ROOT-KNOT NEMATODES ON WILLOWS: SCREENING OF *SALIX* SPECIES, CULTIVARS, AND HYBRIDS FOR RESISTANCE

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Abstract. Five clones of *Salix alba*, two cultivars of *S. babylonica*, and 25 "weeping willow" clones from various arboreta were susceptible to the root-knot nematodes *Meloidogyne arenaria* (Race 1 and Race 2), *M. incognita*, and *M. javanica*. None of these clones, nor those of 16 other taxa, were susceptible to *M. hapla*. Clones of some of the other taxa (*S. arbutifolia*, *S. gracilistyla*, *S. integra*, *S. nigra*, *S. sachalinensis* 'Sekka') were resistant to or tolerant of *all* the nematodes, and a few taxa exhibited differential susceptibilities. Putative hybrids between a susceptible female *S. alba* clone and some resistant or tolerant taxa were susceptible to *all* infective nematode species and races. Short-term greenhouse studies indicated that shoot growth of a *S. alba* clone could be significantly reduced by nematode infestation but growth of *S. babylonica* 'Babylon' was not affected. The fact remains, however, that most of our widely planted landscape willows are highly susceptible to root-knot nematodes and may be more subject to windthrow because of such infestation.

Résumé. Cinq clones de *Salix alba*, deux cultivars de *S. babylonica* et 25 clones de saules pleureurs d'arboreta variés étaient susceptibles aux nématodes des racines *Meloidogyne arenaria* (race 1 et race 2), *M. incognita* et *M. javanica*. Aucun de ces clones, ni ceux de 16 autres taxons, étaient susceptibles au *M.halpa*. Les clones de quelques-uns des autres taxons (*S. arbutifolia*, *S. gracilistyla*, *S.integra*, *S. nigra*, *S.achalinensis* "Sekka') étaient résistants ou tolérants à tous les nématodes et peu de taxons ont montré des susceptibilités différentielles. Des hybrides entre une femelle susceptible de clone *S. alba* et quelques taxons résistants ou tolérants étaient susceptibles à toutes les espèces et races de nématodes. Des études le l'effet de serre à court terme indiquent que la poussée de croissance d'un clone *S.alba* pourrait être significativement reduite par une infestation de nématodes mais la croissance de *S. babylonica* 'Babylon' n'était pas affectée. Il demeure cependant que la plupart de nos saules ornementaux largement plantés sont hautement susceptibles aux nématodes des racines et peuvent êtrë plus sujets aux chablis à cause d'une telle infestation.

On July 27, 1988, we discovered that a tree of *Salix alba* (NA 44016) growing at the U.S. National Arboretum, Washington, D.C. had blown down during a mild overnight storm. Examination of the exposed roots revealed extensive infestation by root-knot nematodes and suggested that the stunting of roots on one side of the tree was the primary cause of the blow-down. Inasmuch as we have been attempting to clarify willow nomenclature and select superior willow cultivars for landscape planting (22), this "new" and potentially serious problem demanded our attention.

The literature concerning root-knot nematodes (*Meloidogyne* sp.) on willows is more extensive than that for most other genera of landscape trees. The first report of any root-knot nematode on *Salix* was in 1889 (17) for an unidentified *Meloidogyne* sp. on *S. babylonica* in Florida and a later (1948) paper also noted an unidentified *Meloidogyne* sp. on the same host plant in Arizona (5). Trees of *S. alba* were reported as hosts of an unidentified *Meloidogyne* sp. in Italy (12) and the USSR (25). The female clone of *S. alba* known as "cricket-bat willow" (distinguished by various authors as cv. 'Caerulea', *var. coerulea* Syme, *var. calva* G.F.W. Meyer, or *S. coerulea* Smith) was reported as a host of *M. javanica* (Treub) Chitwood in Australia (7) and was susceptible to inoculation with *M. incognita* (Kofoid and White) Chitwood in Argentina (16). Three other willow species have been noted as hosts of *M. javanica: S. caprea* L. in Africa (13), *S. caucasica* L. in the USSR (18), and *S. viminalis* in Israel (15). In addition, *S. acmophylla* Boiss. was reported to be a host of an unidentified *Meloidogyne* sp. in the USSR (25). Other willows, unidentified as to species, have been noted as hosts of *M. incognita* in Argentina (16) and Maryland (11) and of *M. javanica* in Italy (8) and Israel (15). Thus, although at least two species of root-knot nematodes have been reported to infest the roots of a few willow taxa, the susceptibility of many commonly planted willows (especially the "weeping" cultivars) was unknown. Furthermore, it was not known whether any of the willows were susceptible to two other widely distributed nematodes: *M. arenaria* (Neal) Chitwood and *M. hapla* Chitwood.

