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Resistance of Auto- and Allotetraploid Triticeae Species and Accessions to *Meloidogyne chitwoodi* based on Genome Composition[1]

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Abstract: The Columbia root-knot nematode *Meloidogyne chitwoodi* parasitizes several plant species, including grasses that have been developed for semiarid environments, and substantially reduces the productivity of cereals and the longevity of perennial grasses growing under semiarid conditions throughout the intermountain region. Thirty-two auto- and allotetraploid (2n = 28) taxa in the perennial Triticeae were evaluated as possible sources of resistance to *M. chitwoodi.* Low levels of root galling were observed on roots of all accessions; root-gall indices ranged from 0 (no galls) to 1.95 in the grasses compared to 4.67 for the susceptible 'Ranger' alfalfa check on a scale of 1 to 6. Even though the gall ratings were low, significant ($P < 0.01$) differences among accessions of the same species, among species, and among genera with different genomes were observed. Within the reproductive indices, which ranged from 0.01 to 1.20 in the grasses compared to 65.38 for the alfalfa check, there was no difference among genera with different genomes and accessions within the same species and genome; however, there was a significant ($P < 0.05$) difference among species with the same genomes. This variation can be traced to *Thinopyrum nodosum* (Jaaska-19), which was the only accession with a reproductive factor greater than 1.00. Based on the data, all auto- and allotetraploids are considered resistant to *M. chitwoodi.*

Key words: Agropyron, Columbia root-knot nematode, *Elymus,* grasses, *Hordeum,, Meloidogyne chitwoodi,* nematode, *Psathyrostachys, Pseudoroegneria,* resistance, *Thinopyrum.*

The perennial grasses of the tribe Triticeae are among the world's most valuable forages and are an important gene source for wheat (*Triticum aestivum*), barley (*Hordeum vulgare*), and rye (*Secale cereale*) breeders (Dewey, 1984). More than 155 million hectares of rangelands in the eight states of the intermountain region provide essential forage for livestock. In addition, these rangelands provide habitat for wildlife and have important recreational value. Surprisingly, only 14% of these rangelands are classified in good condition (Schmautz et al., 1980).

Plant-parasitic nematodes reduce the productivity of cereals and the longevity of perennial grasses growing under semiarid conditions throughout the intermountain region (Griffin, 1985). Several species of root-knot nematodes are associated with the growth of grasses (Griffin 1985, 1992; Riggs et al., 1962). The Columbia root-knot nematode, *Meloidogyne chitwoodi* Golden, O'Bannon, Santo & Finley, is parasitic on several plant species, including grasses that have been developed for semiarid environments. The development of superior forage grasses for revegetation in these harsh environments has been successful in the past and is relatively economical. However, if progress is to continue, additional sources of disease and insect resistance must be identified within the grasses.

Meloidogyne chitwoodi is also a serious parasite on potato (*Solanum tuberosum L.*) in the western United States, causing marked reductions in potato yields, particularly when potato fields are rotated with cereals (Griffin, 1985). Development and use of nematode-resistant cereals would reduce the nematode population density in the soil and thus reduce yield losses in potato production.

Hybridization between and within annual and perennial Triticeae species has been used to transfer disease and insect resistance since the 1930s, when Tsitsin (1960) demonstrated that *Thinopyrum ponticum, T. intermedium,* and *T. junceum* hybridized readily with various species of *Triticum.* Sharma and Gill (1983) published a review on wide hy-

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bridization with wheat and its related grass relatives.

The genomic system of classification within the perennial Triticeae grasses groups species with similar genomes. The term genome is a letter designation (i.e., A, B, C) that identifies the chromosomes within the base chromosome number (i.e. within the Triticeae the base chromosome number is 7). In a true autotetraploid (2n = 28), the genomic formula would be AAAA; in an allotetraploid, the genomic formula would be AABB (two different chromosome groups). Based on the genomic system of classification, the genus *Agropyron* would be limited to those species containing only the P genome. The genus *Pseudoroegneria* is comprised of species with various combinations of the S and P genomes. The genus *Hordeum* contains the H genome. *Psathyrostachys* species are comprised of the N genome. The genus *Thinopyrum* consists of three basic genomes, J, E, and S. The genus *Elymus* consists of approximately 150 allopolyploid species with various genome combinations of the S, H, Y, P, and W genomes. The genus *Leymus* contains species ranging in chromosome number from 2n = 28 to 84, comprised of the N genome and an unidentified genome.

