Resistance of Potato Breeding Clones and Cultivars to Three Species of Potato Cyst Nematode

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Abstract

In the United States, potato cyst nematodes *Globodera rostochiensis* and *G. pallida* are quarantined pests. A new cyst nematode species, *Globodera ellingtonae*, discovered in Oregon and Idaho, reproduces well on potato but is not currently a quarantine pest. Identifying resistance to all three *Globodera* spp. would provide a valuable management tool. Thirteen breeding clones and nine cultivars were evaluated in Oregon, Idaho, and New York laboratories where the nematode populations are maintained. Minutubers or tissue culture plants were planted into pots and inoculated with eggs in replicated experiments. Results indicated that five entries were partially resistant or resistant to all three species, while

another five were resistant or partially resistant to *G. rostochiensis* and *G. ellingtonae*. Resistance to *G. rostochiensis* pathotypes Ro1 and Ro4 is controlled by the H1 gene and this study suggests that H1 may confer resistance to *G. ellingtonae* as well. Observed resistance to *G. pallida* was lower relative to the levels of resistance observed for *G. rostochiensis* and *G. ellingtonae*. Germplasm with *G. pallida* or *G. ellingtonae* resistance will be used in hybridizations to develop russet-skinned cultivars with long tubers which represent the predominant market class in western U.S. production, and to further explore the basis of potato resistance to *Globodera* spp.

Globodera pallida and *G. rostochiensis*, collectively known as potato cyst nematodes (PCN), have a narrow host range, reproducing primarily on solanaceous crops (potato, tomato, eggplant, and pepper) and some solanaceous weeds (den Nijs 2007). Potato plants grown in infested fields grow poorly in aggregated areas of the field, which subsequently increase in size as potato crops are repeatedly grown in those areas (MacGuidwin 2001). If not controlled, both species can cause significant damage to potato yields and, consequently, are under quarantine or regulatory status worldwide (Brodie 1984; Singh et al. 2013). Although chemical control through fumigation can be used to produce a crop in an infested area, the cost of fumigation can reach levels which effectively reduce or remove the profit margin from production, making potato production unsustainable. Host resistance available in cultivars acceptable to the industry provides the best means of long-term management of PCN.

G. rostochiensis was first detected in the United States on Long Island, NY where field symptoms had been noted since the late 1930s (Evans and Brodie 1980). Despite quarantine controls established in New York by 1944, additional infested fields were detected in 1967, 1974, and 1976 in nearby counties (Brodie and Mai 1989; Evans and Brodie 1980). As of September 2014, approximately 126,261 ha were regulated in eight counties in New York and 2,422 ha were considered infested and have an active control and mitigation program in place to prevent the spread of *G. rostochiensis* (APHIS 2014).

In 2006, *G. pallida* was first reported in the United States in eastern Idaho (Hafez et al. 2007). Regulations were put into place through a Federal Order in August 2006 for infested fields in Idaho, with regulatory oversight and controls for the area that encompassed the infested fields. In 2007, an interim rule was put into place to

establish field-by-field regulations as part of the next phase in rule-making (APHIS 2007). Delimiting surveys were conducted in both seed and commercial potato production areas. Although the overall area of infestation in Idaho is relatively small, the number of fields identified as infested has slowly increased. By 2012, the number of *G. pallida*-infested fields was 17, totaling 775 ha (APHIS 2012). In 2013, the number of *G. pallida*-infested fields was 21 with a total area of 931 ha (APHIS 2013). At the end of 2014, the number of *G. pallida* infested fields was 26, with a total area of 1,172 ha (APHIS 2015). In December 2016, a new 61-ha field was identified as infested, bringing the total infested area to 1,233 ha (APHIS 2017a). All newly identified infested fields since the initial identification of *G. pallida* infestation were already under the United States Department of Agriculture (USDA) Animal and Plant Health Inspection Service regulatory program due to their association with an infested field. The infested area represents about 1% of the total potato hectares in Idaho (NASS 2016).

In 2008, a previously unknown *Globodera* nematode population was detected in eastern Idaho and in Powell Butte, OR (Skantar et al. 2011). This nematode was classified as a new species, *G. ellingtonae* (Handoo et al. 2012), and has been shown to reproduce well on potato (Zasada et al. 2013). Since this nematode was described, there has been an additional report of its detection in Argentina (Lax et al. 2014). *G. ellingtonae* is not currently considered a quarantine species but additional research is needed to determine its pathogenicity and impact on potato.

The regulatory programs for the respective *Globodera* spp. in New York and Idaho currently have different goals. In New York, the goal is containment and prevention of spread. *G. rostochiensis* remains in only eight counties in New York and those counties use a strict rotation with resistant cultivars and nonhost crops. In Idaho, which leads in U.S. potato production, containment and eradication of *G. pallida* are the goals. This regulatory program relies upon the use of extensive sampling to delimit the infestation, soil fumigation, trap crops, and a core set of parameters to be met before a field is released for potato production. As of January 2017, 20 of the 27 infested fields no longer had detectable viable eggs, and 8 of these fields are eligible to resume potato production with some regulatory oversight (APHIS 2017b).

Ultimately, host resistance with a potato crop that can produce an economic return for the grower is an excellent method for control of *Globodera* spp. For *G. rostochiensis*, a major gene, H1, provides complete resistance to pathotypes Ro1 and Ro4 (Limantseva et al.

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2014). This major gene, originating from *Solanum tuberosum* subsp. *andigena*, has provided durable resistance since its discovery in 1952, and it has been successfully introgressed into many commercial cultivars (Bakker et al. 2004). Unfortunately, resistance to *G. pallida* is not as well developed as for *G. rostochiensis*, with resistance to *G. pallida* being polygenic, with multiple genes acting in an additive fashion to confer higher levels of resistance (Rigney et al. 2017). Innovator represents a more widely grown potato cultivar with quantitative resistance to *G. pallida* likely derived from *S. vernei* (Bradshaw 2009).

This study was undertaken to conduct an initial screening on existing germplasm and parent material in a potato breeding program for resistance to three *Globodera* spp. Two of these species (*G. pallida* and *G. rostochiensis*) exist in many potato producing countries, including the United States (Brodie and Mai 1989; Hafez et al. 2007; Skantar et al. 2007; Sun et al. 2007). The recent identification of *G. pallida* in the United States and a new detection of *G. rostochiensis* in Canada (Sun et al. 2007; Yu et al. 2010) reinforces the need to introgress *Globodera* resistance into germplasm suitable for the U.S. market. Being newly identified, *G. ellingtonae* has not previously been systematically screened against germplasm to identify sources of resistance. Comparison of screening results to *G. pallida* and *G. rostochiensis* may also help to further understand the biology of *G. ellingtonae*.