According to Agrios (1), root-feeding nematodes "probably decrease the ability of plants to take up water and nutrients from soil and thus cause symptoms of water and nutrient deficiencies in the above ground parts of plants". Reduction in growth of several junipers *(Juniperus)* and hollies *(Ilex)* infested with different nematodes has been documented and illustrated by Benson and Barker (4). Certain wilt fungi *(Fusarium, Verticillium)* and root rots *(Phytophthora, Rhizoctonia)* may also form disease complexes with various nematodes in which the combined effects of the fungus and the nematode cause more damage than either pathogen alone. McArdle and Santamour (14) utilized two root-knot nematodes in combination with the mimosa wilt fungus *(Fusarium)* to screen seedlings of *Albizia julibrissin* Durazz. for wilt resistance. Another well-known influence of certain nematodes on plants is their role as carriers of viruses and the "failure" of grafts (not graft incompatibility) of certain apples and oaks is caused by tomato ringspot virus transmitted to rootstocks by nematodes (21, 24). As far as we know, however, the blow-down of our *S. alba* tree is the first documented instance of a root-knot nematode being responsible for such a potentially dangerous situation.

The purposes of the present study were to identify the root-knot nematode we found on *S. alba* and to utilize this nematode and other common species to screen a wide range of willow species, cultivars, and hybrids for nematode resistance.

Identification of the willow nematode. Freshly collected galls from the infested willow and soil samples taken near infested roots were delivered to Dr. A. Morgan Golden (USDA-ARS, Beltsville, MD) on 1 August 1988. His preliminary observations indicated that the nematode could be either *M. arenaria* or *M. platani* Hirschmann, a species that was first discovered on *Platanus* (sycamore) in 1971 (6) and identified and studied extensively in 1982 (2, 9). Ruehle (19) reported that typical *M. arenaria* did not parasitize sycamore and Al-Hazmi and Sasser (2) found that *M. platani* did not parasitize peanut *(Arachis hypogaea* L. 'Florunner'). Thus, these two host plants might be used to verify the identity of the nematode. Inoculation of peanut seedlings and rooted cuttings of *Platanus* 'Columbia' and 'Liberty' (20) did not result in gall formation on the roots of either potential host. On 27 October 1988, we were able to supply Dr. Golden with inoculated (4 August 1988) potted plants of *S. alba* (Calva' (UM 600375) for a more critical examination. His conclusion was that our nematode was a parthenogenetic (no males produced) race of *M. arenaria.* Inasmuch as Sasser (23) has distinguished the two races of *M. arenaria* on their differing abilities to parasitize peanut, we feel rather confident in considering the root-knot nematode from willow to be *M. arenaria*—Race 2.

Materials and Methods

All of the willows used in this study were grown from stem cuttings in the greenhouses of the National Arboretum. The original trees from which these cuttings were taken were part of the collections growing at the National Arboretum (NA); the Arnold Arboretum of Harvard University, Jamaica Plain, Massachusetts (AA); the Morton Arboretum, Lisle, Illinois (MA); and the University of Minnesota Landscape Arboretum, Chanhassen, Minnesota (UM). Many of the trees from other arboreta had been planted in Glenn Dale, Maryland in 1986. Because of the confused and sometimes dubious species and cultivar designations of these willows, the accession numbers given to the trees at the institutions of origin will be provided when pertinent. Interspecific willow hybrids were derived from controlled pollinations among National Arboretum trees from 1985 to 1987.

Plants of most of the taxa listed in Table 1, and from all of the "weeping" cultivars, were propagated in flats of a peat-perlite mix, under mist, from dormant stem cuttings treated with Hormodin No. 2. These cuttings were stuck between 19 January and 30 January 1989, potted in 2-quart plastic containers in a soil-peat-perlite mix on 2 March 1989, and inoculated on 21 March 1989.

Cuttings of the hybrids and a few of the taxa listed in Table 1 were taken from actively growing plants on 17 April 1989, potted on 15 May 1989, and inoculated on 27 June 1989. Since none of the willows inoculated in March were susceptible to *M. hapla,* no inoculum of this nematode was available for the June inoculations.

