genes found in plum, peach and almonds can be combined in rootstock cultivars for each fruit-producing species (Esmenjaud et al. 2009; Nyczepir and Esmenjaud 2008).

22.2.6 Mapped Genes and QTLs for Resistance to Nematodes in Sugar Beet

Heterodera schachtii, the beet cyst nematode (BCN), is widely distributed in temperate climates. It has a broad host range and attacks many species from the Chenopodiaceae and Brassicaceae families. Monogenic resistance to *H. schachtii* was introgressed in sugar beet (*Beta vulgaris*) from the wild relatives *B. procumbens* and *B. webbiana*, in monosomic addition lines. RFLP mapping studies identified nematode-resistant beet lines resulting from translocation events between the wild chromosome segment carrying the nematode resistance genes $Hs1^{pro\text{-}1}$, $Hs1^{web\text{-}1}$ and $Hs2^{web\text{-}7}$, and the cultivated beet chromosome IV (Heller et al. 1996). Further studies indicated that the translocated alien chromosome fragment carrying the $Hs1^{pro\text{-}1}$ gene, may carry additional genes involved in BCN resistance (Sandal et al. 1997).

Sugar beet is also attacked by several species of RKN. An accession of the wild beet *B. vulgaris* ssp. *maritima*, resistant to six species of RKN, was used to introgress resistance in cultivated sugar beet (Yu et al. 1999). Molecular markers linked to the RKN resistance gene have been designed (Weiland and Yu 2003). A review on the use of genetic resistance to control pests in sugar beet has recently been published (Zhang et al. 2008).

22.2.7 Mapped genes and QTLs for Resistance to Nematodes in Other Species

Resistance to a range of RKN species has been mapped in a small number of other crop species. Resistance to *M. incognita* has been mapped in sweetpotato

(Cervantes-Flores et al. 2008; McHaro et al. 2005) while resistance to *M. arenaria* has been mapped in peanuts (Burow et al. 1996; Chu et al. 2007) and resistance to *M. javanica* in carrot (Boiteux et al. 2000). Finally, resistance to two less widespread RKN species has been mapped: to *M. exigua* in coffee (Noir et al. 2003), and to *M. trifoliophila* in *Trifolium* (Barrett et al. 2005).

The citrus nematode *Tylenchulus semipenetrans* is distributed worldwide in citrus growing areas. Resistance to *T. semipenetrans* was introgressed into a citrus rootstock (Swingle Citrumelo) via intergeneric hybridization between grapefruit (*Citrus paradisi*) and *Poncirus trifoliata*, a close relative of *Citrus* (Hutchison 1974). A major effect QTL originating from Swingle Citrumelo, accounts for more than 50% of the resistance to the citrus nematode (Ling et al. 2000).

Xiphinema index is a migratory root ectoparasite which belongs to the Dorylaimida. In addition to causing direct damage to the root system, it is the vector of Grapevine Fanleaf Virus, the most severe viral disease of grape. Resistance to *X. index* was introgressed from *Vitis arizonica* into the cultivated species, *V. vinifera*. A major effect QTL on chromosome 19 of grape is responsible for almost 60% of the resistance to *X. index* (Xu et al. 2008).

22.3 Molecular Marker-Assisted Breeding for Resistance to Nematodes

With the publication of papers describing DNA-based markers linked to nematode resistance genes or QTL, marker-assisted breeding (MAB) for nematode resistance has become possible. However, compared to the number of publications reporting markers linked to nematode resistance genes or QTLs, there are few publications reporting the use of these markers in breeding programs. One explanation for this disparity might be that many new nematode resistance genes have only been mapped in experimental populations, often in progeny of wild species or in interspecific crosses, which are quite remote from advanced breeding materials. In such 'exotic' materials, the linked markers are diagnostic for resistance only in the descendants of the cross used for mapping but lack general diagnostic value in multiparental advanced breeding populations. Moreover, where a molecular marker indeed proves valuable in commercial breeding programs, this fact is usually not reported in the scientific literature. However, MAB for nematode resistance has many potential advantages compared to conventional bioassays. First, the cost of a bioassay (up to 400 € per genotype for a test of quantitative resistance against a quarantine nematode) is much higher than the cost of a marker based assay. Second, bioassays require more time than MAB, taking somewhere between a few weeks when testing monogenic resistance, or up to several months when testing for quantitative resistance. Finally, bioassays for quantitative resistance require sufficient plant material to perform several replications. For example, a standard resistance bioassay for *G. pallida* in potato requires at least five tubers. These five tubers are usually only available at least two years after sowing of the seeds issued from a

cross. During this time, the first steps of selection occur, mainly on tuber maturity or tuber appearance traits. If a resistance QTL is unfavorably linked to genes or QTLs involved in these tuber traits, genotypes carrying the resistance allele at the QTL will be discarded before the resistance bioassay is performed.