Materials and Methods

Because of the quarantine status of *G. pallida* and *G. rostochiensis*, evaluations were conducted at three different facilities in the United States: *G. pallida* was evaluated at the University of Idaho, Moscow; *G. rostochiensis* was evaluated at the Federal Golden Nematode Quarantine Facility at Cornell University, Ithaca, NY; and the nonregulated species, *G. ellingtonae*, was evaluated at USDA Agricultural Research Service (ARS) Horticultural Crops Research Unit, Corvallis, OR. In general, the same methods were used at each facility, with minor modifications mentioned below.

Inoculum production. *G. pallida* was originally isolated from fields near Shelley, ID, and species confirmation was achieved through morphological and molecular identification (Skantar et al. 2007). To produce inoculum of *G. pallida*, the population was reared in greenhouses on the susceptible potato cultivar Désirée in 15-cm clay pots filled with sterilized 2:1 sandy loam/sand soil. Plants were grown under greenhouse conditions at 18°C with a 16-h light cycle. All plants were maintained at even moisture by watering with 75 ml of water twice daily and fertilized with Jacks Classic 20-20-20 N-P-K all-purpose fertilizer (J. R. Peters Inc., Allentown, PA) three times per week. After 16 weeks, cysts for experimental use were recovered by extracting from soil using the Fenwick Can method (Fenwick 1940). Prior to experimental use, all cysts were incubated at 4°C for a minimum of 16 weeks. Cysts were placed in sealed pouches (2.5 cm²) made of 250-µm nylon mesh (McMaster-Carr, Santa Fe Springs, CA), and were hydrated in sterile distilled water for 3 days prior to use.

G. rostochiensis pathotypes Ro1 and Ro2 were originally isolated from fields in New York. To produce inoculum of both *G. rostochiensis* pathotypes, the populations were reared in a greenhouse on Katahdin (for Ro1) and Pike (for Ro2) potato in 7.6-cm clay pots filled with sterile 1:1 soil/sand. Nematode-inoculated plants were grown under greenhouse conditions at 18 to 23°C with a 16-h light cycle. Plants were fertilized with a combination of Osmocote (Scotts Company, Marysville, OH) and 20-20-20 N-P-K all-purpose fertilizer. After 12 to 14 weeks, cysts for experimental use were recovered by extracting from dried soil using a USDA cyst extractor (Brodie 1996). Similar to *G. pallida*, cysts were stored at 4°C prior to use in experiments. Cysts were hydrated in sterile distilled water for 2 to 3 days, then prepared for egg extraction. Inoculum was further prepared by releasing eggs from cysts by crushing cysts with a rubber stopper on a 250-µm sieve nested over a 25-µm sieve, with eggs being retained on the latter. Eggs were washed with water into a container, adjusted to a desired volume, and eggs per milliliter was determined under a microscope.

G. ellingtonae was originally isolated from Powell Butte, OR. Inoculum was produced the previous field season by inoculating susceptible potato Russet Burbank in the spring with *G. ellingtonae* cysts containing eggs in 22-liter pots (Grip Lip 2800; Nursery

Table 1. Cultivars and advanced breeding lines used for screening trials for *Globodera pallida*, *G. ellingtonae*, *G. rostochiensis*

Number	Cultivar or breeding line	Female parent	Male parent
1	A03873-3	V-15-71	Gemstar Russet
2	A03882-10YN	V-15-71	A98295-3
3	A061008-4	PA03NM3-4	A00731-2
4	A06689-2	V-15-71	A98345-1
5	A06968-4	PA99N2-1	A00731-2
6	A07934-7	A01010-1	A00731-2
7	A08636-7PCN	V-15-71	A02093-1
8	A08636-8PCN	V-15-71	A02093-1
9	A08636-11PCN	V-15-71	A02093-1
10	A08640-2	V-15-71	Rio Grande Russet
11	A08640-8	V-15-71	Rio Grande Russet
12	NY121	E74-7	N43-288
13	V-15-71	Serrana	NY121
14	Albatros	1.293 112-77	1.3014 102-81
15	Avondale	Ulster Glade	A25119
16	Banba	Slaney	Estima
17	Eden	10899 AD 14	Maris Piper
18	Karaka	002/9	V394
19	Moonlight	1463-1	V394
20	Nicola	Clivia	6430 1111
21	Sante	Y66-13-636	AM66-42
22	Slaney	Maris Page	Cara
ck1	Désirée	Urgenta	Depesche
ck2	Russet Burbank	(mutant of Burbank)	...
ck3	Marcy	Atlantic	Q Q155-3

Table 2. Cultivar and advanced breeding line response to *Globodera pallida* in bioassays conducted at Moscow, ID

Number	Breeding line or cultivar	Average cysts/pot ²	
		2013	2014
1	A03873-3	122.2 abcd	6.7 b
2	A03882-10YN	63.4 cd	4.5 b
3	A061008-4	nt	17.4 b
4	A06689-2	262.9 a	25.3 ab
5	A06968-4	60.6 cd	23.8 ab
6	A07934-7	58.1 cd	32.2 ab
7	A08636-7PCN	18.6 d	12.2 b
8	A08636-8PCN	141.2 abcd	12.3 b
9	A08636-11PCN	180.8 abc	12.4 b
10	A08640-2	47.2 cd	21.1 b
11	A08640-8	51.6 cd	24.8 ab
12	NY121	14.2 d	1.7 b
13	V-15-71	104.2 bcd	13.8 b
14	Albatros	94.6 bcd	15.4 b
15	Avondale	94.2 bcd	9.1 b
16	Banba	176.7 abc	nt
17	Eden	8.4 d	11.4 b
18	Karaka	12.3 d	8.6 b
19	Moonlight	6.7 d	6.3 b
20	Nicola	168.4 abc	26.0 ab
21	Sante	7.7 d	3.4 b
22	Slaney	179.7 abc	10.2 b
ck1	Désirée	131.0 abcd	58.2 a
ck2	Russet Burbank	225.5 ab	17.0 b

² Letters in columns that are different from each other are significantly different ($P \leq 0.05$); nt = not tested.

Supplies Inc., McMinnville, OR) buried in the field at Powell Butte, OR. The following spring, pots were removed from the ground and soil was emptied onto tarps, dried under shelter, thoroughly mixed, and sifted to remove rocks and large debris. Cysts were extracted from dried soil using a USDA cyst extractor. Egg inoculum of *G. ellingtonae* was prepared as described for *G. rostochiensis*.