For the March inoculations, potted plants of *S. alba* (Calva' (UM 600375) that had been inoculated with the willow nematode on 4 August

1988 served as the source of inoculum for *M. arenaria*—Race 2. Potted tomato plants (from A.M. Golden) infested with *M. arenaria*—Race 1, *M. hapla, M. incognita,* and *M. javanica* provided the inoculum for those nematode species. Inoculum was prepared by removing the infested plants from their containers, finely chopping the root systems, and thoroughly mixing the chopped roots with the soil medium in which the infested plants had been growing. The inoculum thus contained free-moving juvenile nematodes as well as females and egg masses in the root galls. Inoculum for the June inoculations (except *M. hapla,* as noted earlier) was prepared from infested willows that had been inoculated in March.

Plants were inoculated by removing a small amount of the soil media from two opposite sides of the container and placing a 50-ml beaker-full of inoculum in each depression. The inoculum was covered with the original media and the plant was watered.

Fifty plants of *S. alba* (NA 44016) were inoculated with *M. arenaria*—Race 2 in March. Measurements of height growth were made on 10 inoculated plants and 10 uninoculated controls on the day of inoculation. Five plants of this clone were inoculated with each of the other four nematodes. For *S. babylonica* 'Babylon' (NA 44011), five plants were inoculated with each of the five nematodes, and 10 plants were retained as controls. Only two plants per clone of the other taxa were inoculated with each nematode in March and five plants of each clone served as uninoculated controls.

In the June inoculations, two plants each of *S. nigra* and four *S. alba* clones were inoculated with each of four nematodes (no *M. hapla)* with two controls. Because of the small size of the hybrid plants in the field, the availability of cuttings was limited and, for most of the hybrid clones, only a single plant was inoculated with each nematode, with one of two controls. Also in June, we retested those clones that had exhibited resistance or tolerance to one or more of the infective nematodes and that had been used as male parents inhybridization with *S. alba* (NA 44016). Only a single plant of the previous control group was inoculated with each nematode. We did not test any of the hybrids between susceptible taxa.

Between 70 and 80 days after inoculation, the plants were removed from their containers and the root systems were rinsed relatively free of soil and organic matter. The top of the plant was removed and the roots were labeled and placed in plastic bags and stored briefly in a refrigerator until examined. Only one plant per treatment was evaluated initially. Additional plants were evaluated only if low numbers of galls or egg masses indicated a potential tolerant or resistant response. Because of the observed lack of parasitism by *M. hapla,* all plants inoculated with this nematode were examined.

For each root system, the number of galls was counted (up to 100) and the number of egg masses in 10 randomly selected galls was determined. Egg production signifies that the nematode can complete its life cycle on a particular host and only plants with egg masses can be classified as "susceptible". An explanation of the rating system is given in the footnote to Table 1.

Taxonomy. The nomenclature and classification of *Salix* has always posed problems for the taxonomist, and there is currently no accepted standard for worldwide use. We have provided the authorities for the botanical Sections recognized in this paper but have not included the various synonomies of Sectional classification. There are also many unresolved problems of generic, species, and cultivar nomenclature and these are discussed below in the same order in which the taxa are listed in Table 1.

The blown-down, nematode-infested specimen of *S. alba* (NA 44016) that prompted this study was received by the National Arboretum as the cultivar 'Chrysostela', an upright-growing selection with a form approaching that of Lombardy poplar. Although our clone did exhibit this growth form, it was a female, and 'Chrysostela' is a male clone (3). The typification of 'Babylon' as the standard clone of *S. babylonica* was discussed in an earlier paper (22). The plant we have listed as *S. arbutifolia* has frequently been placed in a separate genus *(Chosenia)* by some authors as *C. arbutifolia* (Pallas) Skvortzov or *C. bracteosa* (Trautv.) Nakai, with *S. bracteosa* Turcz. as another synonym. Within subgenus *Vetrix, S. medemii* from Iran has also been called *S. aegyptiaca* L. The North American taxon *S.*

Table 1. Response of *Salix* (willow) taxa to inoculation with root-knot nematodes *(Meloidogyne* spp.)[1]