The first nematode resistance gene tracked with a marker was the *Mi-1* gene, which confers resistance to RKN in tomato. *Mi-1* was selected using the linked isozyme acid phosphatase marker (APS-1) (Medina-Filho and Stevens 1980; Rick and Fobes 1974). This isozyme marker was then converted to a DNA-based marker (Aarts et al. 1991) and a more closely linked DNA marker, REX-1, was developed and used in MAB (Williamson 1994, 1998). Despite the fact that *Mi-1* was introgressed from *S. peruvianum* into a *S. lycopersicum* background in the 1940s, the molecular marker REX-1 was found to be diagnostic in advanced breeding lines fifty years later. The absence of recombination between REX-1 and *Mi-1* is due to the inversion of a chromosomal segment of 650 kb between *S. lycopersicum* and *S. peruvianum*, allowing a nearly perfect association between REX-1 and *Mi-1* (Seah et al. 2004). With the molecular characterization of the *Mi* gene (Milligan et al. 1998; Vos et al. 1998, see below) new markers were developed from the gene sequence.

Further examples of MAB have been reported in potato for resistance to cyst nematodes (Achenbach et al. 2009; Gebhardt et al. 2006; Moloney et al. 2010; Sattarzadeh et al. 2006) and to root-knot nematodes (Zhang et al. 2007). In soybean (Concibido et al. 1996; da Silva et al. 2007; Ha et al. 2007a; Li et al. 2009; Meksem et al. 2001b; Noel 2004) and wheat (Barloy et al. 2007; Ogbonnaya et al. 2001b; William et al. 2007), MAB is used to select lines carrying resistance to cyst nematodes. In *Prunus*, markers detected in the vicinity of root-knot nematode resistance genes have been used as diagnostic tools in subsequent crosses (Esmenjaud 2009; Lecouls et al. 2004).

22.4 Genes Underlying Resistance to Nematodes

22.4.1 Six Nematode Resistance Genes Molecularly Characterized to Date

Plant genes conferring qualitative resistance to pathogens (*R* genes) respond to specific determinants of an invading pathogen, via direct or indirect recognition of effector molecules encoded by pathogen avirulence (*Avr*) genes (see also Chaps. 13 and 15). After recognition of the *Avr* gene product, the *R* gene activates signaling pathways that result in disease resistance (Jones and Dangl 2006). A common feature of receptors that recognize pathogen effectors is the leucine rich repeat (LRR) domain. The majority of cloned resistance genes encode proteins carrying a LRR in their C-terminal part and also containing a central nucleotide binding site (NBS). Depending on their N-terminal region, NBS-LRR proteins can be subdivided in

TIR-NBS-LRR proteins if they contain a domain sharing homology to the Drosophila Toll and Mammalian Interleukin-1 receptor, or CC-NBS-LRR proteins if they contain a putative coiled-coil or leucine zipper region. Other classes of resistance proteins do not contain the CC, TIR nor NBS domain and possess an extracellular LRR domain at their N terminus, a transmembrane domain, and a cytoplasmic tail (Martin et al. 2003). The structure and function of resistance proteins have recently been reviewed (Caplan et al. 2008; Tameling and Takken 2008; van Ooijen et al. 2007). At the beginning of 2010 six genes conferring resistance to nematodes have been characterized at the molecular level.

The first cloned nematode resistance gene, *Hs1*$^{pro\text{-}1}$, was isolated in sugar beet and acts against the cyst nematode *H. schachtii* (Cai et al. 1997). This was followed by several genes from plants belonging to the Solanaceae family: *Mi-1.2*, conferring resistance to *Meloidogyne* species, was isolated from tomato (Milligan et al. 1998; Vos et al. 1998), its homologue, *CaMi*, was isolated from pepper (Chen et al. 2007), *Gpa2*, conferring resistance to *G. pallida*, was isolated from potato (van der Vossen et al. 2000), *Hero*, conferring resistance to *G. rostochiensis* and *G. pallida*, was isolated from tomato (Ernst et al. 2002) and *Gro1-4*, conferring resistance to the cyst nematode *G. rostochiensis*, was isolated from potato (Paal et al. 2004). *Mi-1.2, CaMi, Gpa2, Hero* and *Gro1-4* belong to the NBS-LRR class of resistance genes, whereas *Hs1*$^{pro\text{-}1}$ has a more unusual structure.