Jensen and Griffin (1994) surveyed 35 accessions representing 15 diploid (2n = 2x = 14) species within the Triticeae for possible sources of resistance to *M. chitwoodi.* They reported that diploid taxa within the genera *Thinopyrum* (*T. bessarabicum*) and *Psathyrostachys* (*P. fragilis, P. juncea,* and *P. stoloniformis*) expressed more resistance to *M. chitwoodi* than other diploid species in the genera *Agropyron, Pseudoroegneria,* and *Hordeum.* However, they concluded that there was enough variation in resistance to *M. chitwoodi* between genera and within species to warrant selection of Triticeae grasses for incorporating increased resistance to *M. chitwoodi* in cereal breeding programs.

The objectives of this study were to evaluate 32 amphiploid taxa in the perennial Triticeae for possible sources of resistance to *M. chitwoodi* and to correlate the resistance reported in the diploid taxa (Jensen and Griffin, 1994) to that observed in the tetraploids.

Materials and Methods

Seeds of 82 accessions representing 32 auto- and allotetraploid (2n = 4x = 28) species (seven genera) within the perennial Triticeae (Table 1) were obtained from the U.S. Living Collection of Perennial Triticeae Grasses (Forage and Range Research Laboratory, USDAARS, Logan, UT). Within each accession, 27 to 42 plants were tested for their responses to *M. chitwoodi* race 2 collected from a potato field at Beryl, Utah, and maintained on tomato (*Lycopersicon esculentum* Mill.) in the greenhouse. Eggs were collected with the NaOCl method (Hussey and Barker, 1973).

Seeds were germinated in moist vermiculite, and one seedling was planted into each plastic tube (6-cm-diam., 30-cm-long) containing 540 cm^3 steam-sterilized Kidman fine sandy loam (coarse-loamy mixed mesic Calcic Haploxeroll; 85% sand, 8% silt, 7% clay; pH 7.1; 0.5% organic matter). Thirty days after planting, each tube was infested with 4 eggs/cm^3 soil. An egg suspension in deionized water was poured into four 10-cm-deep holes in the soil around each plant. Plants were arranged within a greenhouse that was maintained at 24 ± 3 °C in a randomized complete-block design with six replications and seven plants per replication; however, within some replications not all seven plants survived. Supplemental light for a 19-hour daylength was provided by fluorescent lamps. Plants were watered daily and fertilized monthly with a complete nutrient solution (Silvius et al., 1978). Plants were harvested 120 days after inoculation, and root gall indices were determined: 1 = no galling; 2 = trace–10%; 3 = 11–20%; 4 = 21–50%; 5 = 51–80%; and 6 = 81–100% root tissue galled (Cook and Evans, 1987). Nematode eggs were collected from each root system with the NaOCl method (Hussey and Barker, 1973). Eggs were counted and the nematode reproductive factor (Pf/Pi = final nematode population per plant/initial nematode population per plant) was calcu-

TABLE 1. Differences in resistance and susceptibility of polyploid Triticeae species and plant introductions (PI) to *Meloidogyne chitwoodi*.

Species	Genome[c]	n	Root gall rating[a] Mean	Nematode reproductive factor[b] Mean
A. cristatum	PP			
'Ephriam'		41	1.02	0.03
PI180794		41	1.15	0.03
PI222957		39	1.08	0.11
PI273734		41	1.12	0.09
Species mean		162	1.10	0.06
A. desertorum	PP			
PI249143		42	1.02	0.04
PI314057		39	1.03	0.05
PI414666		37	1.16	0.42
Species mean		118	1.07	0.16
A. fragile	PP			
PI314608		33	1.21	0.05
PI429789		40	1.10	0.05
PI547300		40	1.10	0.05
Species mean		113	1.10	0.05
Genome mean	PP	393	1.09	0.09
Pseudoroegneria geniculata	SS			
DJ3882		40	1.40	0.09
DJ3931		37	1.20	0.11
DJ4016		42	1.00	0.03
Species mean		119	1.19	0.07
P. spicata	SS			
PI232124		40	1.00	0.04
PI232125		41	1.05	0.04
PI232126		42	1.02	0.13
Species mean		123	1.02	0.28
P. stipifolia	SS			
PI383560		38	1.12	0.27
PI440095		40	1.18	0.28
Species mean		78	1.17	0.28
P. strigosa	SS			
PI531752		37	1.00	0.01
PI531753		40	1.10	0.04
Species mean		77	1.05	0.02
Genome mean	SS	397	1.11	0.10
P. deweyi	SP			
PI502264		41	1.07	0.03
PI531756		35	1.26	0.71
Species mean		76	1.16	0.34
Hordeum brachyantherum	HH			
D3608		42	1.00	0.10
PI531764		42	1.05	0.10
Species mean		84	1.02	0.10
H. brevisubulatum	HH			
PI229449		38	1.03	0.04
PI401388		38	1.21	0.32
Species mean		76	1.12	0.18
H. bulbosum	HH			
PI343189		42	1.10	0.37
PI414669		42	1.10	0.38
PI531776		42	1.10	0.31
Species mean		126	1.10	0.35
Genome mean	HH	286	1.08	0.23