Source of plant material. Potato cultivars used for nematode screening were maintained at the USDA-ARS potato breeding program at Aberdeen, ID, with breeding clones representing germplasm from the program (Table 1). Plantlets from tissue culture or sprouted tubers were provided to each nematode laboratory for use in the resistance phenotyping. A set of differential plants grown from tissue culture plantlets was also screened against all three nematode species, including the Ro1 and the Ro2 pathotypes of *G. rostochiensis*. Differential entries used were 65.346/19, 62.33.2, D47/11, P55/7, and 12674ab1, originally provided by Dr. Jon Pickup, Science and Advice for Scottish Agriculture.

Potato clone and cultivar evaluations. At each location, evaluations were conducted in either 7.6-cm (New York) or 15-cm (Idaho and Oregon) clay pots that were partially buried in sterilized sand contained in shallow plastic (Idaho and Oregon) or metal (New York) containers to maintain even soil moisture and temperature. Tissue-cultured plantlets, tubers, or sprouted plantlets from tubers were planted in pots containing a 2:1 sandy loam/sand mixture (*G. pallida*) or a 1:1 soil/sand mixture (*G. rostochiensis* or *G. ellingtonae*). At the time of planting, each pot was inoculated with *Globodera* spp. at a density of approximately 5 eggs/g of loam/sand mixture (*G. pallida* or *G. ellingtonae*) and 15 to 20 eggs/g of soil/sand mixture (*G. rostochiensis*). For *G. pallida*, the packet containing encysted eggs was placed directly beneath the roots. For *G. ellingtonae*, freed eggs were pipetted directly onto roots prior to covering with loam/sand mixture. For *G. rostochiensis*, eggs were pipetted into holes made around roots of fully established plants. At each location, the experimental units were arranged in a complete randomized design with genotypes being replicated four to five times. All of the clones and cultivars were evaluated in at least two replicated trials (screenings) at each location. The cultivars Désirée and Russet Burbank were included in

all trials as susceptible controls, with Russet Burbank being the most widely grown cultivar in the United States (41% of fall planted potato) (NASS 2016). The cultivar Marcy was also included in the *G. rostochiensis* trials as a known resistant control to Ro1 (De Jong et al. 2006).

Plants were maintained in greenhouses having temperature ranges of 18 to 23°C with a 16-h light cycle, with the exception of one evaluation in New York which was done in a screenhouse from 25 June to 26 September 2014 with temperatures ranging from 15 to 29°C and natural light. Plants at each location received 20-20-20 N-P-K all-purpose fertilizer alone or combined with a slow-release fertilizer. For *G. rostochiensis* evaluations, plants were removed from pots and the cysts present on the surface of the root ball were counted 8 weeks after nematode egg inoculation. Resistance and susceptibility were determined based on the number of cysts found on the surface of the plant root-ball. Our standard protocol classifies plants with no more than 5 cysts as resistant and plants with more than 5 cysts as susceptible (Plaisted et al. 1984) but, for the objectives of this study, the determination for resistance or susceptibility was based on the relative susceptibility of the controls Désirée and Russet Burbank. For *G. pallida* and *G. ellingtonae* evaluations, plants and soil were removed from pots 16 weeks after nematode inoculation and soil was air dried for 2 weeks. Cysts were then extracted from dried soil using the Fenwick can method (Idaho) or USDA cyst extractor (Oregon). Extracted cysts were counted and recovered for each plant.

Tests for molecular markers. Entries were tested for the presence of markers associated with *G. rostochiensis* resistance using 57R (Finkers-Tomczak et al. 2011) and TG689 (Milczarek et al. 2011) with the protocol outlined in Park et al. (2018), which included visualization of 1.5% agarose gels with a UV transilluminator.

Data analysis. A standard susceptible cultivar was used to calculate relative susceptibility (RS) values as (final cyst density of test cultivar/final cyst density of Désirée) × 100 (OEPP/EPPO. 2006). Désirée was used as the susceptible cultivar for all screenings, with the exception of the second screening for *G. rostochiensis*, when Russet Burbank was used. For *G. rostochiensis*, Désirée had an

Table 3. Cultivar and advanced breeding line resistance to *Globodera ellingtonae* conducted in bioassays at Corvallis, OR

Number	Breeding line or cultivar	Average cysts/pot ^z			
		2012	2013	2013	2014
1	A03873-3	47.8 ef	14.3 fg	...	...
2	A03882-10YN	...	62.7 defg	...	129.8 b
3	A061008-4	145.8 cde	114.0 defg	...	...
4	A06689-2	254.2 b	160.7 cde	...	...
5	A06968-4	242.0 bc	137.7 cde	...	...
6	A07934-7	132.8 de	86.8 defg	...	...
7	A08636-7PCN	...	122.0 def	...	154.8 b
8	A08636-8PCN	...	243.3 bc	...	103.3 b
9	A08636-11PCN	...	350.0 b	...	164.7 ab
10	A08640-2	169.3 bcd	125.8 cdef	...	...
11	A08640-8	128.5 de	53.3 efg	...	...
12	NY121	0.7 f	0.0 g	...	...
13	V-15-71	202.2 bcd	126.8 cdef	...	...
14	Albatros	0.3 f	0.3 g	...	...
15	Avondale	0.0 f	0.0 g	...	...
16	Banba	0.0 f	0.0 g	...	...
17	Eden	0.4 f	0.0 g	...	...
18	Karaka	0.2 f	...	0.2 b	...
19	Moonlight	0.3 f	...	0.0 b	...
20	Nicola	0.0 f	...	0.1 b	...
21	Sante	0.7 f	0.0 g	...	...
22	Slaney	0.0 f	...	...	...
ck1	Désirée	368.9 a	572.2 a	312.2 a	218.7 a
ck2	Russet Burbank	397.3 a	177.3 cd	279.8 a	312.2 a

^z Letters in columns that are different from each other are significantly different ($P \leq 0.05$).