The *Hs1*$^{pro\text{-}1}$ gene was introgressed into sugar beet as an alien chromosomal segment from the wild species *B. procumbens* (Heller et al. 1996). *Hs1*$^{pro\text{-}1}$ was cloned using a positional cloning approach. The protein encoded by *Hs1*$^{pro\text{-}1}$ contains a putative N-terminal extracellular LRR region and a transmembrane domain. It does not have obvious similarities with other resistance genes. *Hs1*$^{pro\text{-}1}$ has been functionally validated using *Agrobacterium rhizogenes*. Hairy roots, regenerated from susceptible beet and expressing *Hs1*$^{pro\text{-}1}$ under the control of the strong, constitutive CaMV35S promoter, expressed the same resistance level to *H. schachtii* as resistant beet lines (Cai et al. 1997). *Hs1*$^{pro\text{-}1}$ is specifically expressed in syncytia of *H. schachtii* and is induced following the formation of the nematode feeding site (Thurau et al. 2003). McLean et al. (2007) reported that the primary published sequence of *Hs1*$^{pro\text{-}1}$ was truncated. Heterologous transformation of susceptible soybean lines with full length *Hs1*$^{pro\text{-}1}$ cDNA enhanced the resistance of the soybean host against the soybean cyst nematode *H. glycines* (McLean et al. 2007).

The tomato *Mi-1.2* gene was cloned simultaneously by two teams, using a positional cloning approach (Milligan et al. 1998; Vos et al. 1998). It belongs to the CC-NBS-LRR class of resistance genes. Interestingly, the *Mi-1.2* gene not only confers resistance to several root-knot nematode species, but also to the potato aphid *Macrosiphum euphorbiae* (Rossi et al. 1998), the tomato psyllid *Bactericerca cockerelli* (Casteel et al. 2006) and to the whitefly *Bemisia tabaci* (Nombela et al. 2003). *Mi-1.2* is constitutively expressed throughout the whole plant and this expression does not vary after inoculation by one of the target pathogens (Goggin et al. 2004; Martinez de Ilarduya and Kaloshian 2001). *Mi-1.2* is one member of a cluster of seven homologues, within 650 kb of the genome (Seah et al. 2004). Expression of *Mi-1* in tobacco or *Arabidopsis* does not confer resistance to *Meloidogyne* species

(Williamson and Kumar 2006), whereas expression of this gene in the more closely related eggplant (*Solanum melongena*) confers resistance to *M. javanica* but not to potato aphids (Goggin et al. 2006). The resistance conferred by *Mi-1.2* is ineffective at high temperatures (Dropkin 1969). Jablonska et al. (2007) demonstrated that *Mi-9*, a nematode resistance gene which is efficient at high temperature, is a homologue of *Mi-1.2*.

A *Mi-1.2* homologue has been cloned from a resistant accession of pepper, by a candidate gene approach, using degenerate primers based on the sequences of *Mi-1.2* and other resistance genes (Chen et al. 2007). This homologue, named *CaMi*, shares 99% identity with *Mi-1.2 at* the amino acid level. Because pepper is a species recalcitrant to genetic transformation, *CaMi* has been functionally validated by transforming susceptible tomato lines with the genomic fragment isolated from pepper: several independent transformed tomato plants exhibited high levels of resistance to *M. incognita*, confirming that *CaMi* is sufficient to confer resistance to this nematode species in tomato. The resistance spectrum of *CaMi* has not yet been investigated and it is not known whether this gene also confers resistance to potato aphid, tomato psyllids or whitefly. As the mapping of *CaMi* has not been reported, its location remains unknown. It would be interesting to know if *CaMi* is located in the pepper nematode resistance gene cluster on chromosome P9 (Djian-Caporalino et al. 2007), which is collinear to tomato chromosome T12, or whether it is located on chromosome P6, collinear to the *Mi-1.2* position on tomato chromosome T6 (Wu et al. 2009b). In potato, another *Mi-1.2* homologue (with 81% identity at the the amino acid level), located in the collinear region on the *S. bulbocastanum* genome, confers resistance to the oomycete *Phytophthora infestans* (van der Vossen et al. 2005).