TABLE 1. *Continued*

Species	Genome[c]	n	Root gall rating[a] Mean	Nematode reproductive factor[b] Mean
Psathyrostachys juncea	NN			
AJC595		42	1.05	0.02
AJC596		42	1.02	0.05
AJC600		35	1.00	0.01
Species mean		119	1.03	0.02
Elymus canadensis	SH			
D3364		41	1.00	0.06
PI531565		42	1.02	0.05
PI531569		42	1.00	0.06
Species mean		125	1.01	0.06
E. caninus	SH			
PI172364		42	1.02	0.04
PI439906		42	1.05	0.18
PI499413		39	1.23	0.38
Species mean		123	1.10	0.20
E. elymoides	SH			
D3341		41	1.07	0.03
PI531602		36	1.00	0.02
PI531605		42	1.02	0.02
Species mean		119	1.03	0.03
E. glaucus	SH			
D3268		42	1.02	0.01
PI232263		41	1.02	0.12
PI232281		38	1.05	0.03
Species mean		121	1.03	0.05
E. lanceolatus	SH			
'Critana'		38	1.03	0.02
PI531623		41	1.00	0.06
PI531624		38	1.00	0.01
Species mean		117	1.01	0.03
E. sibiricus	SH			
PI499458		42	1.10	0.10
PI499613		42	1.00	0.10
Species mean		84	1.05	0.10
E. trachycaulus	SH			
DJ3956		42	1.36	0.70
PI276711		42	1.00	0.04
Species mean		84	1.18	0.37
Genome mean	SH	773	1.05	0.11
E. abolinii	SY			
DJ4133		39	1.03	0.04
PI499585		37	1.05	0.06
PI531555		34	1.06	0.03
Species mean		110	1.05	0.05
E. ciliaris	SY			
PI276395		42	1.12	0.43
PI499415		42	1.05	0.10
PI531575		42	1.36	0.40
Species mean		126	1.17	0.31
E. fedtschenkoi	SY			
DJ3798		32	1.06	0.08
PI531607		41	1.10	0.18
Species mean		73	1.08	0.13

TABLE 1. *Continued*

Species	Genome[c]	n	Root gall rating[a] Mean	Nematode reproductive factor[b] Mean
E. strictus	SY			
PI499474		42	1.00	0.11
PI499477		42	1.02	0.04
PI531682		42	1.00	0.04
Species mean		126	1.01	0.06
Genome mean	SY	435	1.08	0.14
Leymus ambiguus	NX			
PI531795		41	1.00	0.02
PI531796		42	1.02	0.01
Species mean		83	1.01	0.01
L. cinereus	NX			
D2872		41	1.00	0.04
PI547343		42	1.00	0.04
Species mean		83	1.00	0.04
L. karataviensis	NX			
PI314667		41	1.37	0.87
L. multicaulis	NX			
D3773		42	1.26	0.15
PI440321		42	1.26	0.58
PI440324		42	1.10	0.20
Species mean		126	1.21	0.31
L. salinus	NX			
KJ8		39	1.05	0.05
PI531816		40	1.03	0.01
Species mean		79	1.04	0.03
L. triticoides	NX			
D2950		41	1.07	0.11
'Shoshone'		41	1.44	0.76
PI531822		42	1.10	0.05
Species mean		124	1.20	0.30
Genome mean	NX	536	1.13	0.22
Thinopyrum caespitosum	ES			
PI383579		39	1.05	0.03
PI531715		27	1.33	0.06
Species mean		66	1.17	0.04
T. nodosum	ES			
Jaaska-19		40	1.95	1.20
PI531735		39	1.08	0.09
PI531736		41	1.02	0.03
Species mean		120	1.35	0.44
Genome mean	ES	186	1.28	0.30
T. junceiforme	JE			
D3463		35	1.00	0.01
PI297873		39	1.00	0.02
Species mean		74	1.00	0.01
M. sativa				
Ranger alfalfa	(susceptible)	12	4.67	65.38
Syn XX	(resistant)	12	1.08	0.02
Syn YY	(resistant)	12	1.00	0.21
Genome LSD (P = 0.05)			0.26	0.12