Table 4. Cultivar and advanced breeding line resistance to *Globodera rostochiensis* (Ro1) conducted in bioassays at Ithaca, NY

Number	Breeding line or cultivar	Average cysts/rootball ^z	
		2014 assay 1	2014 assay 2
1	A03873-3	6.8 ab	4.8 bcd
2	A03882-10YN	0.2 b	2.4 de
3	A061008-4	3.1 ab	15.0 a
4	A06689-2	2.4 ab	3.6 cde
5	A06968-4	0.5 ab	14.8 a
6	A07934-7	6.2 ab	15.0 a
7	A08636-7PCN	0.0 b	7.0 bc
8	A08636-8PCN	0.0 b	7.9 b
9	A08636-11PCN	1.0 b	14.6 a
10	A08640-2	2.2 ab	8.3 b
11	A08640-8	2.1 ab	13.8 a
12	NY121	0.0 b	0.0 e
13	V-15-71	0.0 b	0.0 e
14	Albatros	0.0 b	0.0 e
15	Avondale	0.0 b	0.5 e
16	Banba	0.0 b	0.7 de
17	Eden	0.0 b	0.0 e
18	Karaka	1.2 b	0.8 de
19	Moonlight	0.0 b	0.3 e
20	Nicola	0.0 b	0.0 e
21	Sante	0.3 b	0.0 e
22	Slaney	0.0 b	0.9 de
ck1	Désirée	8.9 a	nt
ck2	Russet Burbank	8.6 ab	15.0 a
ck3	Marcy	0.5 b	0.2 e

^z Letters in columns that are different from each other are significantly different ($P \leq 0.05$); nt = not tested.

average of 9 cysts per root ball and Russet Burbank had an average of 15. RS values were then converted to a 0-to-9 scale based on the European and Mediterranean Plant Protection Organization (EPPO) scale, with 0 being the most susceptible and 9 being the most resistant, in order to rank and compare the entries (OEPP/EPPO 2006). For purposes of comparing resistance results for each entry, scatter plots were created for each nematode species. The first-screening resistant rankings were plotted on the x-axis and the second-screening resistant rankings were plotted on the y-axis. Entries were rated as resistant (RS value ≥ 7), partially resistant (RS value 4 to 6), or susceptible (RS value ≤ 3). For comparison of cyst numbers per pot or rootball, means separation was done using Tukey's honestly significant difference test and are reported as LS means ($P \leq 0.05$) (SAS Institute 2015).

Results

All of the *Globodera* spp. reproduced well on the susceptible controls Russet Burbank and Désirée. Désirée ranked eighth and first in two assays and Russet Burbank ranked second and ninth for the highest number of cysts produced for *G. pallida*; for *G. ellingtonae*, Désirée ranked first or second in all assays and Russet Burbank ranked first, second, or fourth; and, for *G. rostochiensis*, Désirée ranked first in one assay and Russet Burbank ranked second and first in two assays (Tables 2, 3, and 4). Resistant variety Marcy ranked fourth (with an average of 0.4 cysts/rootball) for the lowest number of cysts (Table 4).

For *G. pallida* resistance, five entries (A08636-7PCN, Sante, Moonlight, Eden, and Karaka) were partially resistant in both screenings (Fig. 1; Table 2). One entry (NY121) was partially resistant in the first screening and resistant in the second screening. The

remaining entries were all classified as susceptible in at least one screening when compared with Désirée.

For *G. ellingtonae*, nine entries (NY121, Albatros, Avondale, Banba, Eden, Karaka, Moonlight, Nicola, and Sante) were resistant to *G. ellingtonae* in both screenings, with all having an average of fewer than one cyst per pot (Fig. 2; Table 3). Slaney also had fewer than one cyst per pot but was only screened once. One entry (A03873-3) was rated as resistant and partially resistant in two screenings. The remaining entries were all classified as susceptible in at least one screening compared with Désirée.

For *G. rostochiensis*, entries NY121, V-15-71, Albatros, Avondale, Banba, Eden, Moonlight, Nicola, and Sante were resistant in both screenings. Two entries (A03882-10YN and Slaney) were resistant in one screening and partially resistant in the other. Karaka was partially resistant in both screenings (Fig. 3; Table 4). The remaining entries were susceptible in at least one screening compared with Désirée or Russet Burbank. Although plants with a root ball count of >5 cysts have been rated as susceptible based on experience from previous evaluations (Plaisted et al. 1984), the ratings here were based on the number of cysts relative to the susceptible cultivars Désirée or Russet Burbank. The cultivar Marcy, included as a control with Ro1 resistance (De Jong et al. 2006), had, on average, fewer than one cyst per root ball (Table 4). This low cyst density also indicates that there were no *G. rostochiensis* Ro2 present in the eggs used for inoculation. Marcy consistently supports high *G. rostochiensis* Ro2 reproduction (X. Wang, unpublished data).

Nine entries (NY121, Sante, Eden, Moonlight, Albatros, Avondale, Nicola, Slaney, and Banba) with resistance to *G. rostochiensis* and *G. ellingtonae* also had either the TG689 or 57R marker associated with the H1 resistance gene. There were also six other entries

Fig. 1. *Globodera pallida* resistance scores (0 to 9) for screenings conducted in 2013 and 2014. Each data point represents two replications of the screening done for each entry (breeding line or cultivar); data points 3 (score of 3) and 16 (score of 1) not included, due to one screening. S = sensitive, PR = partially resistant, and R = resistant. Numbers in figure correspond to entries listed in Table 1.

(Karaka, V-15-71, A03382-10YN, A03873-3, A08636-8PCN, and A08636-11PCN) with marker presence that had different levels of resistance for both nematode species. Generally, these six entries had lower *G. rostochiensis* and *G. ellingtonae* resistance scores, with the exception of V-15-71, which had a high *G. rostochiensis* (9) score and a low *G. ellingtonae* (3) score (Table 5).

When screening results were compiled and averaged across all three *Globodera* spp., entries with the highest resistance were Eden, NY121, Moonlight, and Sante (Table 5). Comparing EPPO scores, NY121, Sante, Eden, and Moonlight, all had resistance to *G. ellingtonae* and *G. rostochiensis* and partial resistance to *G. pallida*. Karaka was resistant to *G. ellingtonae* and partially resistant to *G. pallida* and *G. rostochiensis*.

A pattern of resistance to *G. ellingtonae* and *G. rostochiensis* and susceptibility to *G. pallida* was noted in five entries: Albatros, Avondale, Banba, Nicola, and Slaney (Table 5). V-15-71 had a high level of resistance to *G. rostochiensis* but was susceptible to the other two *Globodera* spp.

Comparison of the average resistance values for each *Globodera* sp. showed that the lowest amount of resistance was against *G. pallida* at 3.4, with *G. ellingtonae* at 5.6 and *G. rostochiensis* at 5.7 (Table 5). A strong correlation existed between *G. ellingtonae* and *G. rostochiensis* ($r = 0.74$, $P < 0.001$), whereas weak to moderate correlations existed between *G. pallida* and *G. ellingtonae* ($r = 0.39$, $P = 0.06$) and *G. pallida* and *G. rostochiensis* ($r = 0.38$, $P = 0.07$). The strong correlation between *G. ellingtonae* and *G. rostochiensis* was noted in the entries Albatros, Avondale, Banba, Eden, Moonlight, Nicola, NY121, Sante, and Slaney.