Subgenus / *Section* / *Species, 'Cultivar', Acc. No.*	*M. arenaria* *Race 1*	*M. arenaria* *Race 2*	*M. hapla*	*M. incognita*	*M. javanica*
Salix					
Salix					
S. alba L. (NA 44016)	**S** (5-9)	**S** (4-5)	**T** (1-0)	**S** (5-3)	**S** (5-4)
'Calva' (UM 600375)	**S** (5-10)	**S** (5-10)	- - -	**S** (5-9)	**S** (5-6)
'Rockanje' (MA 0310-65)	**S** (5-9)	**S** (5-5)	- - -	**S** (5-2)	**S** (5-4)
'St. Oedenrode' (NA 57833)	**S** (5-9)	**S** (5-9)	- - -	**S** (5-9)	**S** (5-8)
'Vitellina' (MA 0466-23)	**S** (4-10)	**S** (5-9	- - -	**S** (5-5)	**S** (5-2)
Subalbae Koidzumi					
S. babylonica L.					
'Babylon' (NA 44011)	**S** (4-10)	**S** (3-6)	**R** (0-0)	**S** (4-5)	**S** (3-4)
'Tortuosa' (NA 44014)	**S** (5-2)	**S** (4-4)	**R** (0-0)	**S** (4-10)	**S** (4-2)
Urbanianae Seemen					
S. arbutifolia Pallas (NA 40139)	**T** (1-0)	**R** (0-0)	**R** (0-0)	**R** (0-0)	**R** (0-0)
Salicaster Dumortier					
S. pentandra L. (NA 44015)	**S** (5-5)	**S** (4-4)	**R** (0-0)	**S** (5-2)	**S** (5-7)
Humboldtianae Pax					
S. nigra Marshall (MA 0062-61)	**T** (1-0)	**T** (1-0)	- - -	**T** (1-0)	**R** (0-0)
Amygdalinae K. Koch					
S. triandra L. (NA 54186)	**S** (5-2)	**S** (4-4)	**R** (0-0)	**S** (5-4)	**S** (5-4)
Vetrix Dumortier					
Vetrix					
S. humilis Marshall (NA 43997)	**S** (5-3)	**S** (3-4)	**R** (0-0)	**T** (2-0)	**S** (3-9)
S. medemii Boiss. (NA 43998)	**S** (5-7)	**S** (5-4)	**R** (0-0)	**S** (5-3)	**S** (5-3)
Canae Kern					
S. elaeagnos Scop. (NA 44020)	**S** (4-5)	**S** (4-2)	**R** (0-0)	**S** (4-2)	**S** (4-4)
Cordatae Barratt *ex* Hook.					
S. glaucophylloides Fern. (NA 44019)	**S** (4-6)	**T** (2-0)	**R** (0-0)	**T** (1-0)	**T** (1-0)
Helix Dumortier					
S. integra Thunb. (NA 40005)	**T** (2-0)	**R** (0-0)	**R** (0-0)	**R** (0-0)	**R** (0-0)
S. purpurea L.					
'Eugenei' (NA 44002)	**S** (5-7)	**S** (4-9)	**R** (0-0)	**S** (5-4)	**S** (4-5)
Nigricantes Kern					
S. apennina Borzi (NA 44005)	**S** (5-5)	**S** (5-7)	**R** (0-0)	**R** (0-0)	**S** (5-2)
Subviminales Seemen					
S. gracilistyla Miq. (NA 44013)	**T** (1-0)	**R** (0-0)	**R** (0-0)	**R** (0-0)	**T** (3-0)
S. melanostachys Makino (NA 18960)	**S** (4-2)	**S** (4-4)	**T** (1-0)	**S** (3-1)	**S** (4-2)
Vimen Dumortier					
S. sachalinensis F. Schmidt					
'Sekka' (NA 44010)	**R** (0-0)	**R** (0-0)	**R** (0-0)	**R** (0-0)	**T** (3-0)
S. viminalis L. (NA 54188)	**S** (5-2)	**S** (4-2)	**R** (0-0)	**S** (5-3)	**S** (5-10)
Vulpinae Kimura					
S. vulpina Kimura (NA 51338)	**S** (5-6)	**S** (5-2)	**T** (1-0)	**S** (5-7)	**S** (5-3)