The *Gpa2* gene, originating from *S. tuberosum* ssp. *andigena*, also belongs to the CC-NBS-LRR class of resistance genes. While *Mi-1.2* exhibits a broad resistance spectrum, resistance conferred by *Gpa2* in potato is restricted to a few populations of the potato cyst nematode *G. pallida*. Interestingly, *Gpa2* is highly similar (88% identity at the amino acid level) and is closely linked to the potato resistance gene *Rx* which confers resistance to *Potato Virus X* (PVX) (van der Vossen et al. 2000). Eight *Gpa2/Rx* homologues are present in an interval of less than 200 kb on chromosome XII in the diploid resistant parent from which *Gpa2* was cloned (Bakker et al. 2003). In *S. accaule*, a *Gpa2* homologue (named *Rx2*), with the same specificity as *Rx*, mapped on chromosome V (Bendahmane et al. 2000). The main differences between *Gpa2*, on one hand and *Rx* and *Rx2* on the other hand, reside in the LRR domain, which is a major determinant of specificity in NBS-LRR proteins (Caplan et al. 2008; Ellis et al. 1999). Due to its narrow pathotype spectrum, *Gpa2* is not a target for breeding or for creation of transgenic plants.

The *Hero* gene, characterized in tomato, confers resistance to both potato cyst nematode species, *G. rostochiensis* and *G. pallida*. It encodes a CC-NBS-LRR protein, with an unusual stretch of 22 negatively charged amino acids in the LRR domain. *Hero* is a member of a cluster of 14 paralogues distributed within 118 kb (Ernst et al. 2002). It is constitutively expressed in all plant tissues, but the expression level increases in roots following inoculation with cyst nematodes (Sobczak et al. 2005). The *Hero* expression level reaches a peak as the syncytium begins to

degenerate. Because *G. rostochiensis* and *G. pallida* are more damaging in potato than in tomato cultivation, transgenic potato lines carrying the *Hero* gene have been created. Unfortunately, the *Hero* gene was unable to confer resistance to cyst nematodes in potato (Sobczak et al. 2005).

The *Gro1-4* gene, originating from the potato relative *S. spegazzinii*, has been cloned following a candidate gene approach. It belongs to the second NBS-LRR subfamily, carrying a TIR domain at its N-terminus and is a member of a gene family of nine homologues. Eight of these homologues, including the functional *Gro1-4* gene are spread over a region of more than 450 kb on chromosome VII. The ninth homologue is located in a similar region to *Hero* on chromosome IV (Paal et al. 2004). The *Gro1* gene family was identified using a probe derived from the sequence of the NBS domain of the *N* gene (Leister et al. 1996). The *N* gene confers resistance to *Tobacco Mosaic Virus* (TMV) in tobacco and is located in a region collinear to potato chromosome XI. Therefore, the *Gro1-4* gene is more related to *N* (38% sequence identity) than to other nematode resistance genes (Paal et al. 2004). *Gro1-4* is constitutively expressed in uninfected roots, and expression of *Gro1* family members has been detected in all plant tissues.,The plant source of the *Gro1-4* gene exhibits a broad spectrum resistance to all known pathotypes of *G. rostochiensis*. Cloned *Gro1-4* confers resistance to the Ro1 pathotype of *G. rostochiensis* but its effectiveness on pathotypes other than Ro1 has not been tested.

22.4.2 New Resistance Genes

Progress has been made towards the identification of other nematode resistance genes in several plant species. High resolution mapping studies and/or candidate gene approaches have been reported to characterize resistance genes, in tomato and Myrobolan plum, for genes conferring resistance to root-knot nematodes, and in potato, soybean and wheat, for genes conferring resistance to cyst nematodes.

In tomato, Jablonska et al. (2007) demonstrated that the *Mi-9* gene, originating from *S. arcanum* and conferring resistance to *Meloidogyne* sp., is a *Mi-1* homologue located on chromosome 6. The identification of the functional homologue has not yet been reported. Once this has been achieved, a comparison of the sequences of both genes and the generation of chimeras between the homologues may explain why one gene is temperature-sensitive whereas the other one is not. The *Mi-3* gene, which maps onto tomato chromosome 12, originates from *S. peruvianum*. This gene is temperature-insensitive and also confers resistance to *Meloidogyne* strains which are virulent on plants carrying *Mi-1* (Yaghoobi et al. 1995). Yaghoobi et al. (2005) mapped *Mi-3* in a genetic interval of less than 0.25 cM. The authors estimated the physical distance corresponding to this interval to be 25–30 kb. However, as the physical mapping was performed on a BAC library from *S. lycopersicum*, a new BAC library from *S. peruvianum* will have to be used to isolate the *Mi-3* resistance allele.