Five PCN differential lines were evaluated against the three *Globodera* spp. (Table 6). Two of the five differential lines (*S. vernei*

65.346/19 and *S. multidissectum* P55/7) were susceptible to *G. pallida* and the remaining three lines were partially resistant. Of the five lines, four were resistant to *G. rostochiensis* Ro1 and *S. multidissectum* P55/7 was partially resistant. *S. multidissectum* P55/7 was susceptible to *G. rostochiensis* Ro2, *S. tuberosum* subsp. *andigena* 12674ab1 and *S. vernei* 62.33.3 were resistant, and *S. vernei* 65.346/19 and *S. tuberosum* subsp. *andigena* D47/11 were partially resistant. Two lines (*S. vernei* 65.346/19 and *S. multidissectum* P55/7) were susceptible to *G. ellingtonae* and the remaining three were resistant. Of note was differential line *S. multidissectum* P55/7, which was susceptible to *G. pallida*, *G. rostochiensis* Ro2, and *G. ellingtonae* and partially resistant to *G. rostochiensis* Ro1; no high level of resistance to *Globodera* spp. was observed in this line relative to the other differential lines included in the assessment.

Discussion

The ability to manage the introduction of *G. pallida* in Idaho is greatly limited due to an absence of resistant cultivars having the russet skin, long tuber type, and necessary processing qualities that characterize the predominant market class in the western United States. In fact, a relatively small percentage of the cultivars available worldwide have durable resistance to *G. pallida*. This, coupled with the presence of *G. rostochiensis* and *G. ellingtonae* in the United States, demonstrates the need for the identification of breeding material with broad-spectrum resistance to multiple *Globodera* spp. Resistant cultivars could be used as a management tool for current infestations and to be prepared for future introductions or further expansion of infested acreage, should they occur. This study was initiated as an initial screening of cultivars and breeding lines in the USDA-ARS potato breeding program in Aberdeen, ID identified as having potential

Fig. 2. *Globodera ellingtonae* resistance scores (0 to 9) for screenings conducted from 2012 to 2014. Each data point represents two replications of the screening done for each entry (breeding line or cultivar); data point 22 (score of 9) not included due to one screening. Numbers in figure correspond to entries listed in Table 1.

resistance to *Globodera* based on literature and genetic background. Although previous studies and available literature helped in the identification of material having *G. pallida* and *G. rostochiensis* resistance for this study, no such source of information was yet available for *G. ellingtonae*, with its recent discovery and identification as a new species (Handoo et al. 2012). The results obtained for the susceptible and resistant controls are consistent with previous published work, giving confidence to the test subject results (Blok and Phillips 2012; Park et al. 2018; Zasada et al. 2013).

Resistant germplasm identified in this study (now including material resistant to *G. ellingtonae*) will be used in the development of *Globodera*-resistant varieties suitable for the primary potato market classes in the United States; most notably, the market class unique to North America that is represented by cultivars having long tubers with russet skin.

An examination of the genetic background of the cultivars and the breeding clones with resistance to all three *Globodera* spp. suggest some commonalities and potential broad-spectrum resistance.

New Zealand cultivars Moonlight and Karaka have resistance or partial resistance to all three *Globodera* spp. These cultivars have a common parent, V394, which has the H1 gene (Anderson et al. 1993, 2004). They both also have great-grandparents (K5/2 and K3/5) that are reported to have H1 and H2 genes from *S. multidissectum*. Going back two more generations along the same line is a common parent, CPC 2802, with the H3 gene for *G. pallida* pathotype 2/3 (Pa2/3) resistance. CPC 2802 is an accession in the Commonwealth Potato Collection with a high level of resistance to *G. pallida* (Anderson et al. 1993).

Scottish cultivar Eden has resistance to *G. ellingtonae* and *G. rostochiensis* and a connection of common parentage to Karaka and

Moonlight. Eden's great grandparents are G20/26 and K5/2 and, again, going two generations back from G20 is the common parent CPC 2802 (Bradshaw 2009). Resistance data reported by the European Cultivated Potato Database (<https://www.europotato.org/>) indicates that Eden has resistance to both *G. rostochiensis* and *G. pallida*. Our research also now confirms that Eden has high levels of resistance to *G. ellingtonae* as well.

Breeding clone NY121 from the Cornell University potato breeding program was resistant to *G. ellingtonae* and *G. rostochiensis* and partially resistant to *G. pallida*. The sources of resistance in NY121 to *G. pallida* are most likely derived from ancestral crosses involving bulk *S. tuberosum* subsp. *andigena* pollen (W. De Jong, personal communication). In addition, the paternal grandparent was Stueben, which was derived from a *G. rostochiensis*-resistant parent (Plaisted et al. 1990).

Sante's genetic background includes *S. tuberosum* subsp. *andigena* and *S. vernei* in its ancestry; both species possibly contribute to its observed resistance to *G. ellingtonae* and *G. rostochiensis* and partial resistant to *G. pallida*. Findings of resistance are also corroborated by data reported in the European Cultivated Potato Database that indicates that Sante has high levels of resistance to *G. rostochiensis*, with three references of high to very high resistance to *G. pallida* pathotype 2 and one reference of low to moderate resistance for pathotypes 2 and 3. Our results showed Sante as partially resistant in two different screenings to *G. pallida* from Idaho, which is classified as having the same virulence as European populations in the *G. pallida* Pa2/3 virulence group (Blok and Phillips 2012).

The cultivars Albatros, Avondale, Banba, Nicola, and Slaney were resistant to *G. rostochiensis* and *G. ellingtonae* but susceptible to *G. pallida* (Table 5). These findings are supported by data reported

Fig. 3. *Globodera rostochiensis* resistance scores (0 to 9) for screenings conducted in 2014. Each data point represents two replications of the screening done for each entry (breeding line or cultivar). Data point ck1 (score of 2) not included due to one screening. S = sensitive, PR = partially resistant, and R = resistant. Numbers in figure correspond to entries listed in Table 1.

by the European Cultivated Potato Database where Avondale, Nicola, and Slaney are listed as having high resistance to *G. rostochiensis* Ro1 and low resistance to *G. pallida* Pa1 and Pa2. Interestingly, Avondale and Slaney both have Cara in their pedigrees, and Cara has the same resistance pattern of high resistance to *G. rostochiensis* Ro1 and low resistance to *G. pallida* Pa1 and Pa2.