[1]Key to Table. **S** = susceptible, galls and egg masses noted; **T** = tolerant, some galls but no egg masses; **R** = resistant, no galls and no egg masses. First figure in parentheses refers to gall rating: 0 = no galls; 1 = from one to two galls; 2 = three to 10 galls; 3 = 11 to 30 galls; 4 = 31 to 100 galls; 5 = more than 100 galls per root system. Second figure is the number of egg masses found in 10 randomly selected galls (or in all galls when fewer than 10 were found).

glaucophylloides has been listed as *S. myricoides* Muhlenb. in some recent works. The cultivar 'Eugenei' is considered by Bean (3) to be a male clone of *S* x *rubra* Huds. *(S. purpurea* x *S. viminalis)*. The taxon (with purple-black catkins) we have listed as *S. melanostachys* is sometimes considered as a variety of *S. gracilistyla*. The clone 'Sekka', with fasciated and contorted stem growth, was received as *S. udensis* Trautv. & Mey. but should be placed under *S. sachalinensis* (3). The clone of *S. alba* 'Calva' (UM 600375) we used as a susceptible host to build up populations of the willow nematode may (or may not) be the famous "Cricket Bat Willow" ('Caerulea') grown in England (3).

Results and Discussion

The data from inoculation of the non-weeping and non-hybrid taxa are given in Table 1. *All* taxa exhibited a tolerant or resistant response to inoculation with *M. hapla*. Most of the other willow taxa were susceptible to the other nematodes, with some notable exceptions. Chief among these was the American black willow *(S. nigra)*, which has a broad geographic range and can become a large, single-trunked tree. Among the other resistant or tolerant taxa, *S. arbutifolia* and *S. integra* grow as large, multiple-stemmed shrubs at the National Arboretum, while *S. sachalinensis* 'Sekka' *S. gracilistyla*, and *S. glaucophylloides* are low-growing shrubs. Both *S. apennina* and *S. humilis* (with resistance or tolerance to *M. incognita)* are more upright in growth habit but tend to be multiple-stemmed. It should be noted that all taxa given a resistant or tolerant rating to one or more of the nematodes were tested twice (except *S. nigra)*.

"Weeping" Cultivars. As noted in an earlier work on the nomenclature of weeping willows (22), we had obtained cuttings (in 1983) of numerous weeping willows (under various names) from other arboreta. Also, as noted earlier, virtually all of these clones were considered to be hybrids of *S. babylonica* 'Babylon' with either *S. alba* or *S. fragilis*. The 25 clones we tested are listed below, under the arboretum of origin. The accession number and identification (as of 1983) are given for each clone. *All* of the clones listed were susceptible to inoculation with *M. incognita*, *M. javanica*, and both races of *M. arenaria*. *All* of the clones were resistant to or tolerant of inoculation with *M. hapla*.

Arnold Arboretum	
AA 7235	*S. alba* var. *tristis*
AA 17950	*S. alba* var. *tristis*
AA 2654-5	*S. alba* var. *tristis*
AA 13-46	*S.* x *blanda*
AA 386-62	*S.* x *blanda*
AA 19-64	*S. elegantissima*
AA 719-71	*S. elegantissima*
AA 175-61	*S. matsudana* 'Pendula'
AA 178-63	*S.* x *sepulcralis*
Morton Arboretum	
MA 0183-53 (MA 0830-55)	*S. alba* 'Tristis'
MA 0128-44 (MA 0262-59)	*S. alba* 'Tristis'
MA 0463-48	*S. babylonica*
MA 0716-58	*S. babylonica*
MA 0564-23	*S. blanda* 'Niobe'
MA 0055-61	*S.* x *elegantissima*
MA 0068-61	*S.* x *sepulcralis*
National Arboretum	
NA 43995	*S. alba* 'Tristis'
NA 46452	*S.* x *blanda* 'Niobe'
NA 60127	*S.* x *blanda* 'Niobe'
NA 8929	*S.* x *chrysocoma*
NA 46451	*S. matsudana 'Pendula'*
University of Minnesota	
UM 580495	*S. alba* 'Tristis'
UM 660586	*S. babylonica*
UM 600376	*S.* x *blanda*
UM 660585	*S.* x *blanda*

Correspondence with the Arnold Arboretum has indicated that the three clones formerly identified as *S. alba* var. *tristis* are now called *S. alba* var. *vitellina* 'Pendula'; those named *S. elegantissima* and one of the *S.* x *blanda* clones are now considered to be *S.* x *blanda* 'Elegantissima'; and the *S. matsudana* 'Pendula' is now called *S.* x *sepulcralis*. We consider it doubtful that these nomenclatural changes reflect any closer approach to reality.