In Myrobolan plum, a high resolution mapping study allowed chromosome landing on a single BAC clone carrying the *Ma* gene for resistance to several *Meloido-*

gyne species (Claverie et al. 2004b). Further recombinant analysis and BAC sequencing identified a cluster of three TIR-NBS-LRR genes, one of which is probably the *Ma* gene (Esmenjaud 2009). Functional validation of these three candidate genes is in progress. Assuming these experiments are successful, the *Ma* gene will be the second nematode resistance gene belonging to the TIR-NBS-LRR class.

In potato, most of the major genes or major effect QTLs involved in nematode resistance have been mapped onto chromosome V. Cloning of several of these is in progress. A recent study (Achenbach et al. 2010) demonstrated that this chromosome was previously misoriented (Dong et al. 2000) and here we use the new orientation as defined by Achenbach et al. (2010). The *H1* gene, mapped on the short arm of chromosome V, confers resistance to the cyst nematode *G. rostochiensis*. Using a progeny of 1,209 genotypes, and information from an ultra high density map of potato (van Os et al. 2006), Bakker et al. (2004) mapped the *H1* gene to an interval less than 1 cM. On the long arm of chromosome V, major effect QTLs acting on resistance to *G. pallida* only (Bryan et al. 2002; Caromel et al. 2003, 2005; Kreike et al. 1994; Rouppe van der Voort et al. 2000) or to *G. pallida* and *G. rostochiensis* (Rouppe van der Voort et al. 1998) have been mapped. Using a progeny of 1,536 individuals, Finkers-Tomczak et al. (2009) mapped the *Grp1* major effect QTL in an interval of 1.08 cM. Even with such huge progeny, the authors were not able to separate the resistance to the two *Globodera* species, conferred by the *Grp1* locus. Thus, this dual specificity may be conferred by a single gene or by two closely linked genes. The $GpaV_{spl}$ major effect QTL, in combination with the $GpaXI_{spl}$ low effect QTL, confers almost complete resistance to *G. pallida* (Caromel et al. 2005). $GpaV_{spl}$ and *Grp1* are collinear. Taking into account the effect of both $GpaV_{spl}$ and $GpaXI_{spl}$ *QTLs,* it has been possible to map the $GpaV_{spl}$ QTL as a major gene, in a 0.8 cM interval in the original progeny of 239 genotypes (B. Caromel, unpublished results). By increasing the size of the progeny to 1,632 genotypes $GpaV_{spl}$ was mapped to an interval of 0.12 cM. The sizes of the progenies used to map *Grp1* and $GpaV_{spl}$ were similar, but the resolution obtained for the $GpaV_{spl}$ map was higher. This better resolution was due to higher recombination rates resulting from meiosis in the pure *S. sparsipilum* resistant clone, compared to the recombination rates occurring in the complex interspecific clone used as resistance source by Finkers-Tomczak et al. (2009).

The strategy used to characterize cyst nematode resistance genes in wheat has been based on a candidate gene approach, using a NBS-LRR coding sequence. Sequences have been isolated from the *Cre3* locus (Lagudah et al. 1997). Derived sequences were further used by the same team to tag other nematode resistance genes in wheat and barley (de Majnik et al. 2003; Seah et al. 1998, 2000). Functional demonstration of the role of these NBS-LRR sequences in nematode resistance has not yet been reported.

In soybean, the *rhg1* and *Rhg4* locus, acting on resistance to *Heterodera glycines*, have been extensively studied. Receptor-like kinase (RLK) sequences have been patented as candidate genes for both loci (Hauge et al. 2001; Lightfoot and Meksem 2000), but functional evidence for the role of RLK in nematode resistance has not yet been reported. In fact, further studies suggest that *rhg1* is a "multigenic" QTL, comprising an RLK, an unusual laccase, and a 46.1 kDa hypothetical transporter protein (Iqbal et al. 2009; Lightfoot et al. 2008; Ruben et al. 2006).

22.5 Breeding for Durable Resistance to Nematodes

There are many practical issues that need to be considered when breeding for nematode resistance. Even for major genes, differences in resistance levels have been noticed depending on the genetic background of the host (Jacquet et al. 2005; Mugniéry, personal communication). These differences could be explained by unmapped genetic factors acting additively or epistatically on resistance (unmapped QTLs). Several genes and QTLs have been overcome by certain nematode populations or are population-specific (Kaloshian et al. 1996; Montes et al. 2008; Rouppe van der Voort et al. 1997). Thus, cultivars with resistance to all populations of a given nematode species are more likely able to control this species over long period of time.