[a] Root galling index: 1 = no galls, 2 = 1–10% root tissue galled, 3 = 11–30% root tissue galled, 4 = 31–50% root tissue galled, 5 = 51–80% of the root tissue galled, and 6 = 81–100% root tissue galled.

[b] Reproductive factor = Pf/Pi, where Pf = the final number of nematodes per plant and Pi = the initial number of nematodes per plant.

[c] Letter designation denoting chromosome sets within each genus.

lated. Data were analyzed as a randomized complete block with unequal sample sizes (SAS, SAS Institute, Cary, NC). The main effects were genomes, species within genomes, and accessions within species and genomes. The error term was replications × accessions within species and genomes. An LSD was computed for genomes but, due to plant mortality during the experiment resulting in unequal sample sizes, an LSD was not computed for species and accessions. The alfalfa cultivar Ranger was used as a susceptible check with Syn XX and Syn YY as resistant alfalfa checks.

Results and Discussion

Low levels of root galling were observed on roots of all accessions. Root-gall indices ranged from 1.0 to 1.9 in the grasses compared to 4.7 for the susceptable alfalfa (Table 1). All accessions except *Thinopyrum nodosum* (Jaaska-19), which had a reproductive factor of 1.2, had reproductive factors less than 1.0, demonstrating the inability of the nematode to reproduce on all grass accessions studied (Table 1). The susceptible alfalfa cultivar Ranger had a reproductive factor of 65.4, confirming that environmental conditions were suitable for nematode reproduction.

Throughout this study all polyploids, regardless of genome and taxonomic placement, had lower reproductive factors (Table 1) than the representative diploids (Jensen and Griffin, 1994). In general, polyploid plants are larger, more vigorous, and more adaptable than diploids growing under a wide range of changing environments (Zeven, 1979).

The genus *Agropyron* sensu stricto contains three ploidy levels: diploid (2n = 2x = 14; *A. cristatum* and *A. mogolicum*), tetraploid (2n = 4x = 28; *A. cristatum, A. desertorum,* and *A. fragile*), and hexaploid (2n = 6x = 42; *A. cristatum*), all comprised of the P genome. Unlike the diploids *Agropyron cristatum* and *A. mongolicum,* which had reproductive factors of 16.5 and 4.5, respectively (Jensen and Griffin, 1994), the tetraploid accessions of *Agropyron* (Table 1) had reproductive factors that averaged 0.5. The reproductive factors obtained for the tetraploid *Agropyron* accessions were different from those previously reported by Griffin and Asay (1989) for the tetraploid cultivars Hycrest and Nordan, which had reproductive factors of 7.0 and 8.5, respectively. However, the results of Jensen and Griffin (1994) and Griffin and Asay (1989) are in agreement for reproductive factors within the *Agropyron* diploids, which appear to have higher reproductive factors. In selecting appropriate parental material, emphasis should be placed on the autotetraploids rather than diploids as a potential source of resistance.

Pseudoroegneria, a recently constructed genus, consists of about 15 species previously included in *Agropyron* or *Elytrigia.* All taxa are diploid (2n = 14) or autotetraploid (2n = 28) and contain the S genome. Two additional allotetraploid taxa included in the genus *Pseudoroegneria* but comprised of the S and P genomes are *P. pretenuis* and *P. deweyi.* Jensen and Griffin (1994) and Griffin et al. (1984) reported a low reproductive factor of 1.2 for *M. chitwoodi* on the North American diploid bluebunch wheatgrasses, which is consistent with reproductive factors in the autotetraploid bluebunch wheatgrass *P. spicata* of North America (Table 1). However, autotetraploid accessions of bluebunch wheatgrasses from Eurasia, *P. geniculata, P. stipifolia,* and *P. strigosa* exhibited lower reproductive factors for *M. chitwoodi* than previously observed in the diploid bluebunch wheatgrasses from Eurasia (Jensen and Griffin, 1994). Species comprised of the SP genomes (Table 1) demonstrated levels of resistance to *M. chitwoodi* similar to those in other *Pseudoroegneria* species. Thus, the best sources of resistance appear in North American diploid and tetraploid *P. spicata* and tetraploid Eurasian bluebunch wheatgrasses.