Hybrids of *Salix alba*. From 1985 to 1987, we made numerous attempts at controlled hybridization of willows, many involving the nematode-infested female clone of *S. alba* (NA 44016) that prompted this study. The hybrids tested must be considered "putative", since *absolute* verification of hybridity of these young plants was not achieved. However, morphological and biochemical (isozyme) analyses indicated a high probability that they were true hybrids. Included in our inoculations were three hybrids of *S. alba* and *S. sachalinensis* 'Sekka' (NA 44010—male parent showing resistance or tolerance to all nematodes); six hybrids of *S. alba* with *S. glaucophylloides* (NA 44019—male parent susceptible only to *M. arenaria*—Race 1); two hybrids of *S. alba* x *S. humilis* (NA 43997—male parent tolerant of *M. incognita);* and seven hybrids of *S. alba* x *S. apennina* (NA 44005—male parent resistant to *M. incognita). All* of the hybrids were susceptible to *M. incognita, M. javanica,* and both races of *M. arenaria.*

Nematode effects on growth. When this study was initiated, we were certain of only the parasite-host relationship between the infested *S. alba* (NA 44016) clone and the nematode *(M. arenaria*—Race 2) isolated from it. Therefore, we made initial stem growth determinations on only that clone. The average shoot extension of 10 inoculated plants and 10 uninoculated controls on the date of inoculation (21 March 1989) was 10.6 cm. Significant growth reduction of the inoculated plants was noted after only 20 days, when they averaged 20.6 cm as opposed to 32.1 cm for the controls. After 60 days, the inoculated plants averaged 35.1 cm in shoot length and the controls were 70.2 cm tall. Thus nematode infestation had reduced growth by nearly 60%.

Although early height growth measurements had not been made on plants of NA 44016 inoculated with other nematodes, significant growth reduction after 60 days can be inferred in plants inoculated with *M. hapla* (44.6 cm), *M. incognita* (35.1 cm), and *M. javanica* 42.2 cm). Apparently, *M. arenaria*—Race 1 had no detrimental effect on growth and plants inoculated with this nematode averaged 72.4 cm, similar to the controls.

Nematode inoculation did not appear to reduce the growth of *S. babylonica* 'Babylon' (NA 44011), although the lack of pre-inoculation measurements precluded any precise judgements. Forty days after inoculation, plants in all of the nematode-inoculated groups had grown more than the controls, with those treated with the *Salix* isolate of *M. arenaria*—Race 2 being the most vigorous. After 60 days, the controls were still smaller (42.8 cm) than those plants inoculated with *M. arenaria*—Race 2 (57.2 cm), *M. arenaria*—Race 1 (52.0 cm), *M. hapla* (48.3 cm), *M. javanica* (47.3 cm), or *M. incognita* (45.3 cm).

Because of the small numbers (two per treatment) of plants of the other clones, it was not possible to make any inferences about the effects of nematodes on shoot growth but no differences were apparent. Growth reduction of nematode-infested crop plants is a common phenomenon. However, increased top growth of potato infested with *M. hapla* has been noted (10). It is likely that growth effects would vary with the nematode species and their abundance, the host genotype, and various aspects of the below-ground and above-ground environment. Of special interest is the fact that growth of clone NA 44016 was reduced by inoculation with *M. hapla* (which produced no galls) while the heavily-galled plants inoculated with *M. arenaria*—Race 1 grew normally.

Conclusions

Most of our commonly planted landscape willow, especially the "weeping" selections, are highly susceptible to root-knot nematodes that are widely distributed in the soils of temperate United States. Even though our hybrids of *S. alba* and nematode-resistant shrubby willow species were all susceptible, there still may be a possibility of developing hardy, weeping, nematode-resistant cultivars for the future. Our resistant native black willow *(S. nigra)* is, however, a diploid (2n=38 chromosomes) while *S. babylonica* (and the *S. alba* x *S. babylonica* hybrids) are tetraploid. Thus, the first-generation hybrids from *S. nigra* x "Weeping" are likely to be susceptible because of the preponderance of genes from the susceptible parent. Advanced generation breeding and backcrossing to *S. nigra* would be necessary to create populations for eventual selection of nematode-resistant individuals.

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