The observed similarity and strong correlation of *G. ellingtonae* and *G. rostochiensis* resistance scores suggests a common mechanism of resistance to both species, with the H1 gene being a possible candidate (Table 5). Support for the H1 gene conferring resistance to both *G. ellingtonae* and *G. rostochiensis* is further provided by Zasada et al. (2013), with reports of Maris Piper, Satina, and Atlantic, all having the H1 gene, also having resistance to *G. ellingtonae*.

In general, differential line results are in agreement with published results for *G. pallida*. Blok and Phillips (2012) reported that the Idaho population of *G. pallida* had a virulence pattern similar to that of the *G. pallida* Pa2/3 European population. Results presented from our research support this designation; however, partial resistance of three lines to *G. pallida* might be interpreted differently based on previous publications. Differential line *S. vernei* 62.33.3 was previously shown to be resistant to *G. pallida* Pa1 and Pa2 but susceptible to *G. pallida* Pa3 (Kort et al. 1977). *S. tuberosum* subsp. *andigena* D47/11 and 12674ab1 were characterized as resistant to *G. pallida* Pa2 and Pa3 populations (Bryan et al. 2002; Stone et al. 1979);

however, in this study, the differential lines were only partially resistant to the Idaho *G. pallida* population. Although 3 years of *G. pallida* data were available for four of the differential lines, only 1 year was available for *S. tuberosum* subsp. *andigena* 12674ab1 in this study. Subsequent experiments which included this line suggest that *S. tuberosum* subsp. *andigena* 12674ab1 has a high level of resistance to the Idaho *G. pallida* population (unpublished data).

When the *Globodera* differential lines were challenged with *G. rostochiensis* Ro1, previous results showing resistance to *G. rostochiensis* Ro1 populations were supported, except for partially resistant *S. multidissectum* P55/7, which was reported as being susceptible (Fuller et al. 1977; Kort et al. 1977). Response of the differential lines to *G. rostochiensis* Ro2 again confirms previous results; however, partially resistant line *S. vernei* 65.346/19 was expected to be resistant (Kort et al. 1977). No previous reports are available for the response of these differential lines to *G. ellingtonae*, with its relatively recent identification as a new species (Handoo et al. 2012). Although *G. ellingtonae* is more similar to *G. rostochiensis* in its ability to reproduce on the differential lines, there are differences. Specifically, *S. vernei* 65.346/19 is resistant to *G. rostochiensis* Ro1 whereas it was susceptible to *G. ellingtonae*. A similar response with respect to these two species was also observed with breeding line V-15-71, which showed a high level of resistance to *G. rostochiensis* and susceptibility to *G. ellingtonae*. These data, combined with

Table 5. Comparison of resistance ratings across three potato cyst nematode species^z

Number	Breeding line or cultivar	<i>G. pallida</i>	<i>G. ellingtonae</i>	<i>G. rostochiensis</i>	Average
12	NY 121	6.5	9	9*	8.2
21	Sante	6	9	8.5*	7.8
17	Eden	5	9	9*	7.7
19	Moonlight	5.5	9	8.5*	7.7
14	Albatros	2.5	9	9*	6.8
15	Avondale	3	9	8*	6.7
18	Karaka	5.5	9	5.5*	6.7
20	Nicola	2	9	9*	6.7
22	Slaney	2.5	9	7.5*	6.3
16	Banba	1	9	8*	6.0
13	V-15-71	3	3	9*	5.0
2	A03882-10YN	4.5	3.5	6*	4.7
7	A08636-7PCN	4.5	3	6	4.5
1	A03873-3	3.5	6.5	2.5*	4.2
8	A08636-8PCN	2.5	3	5.5*	3.7
11	A08640-8	3	4.5	3	3.5
5	A06968-4	3	3	4	3.3
10	A08640-2	3	3.5	3	3.2
3	A061008-4	3	3.5	2.5 nt	3.0
4	A06689-2	2	2.5	3.5	2.7
6	A07934-7	2.5	3.5	2	2.7
9	A08636-11PCN	2.5	2	3.5*	2.7
ck1	Désirée	2	2	2	2.0
ck2	Russet Burbank	2	2	2	2.0
Average	...	3.4	5.6	5.7	...

^z Asterisk (*) indicates presence of H1 marker 57R or TG689 and nt = not tested for markers.

Table 6. Host status of a set of *Solanum* differentials for *Globodera* spp. found in the United States^y

Differential ^z	<i>Globodera pallida</i> (n = 17)	<i>G. rostochiensis</i> Ro1 (n = 8)	<i>G. rostochiensis</i> Ro2 (n = 8)	<i>G. ellingtonae</i> (n = 12)
65.346/19 (<i>Solanum vernei</i>)	+	—	±	+
62.33.3 (<i>S. vernei</i>)	±	—	—	—
D47/11 (<i>S. tuberosum</i> subsp. <i>andigena</i>)	±	—	±	—
P55/7 (<i>S. multidissectum</i>)	+	±	+	+
12674ab1 (<i>S. tuberosum</i> subsp. <i>andigena</i>)	±	—	—	—
Désirée	+	+	+	+

^y Based on reproduction factor values. Relative susceptibility (RS): — indicates RS 7 to 9 (resistant), ± indicates RS 4 to 6 (partially resistant), and + indicates RS 1 to 3 (susceptible) in each year of testing. Calculated from ability to reproduce on a differential based upon the European Plant Protection Organization RS score, calculated as (final population of test plant/final population on susceptible control (Désirée) × 100; 9 = resistant and 1 = susceptible.

^z Full-size plants derived from tissue culture plantlets.

previously published molecular phylogenies (Handoo et al. 2012; Skantar et al. 2011; Zasada et al. 2015), continue to support the elevation of *G. ellingtonae* to the species level.

In general, the response of differential lines to *G. pallida* and *G. rostochiensis* agrees with the published literature; however, results for partial resistance observed in the current study were previously reported as resistant or susceptible. This may reflect more variable results in the current study or, alternatively, the Idaho *G. pallida* population used in this study may differ slightly in virulence from the European populations used in previous studies. Another possible explanation is somaclonal variation of the five lines in tissue culture. Although no dramatic phenotypic variation occurred in any of the lines, more subtle disease resistance changes cannot be ruled out.