Hordeum is genomically heterogeneous and comprised of taxa that are diploid, tetraploid, and hexaploid. Jensen and Griffin (1994) reported reproductive factors for *M. chitwoodi* within diploid *Hordeum* species ranging from 0.1 in *H. chilensis* to 96.9 in *H. bogdanii,* with an overall reproductive factor of 38.3. The tetraploid *Hordeum* species, *H.*

brachyantherum, H. brevisubulatum, and *H. bulbosum,* showed little variation in reproductive factors (Table 1) compared to the diploids (Jensen and Griffin, 1994). In identifying sources of resistance, emphasis should be placed on the tetraploid species.

Psathyrostachys is a small genus of about 10 species, all of which contain the basic N genome. *Psathyrostachy juncea* (Russian wildrye) is one of only two known, naturally occurring autotetraploids within this genus. Reproductive factors within the tetraploid accessions (Table 1) are consistent with those reported for the diploid *P. juncea* (RF = 1.2), *P. fragilis* (RF = 1.8), and *P. stoloniformis* (RF = 0.6) (Jensen and Griffin, 1994). The accessions of tetraploid Russian wildrye (NN) had nematode reproductive factors (RF = 0.02) lower, but not significantly so, than those observed in *Leymus* tetraploids (Table 1), where the N genome is one of the progenitors to the genus *Leymus.* There appeared to be no difference in the reproduction of *M. chitwoodi* on either the diploid or tetraploid taxa within *Psathyrostachys.*

Elymus is by far the largest genus of the Triticeae when defined according to genomic content (Jensen and Salomon, 1995). It contains approximately 150 species with various combinations of the S, H, Y, P, and W genomes. The majority of the species within *Elymus* are allotetraploids comprised of the SH and SY genomes, where the diploid progenitor of the Y genome is still unknown. Eight SH genome and four SY genome species (Table 1) were screened for resistance to *M. chitwoodi.* Regardless of the genome combination, the nematodes were not able to reproduce. This level of resistance in the SH and SY tetraploids is consistent with the lower reproductive factors observed in each of the S and H genome diploid progenitors (Jensen and Griffin, 1994), suggesting that resistance to the root-knot nematode can be manipulated through hybridization and selection of appropriate parents.

Leymus is a polyploid genus of about 30 species worldwide. All species of *Leymus* are based on the N genome from *Psathyrostachys* and a genome X of unknown origin. None of the six *Leymus* species (*L. ambiguus, L. cinereus, L. karataviensis, L. multicaulis, L. salinus,* and *L. triticoides*) had reproductive factors greater than one. Our data confirm those of Griffin et al. (1984), who reported low nematode reproduction on *L. cinereus* inoculated with 5,000 *M. chitwoodi* eggs. The high level of resistance is in part due to the presence of the N genome from *Psathyrostachys,* which has demonstrated a high level of resistance (Jensen and Griffin, 1994).

Thinopyrum is a recently erected genus that, according to Dewey's (1984) definition, encompasses about 20 species that originated near the Mediterranean. This genus is centered around the diploid J^b genome from *T. bessarabicum* and the J^e genome from *T. elongatum.* Jensen and Griffin (1994) reported significantly different ($P < 0.01$) reproductive factors for the above taxa with *T. bessarabicum* being more resistant. Griffin et al. (1984) reported no Columbia root-knot nematode reproduction on *T. intermedium.* The only accession in the study to have a reproductive factor greater than one was *T. nodosum* (Table 1); however, the reproductive factor was low enough to be classified as moderately resistant. All other accessions would not allow the root-knot nematode to reproduce (Table 1). Based on the available data, and the ability to transfer genes from *Thinopyrum* species into the cereal crops, emphasis should be placed at the tetraploid and higher ploidy levels.

Despite the differences in reproductive factors, which ranged from 0.01 to 1.2 across all 82 accessions, the auto- and allotetraploids studied all would be considered resistant to the root-knot nematode when compared to the alfalfa check with a reproductive factor of 65.4 (Table 1). The lack of variation for resistance within and between genera suggests that gains in resistance to the root-knot nematode within these grasses through conventional breeding will be slow; however, they may serve as a valuable gene source in breeding programs for developing root-knot nematode resistance within the cereal crops wheat, barley, and rye.

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