It is important to accumulate several QTLs or one major gene and QTLs in order to broaden the resistance spectrum of resistance genes or major effect QTLs and to increase durability. Indeed, the pathotype spectrum or the durability of resistance to nematodes, in plants carrying single genes or major effect QTLs, are usually weaker than those of the resistance sources (Turner et al. 2006). This reflects a partial transfer of genetic factors involved in resistance in the selected plants. Evaluation of the spectrum of resistance in individuals carrying different QTL combinations gives an indication of the potential durability of such QTL combinations. In the wild potato relative *S. sparsipilum*, resistance to *G. pallida* is conferred by one major ($R^2 = 76\%$) and one minor ($R^2 = 12.7\%$) effect QTL (Caromel et al. 2005). We evaluated the resistance level conferred by the four QTL combinations on eight populations of *G. pallida* originating from four European countries and from New Zealand. In plants carrying the resistance allele at the single major effect QTL the number of newly formed cysts that developed varied between two and fifty, depending on the nematode population, while in plants carrying resistance alleles at both QTL, this number never exceeded four cysts (Caromel 2004; Caromel et al. 2008).

In other pathosystems, Brun et al. (2009) and Palloix et al. (2009) demonstrated that the durability of major genes is higher in a genetic background carrying minor resistance QTLs than in a fully susceptible genetic background. Furthermore, Palloix et al. (2009) showed that growing cultivars with monogenic resistance promote further evolution of pathogens allowing adaptation to complex resistances combining the major gene and QTLs.

Even though quantitative phenotyping is more labour intensive than qualitative phenotyping, the resistance to nematodes can be evaluated by counting the numbers of galls or eggs or the numbers of newly formed cysts, in individuals of a plant progeny. Together with a genetic map, these quantitative data allow QTL detection. In several species, evenly distributed markers are available to build extensive genetic maps and the sequences of whole genomes, for the most studied species, will also help in designing new makers for mapping experiments. With a progeny of 150–300 individuals and appropriate detection methods, low effect QTLs can be detected even in the presence of major effect QTL (Caromel et al. 2005; Tan et al. 2009; Wu et al. 2009a). Markers flanking major and minor QTLs can further be used to assist the breeding process.

Another alternative to select for durable resistance is to select for plant resistance genes recognising nematode effectors encoded by genes which are under high selective pressure. Mutation in such genes would probably affect the fitness of the new nematode isolate, which would be counter-selected. In plant-virus interactions, Janzac et al. (2009) demonstrated that durability of resistance of major genes is a function of the selective constraints applied on the corresponding avirulence factors. Nematode avirulence genes are probably secreted or excreted into the plant tissue. With the increasing characterization of nematode-secreted molecules (Adam et al. 2009; Bellafiore et al. 2008; Davis et al. 2008; Jones et al. 2009; Patel et al. 2008; Roze et al. 2008; Sacco et al. 2007), selective pressure on the corresponding genes can be evaluated (Sacco et al. 2009). Transient expression of the products of the constrained nematode secreted genes, in plant tissues originating from a collection of plant genetic resources, would allow the identification of the corresponding resistance genes, as it has been shown for *Phytophthora infestans* avirulence products in potato (Vleeshouwers et al. 2008).

22.6 Conclusions

The past twenty years have seen substantial progress in the genetic dissection and molecular characterization of plant resistance to nematodes, thanks to the molecular genetic tools that became available to plant geneticists around 30 years ago (Tanksley 1983). Some of the results of this research have been translated in commercial breeding programs. We are confident that this process will continue.

Accumulating evidence suggests that major resistance genes or QTLs need to be introgressed together with low effect QTLs to build cultivars with durable resistance. Our next challenge is to accurately detect such low effect QTLs. This implies the need to consider all resistance as quantitative (by counting nematodes or galls), to genotype and phenotype larger progenies (typically 150–300 individuals) and to use enough replicates in the resistance assay to obtain a high heritability for the trait.

Combining accurate phenotyping on large progenies with high density marker coverage will allow detection and tagging of large and low effect QTLs involved in nematode resistance. The availability of whole genome sequences of the most important crop plants, a goal which is likely to be achieved in the near future, will provide new opportunities to identify, localize, diagnose and clone nematode resistance genes, providing breeders with a versatile instrument for precision resistance breeding.

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