Results from this study show that parental cultivars or clones are available for focused breeding efforts in the United States to produce well-adapted cultivars with resistance to *Globodera* spp. for the U.S. potato industry. The identification of nine entries expressing resistance to both *G. rostochiensis* and *G. ellingtonae* suggest that similar resistance genes may be involved, with H1 being a primary candidate gene. These nine entries have been screened and confirmed as having one or both molecular markers (TG689 and 57R) associated with H1. Breeding line V-15-71 is different from these nine in that it has high resistance to *G. rostochiensis* (9.0) and susceptibility to *G. ellingtonae* (3.0) and has the TG689 molecular marker associated with H1. This observation suggests that there may be a resistance locus specific to *G. ellingtonae* that is tightly linked to H1, with that linkage having been broken through genetic recombination in V-15-71. Further molecular characterization of V-15-71 in the region of H1 would help in elucidating whether joint resistance to *G. ellingtonae* and *G. rostochiensis* is conferred by H1 or by H1 in concert with another tightly linked resistance locus. The resistance in V-15-71 is likely coming from the male parent NY121, which also has the TG689 marker. There are four entries with the marker that have V-15-71 as the female parent, yet they have lower levels of resistance to both nematodes. Discordant responses between the marker and lack of resistance need further evaluation. These different responses may be caused by recombination between H1 and the marker, or the presence of other resistance genes or modifier genes. There are other cases where marker presence and a susceptible phenotype exist. In work done by Park et al. (2018), there are five cases where one or both markers (57R and TG689) were present yet each had a susceptible phenotype. Another example is noted by Milczarek et al. (2014), where 7.7% of the breeding clones were susceptible even when TG689 was present and 5.1% were susceptible when 57R was present.

The first-time detection of *G. pallida* in Idaho and *G. ellingtonae* in Oregon and Idaho, United States and the new detection of *G. rostochiensis* in Quebec, Canada highlight the need for renewed efforts to develop cultivars with resistance to more than one *Globodera* sp.

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Literature Cited

Anderson, J. A. D., Lewthwaite, S. L., Genet, R. A., and Braam, F. 2004. Moonlight: A dual-purpose main crop potato (*Solanum tuberosum*) cultivar. N. Z. J. Crop Hortic. Sci. 32:153-156.

Anderson, J. A. D., Lewthwaite, S. L., Genet, R. A., Gallagher, D., and Braam, F. 1993. Karaka: A new fresh market potato with high resistance to *Globodera pallida* and *G. rostochiensis*. N. Z. J. Crop Hortic. Sci. 21:95-97.

APHIS. 2007. 7 CFR Parts 301 and 305 [Docket No. APHIS-2006-0143] RIN 0579-AC54. Potato Cyst Nematode; Quarantine and Regulations. Online publication. United States Department of Agriculture–Animal and Plant Health Inspection Service. http://www.aphis.usda.gov/plant_health/plant_pest_info/potato/downloads/pcndocs/9-07_interim_rule.pdf

APHIS. 2012. Addition of Pale Cyst Nematode, *Globodera pallida*, Regulated Areas in Idaho. Online publication. SPRO Letters and Federal Orders. http://www.aphis.usda.gov/plant_health/plant_pest_info/potato/downloads/pcndocs/DA-2012-24.pdf

APHIS. 2013. APHIS Adds Pale Cyst Nematode, *Globodera pallida*, Regulated Areas in Idaho. Online publication. SPRO Letters and Federal Orders. http://www.aphis.usda.gov/plant_health/plant_pest_info/potato/downloads/pcndocs/DA-2013-20.pdf

APHIS. 2014. APHIS Removes Golden Nematode (*Globodera rostochiensis*) Regulated Areas in Orleans, Nassau, and Suffolk Counties in New York. Online publication. Federal Order: Removal of regulated areas for GN in New York. https://www.aphis.usda.gov/plant_health/plant_pest_info/nematode/downloads/DA-2014-43.pdf

APHIS. 2015. APHIS Adds Pale Cyst Nematode (*Globodera pallida*) Regulated Areas in Idaho. Online publication. SPRO Letters and Federal Orders. http://www.aphis.usda.gov/plant_health/plant_pest_info/potato/downloads/pcndocs/DA-2015-03.pdf

APHIS. 2017a. APHIS Adds Pale Cyst Nematode (*Globodera pallida*) Infested Field in Idaho. Online publication. SPRO Letters and Federal Orders. https://www.aphis.usda.gov/plant_health/plant_pest_info/potato/downloads/pcndocs/DA-2017-01.pdf

APHIS. 2017b. Pale Cyst Nematode (PCN) Eradication Program – Idaho Falls, Idaho 2017 1st Quarter Report (January 1–March 31). Online publication. United States Department of Agriculture. https://www.aphis.usda.gov/plant_health/plant_pest_info/potato/downloads/pcndocs/surveyupdates/2017/pcn-1st-quarter-2017.pdf

Bakker, E., Achenbach, U., Bakker, J., Vliet, J., Peleman, J., Segers, B., Heijden, S., Linde, P., Graveland, R., Hutten, R., Eck, H., Coppoolse, E., Vossen, E., Bakker, J., and Govers, A. 2004. A high-resolution map of the H1 locus harbouring resistance to the potato cyst nematode *Globodera rostochiensis*. Theor. Appl. Genet. 109:146-152.

Blok, V. C., and Phillips, M. S. 2012. Biological characterisation of *Globodera pallida* from Idaho. Nematology 14:817-826.

Bradshaw, J. E. 2009. Potato breeding at the Scottish Plant Breeding Station and the Scottish Crop Research Institute: 1920-2008. Potato Res. 52:141-172.

Brodie, B. B. 1984. Nematode parasites of potato. Pages 167-212 in: Plant and Insect Nematodes. W. R. Nickle, ed. M. Dekker, New York.

Brodie, B. B. 1996. Effect of initial nematode density on managing *Globodera rostochiensis* with resistant cultivars and nonhosts. J. Nematol. 28:510-519.

Brodie, B. B., and Mai, W. F. 1989. Control of the golden nematode in the United States. Annu. Rev. Phytopathol. 27:443-461.

Bryan, G. J., McLean, K., Bradshaw, J. E., De Jong, W. S., Phillips, M., Castelli, L., and Waugh, R. 2002. Mapping QTLs for resistance to the cyst nematode *Globodera pallida* derived from the wild potato species *Solanum vernei*. Theor. Appl. Genet. 105:68-77.

De Jong, W. S., Donald, E. H., Brodie, B. B., Perry, K. L., Sieczka, J. B., Christ, B. J., Porter, G. A., Paddock, K. M., Peck, M. W., and Plaisted, R. L. 2006. Marcy: A chipping variety with resistance to common scab and the golden nematode. Am. J. Potato Res. 83:189-193.

den Nijs, L. J. M. F. 2007. The canon of potato science: 14. Cyst nematodes. Potato Res. 50:259-262.

Evans, K., and Brodie, B. B. 1980. The origin and distribution of the golden nematode and its potential in the U.S.A. Am. Potato J. 57:79-89.

Fenwick, D. W. 1940. Methods for the recovery and counting of cysts of *Heterodera schachtii* from soil. J. Helminthol. 18:155-172.

Finkers-Tomczak, A., Bakker, E., de Boer, J., van der Vossen, E., Achenbach, U., Golas, T., Suryaningrat, S., Smant, G., Bakker, J., and Govers, A. 2011. Comparative sequence analysis of the potato cyst nematode resistance locus H1 reveals a major lack of co-linearity between three haplotypes in potato (*Solanum tuberosum* ssp.). Theor. Appl. Genet. 122:595-608.

Fuller, J. M., Howard, H. W., and Stone, A. R. 1977. A new pathotype of the potato cyst nematode *Globodera pallida*. Plant Pathol. 26:135-138.

Hafez, S. L., Sundararaj, P., Handoo, Z. A., Skantar, A. M., Carta, L. K., and Chitwood, D. J. 2007. First report of the pale cyst nematode, *Globodera pallida*, in the United States. Plant Dis. 91:325.

Handoo, Z. A., Carta, L. K., Skantar, A. M., and Chitwood, D. J. 2012. Description of *Globodera ellingtonae* n. sp. (Nematoda: Heteroderidae) from Oregon. J. Nematol. 44:40-57.

Kort, J., Ross, H., Rumpfenhorst, H. J., and Stone, A. R. 1977. An international scheme for identifying and classifying pathotypes of potato cyst-nematodes *Globodera rostochiensis* and *G. pallida*. Nematologica 23:333-339.

Lax, P., Rondan Duenas, J. C., Franco-Ponce, J., Gardenal, C. N., and Doucet, M. E. 2014. Morphology and DNA sequence data reveal the presence of *Globodera ellingtonae* in the Andean region. Contrib. Zool. 83:227-243.

Limantseva, L., Mironenko, N., Shuvalov, O., Antonova, O., Khiutti, A., Novikova, L., Afanasenko, O., Spooner, D., and Gavrilenko, T. 2014. Characterization of resistance to *Globodera rostochiensis* pathotype Ro1 in cultivated and wild potato species accessions from the Vavilov Institute of Plant Industry. Plant Breed. 133:660-665.

MacGuidwin, A. E. 2001. Diseases caused by plant-parasitic nematodes. Pages 48-51 in: Compendium of Potato Diseases. W. R. Stevenson, R. Loria, G. D. Franc, and D. P. Weingartner, eds. American Phytopathological Society, St. Paul, MN.

Milczarek, D., Flis, B., and Przetakiewicz, A. 2011. Suitability of molecular markers for selection of potatoes resistant to *Globodera* spp. Am. J. Potato Res. 88:245-255.

- Milczarek, D., Przetakiewicz, A., Kamiński, P., and Flis, B. 2014. Early selection of potato clones with the H1 resistance gene – The relation of nematode resistance to quality characteristics. *Czech J. Genet. Plant Breed.* 50:278-284.
- NASS. 2016. Page 15 in: Potato Area Planted and Harvested, Yield, and Production by Seasonal Group – States and United States: 2015 and Forecasted November 1, 2016. Online publication. National Agricultural Statistics Service (NASS), Agricultural Statistics Board, United States Department of Agriculture (USDA). <http://usda.mannlib.cornell.edu/usda/nass/CropProd//2010s/2016/CropProd-11-09-2016.pdf>
- OEPP/EPPO. 2006. European and Mediterranean Plant Protection Organization. Testing of potato varieties to assess resistance to *Globodera rostochiensis* and *Globodera pallida*. *Eur. Medit. Plant Prot. Org. Bull.* 36:419-420.
- Park, J., Yang, H., De Jong, W. S., and Wang, X. 2018. An evaluation of two H1-linked markers and their suitability for selecting *Globodera rostochiensis* resistant potatoes in the New York breeding program. *Am. J. Potato Res.* 95: 170-177.
- Plaisted, R. L., Halseth, D. E., Brodie, B. B., Thurston, H. D., Slack, S. A., Loria, R., Jones, E. D., and Sieczka, J. B. 1990. Steuben: A golden nematode resistant variety with wide adaptation. *Am. Potato J.* 67:239-243.
- Plaisted, R. L., Thurston, H. D., Brodie, B. B., and Hoopes, R. W. 1984. Selecting for resistance to diseases in early generations. *Am. Potato J.* 61:395-403.
- Rigney, B., Blok, V., Griffin, D., Dalton, E., and Milbourne, D. 2017. Consistent action of two partially effective loci conferring resistance to *Globodera pallida* Pa2/3 across multiple nematode field populations. *Plant Pathol.* 66:1031-1040.
- SAS Institute. 2015. JMP Statistical Discovery software, version 12.2.0. SAS Institute Inc., Cary, NC.
- Singh, S. K., Hodda, M., and Ash, G. J. 2013. Plant-parasitic nematodes of potential phytosanitary importance, their main hosts and reported yield losses. *EPPO Bull.* 43:334-374.
- Skantar, A. M., Handoo, Z. A., Carta, L. K., and Chitwood, D. J. 2007. Morphological and molecular identification of *Globodera pallida* associated with potato in Idaho. *J. Nematol.* 39:133-144.
- Skantar, A. M., Handoo, Z. A., Zasada, I. A., Ingham, R. E., Carta, L. K., and Chitwood, D. J. 2011. Morphological and molecular characterization of *Globodera* populations from Oregon and Idaho. *Phytopathology* 101:480-491.
- Stone, A. R., Fuller, J. M., and Howard, H. W. 1979. The presence of pathotype Pa2 of *Globodera pallida* in the United Kingdom. *Plant Pathol.* 28:134-137.
- Sun, F., Miller, S., Wood, S., and Cote, M. J. 2007. Occurrence of potato cyst nematode, *Globodera rostochiensis*, on potato in the Saint-Amable region, Quebec, Canada. *Plant Dis.* 91:908.
- Yu, Q., Ye, W., Sun, F., and Miller, S. 2010. Characterization of *Globodera rostochiensis* (Tylenchida: Heteroderidae) associated with potato in Quebec, Canada. *Can. J. Plant Pathol.* 32:264-271.
- Zasada, I. A., Ingham, R. E., and Phillips, W. S. 2015. Biological insights into *Globodera ellingtonae*. *Asp. Appl. Biol.* 130:1-8.
- Zasada, I. A., Peetz, A., Wade, N., Navarre, R. A., and Ingham, R. E. 2013. Host status of different potato (*Solanum tuberosum*) varieties and hatching in root diffusates of *Globodera ellingtonae*. *J. Nematol.* 45:195-201.