Insights into the Host Range, Population Decline, and Pathogenicity to Potato of *Globodera ellingtonae*

by
Hannah V. Baker

A THESIS

submitted to

Oregon State University

Honors College

in partial fulfillment of
the requirements for the
degree of

Honors Baccalaureate of Science in Bioresource Research
(Honors Associate)

Presented May 9, 2018
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Hannah V. Baker for the degree of Honors Baccalaureate of Science in Bioresource Research presented on May 9, 2018. Title: Insights into the Host Range, Population Decline, and Pathogenicity to Potato of *Globodera ellingtonae*.

Abstract approved:_____

Inga Zasada

This thesis project has the following specific objectives: (i) Determine pathogenicity of *Globodera ellingtonae* to potato utilizing two trials conducted over a 16 week period, (ii) Elucidate the host range of *G. ellingtonae* using a variety of different *Solanum* weed species and crop species, and (iii) Characterize population decline of *G. ellingtonae* under field conditions at Powell Butte, Oregon over an 18 month period. Data collected is intended to be used to encourage, as warranted based on the data, the application of quarantine measures for *G. ellingtonae* within the U.S. or to provide more robust support of the effectiveness of the existing management plan. In the pathogenicity study, *G. ellingtonae* caused minimal or no impact to the yield of potato compared to impacts reported in the literature for *G. pallida* and *G. rostochiensis*. The host range of *G. ellingtonae* was determined to be restricted to plants within the Solanaceae family. Lastly, reductions in population densities of *G. ellingtonae* were observed in areas with higher initial populations of *G. ellingtonae* while areas with lower initial densities showed little to no reduction. The findings of this thesis project furthered the understanding of the pathogenicity to potato, the host range, and population decline of *Globodera ellingtonae*. The minimal impact of *G.*

ellingtonae on the growth and yield of potato observed in this study is in contrast to what have been observed for the quarantine nematodes *G. pallida* and *G. rostochiensis*, a result which warrants additional research under different environmental conditions. The existing knowledge of the host range of *G. ellingtonae* was expanded to include more members of the Solanaceae family, demonstrating further similarities and differences between *G. ellingtonae*, *G. pallida*, and *G. rostochiensis*. The population decline data supports a need for improved characterization of the population decline of *G. ellingtonae* over longer periods.

Key Words: Pathogenicity, *Globodera ellingtonae*, Potato Cyst, Nematode, Host Range, Population Decline

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Honors Baccalaureate of Science in Bioresource Research project of Hannah V. Baker presented on May 9, 2018.

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I understand that my project will become part of the permanent collection of Oregon State University, Honors College. My signature below authorizes release of my project to any reader upon request.

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ABSTRACT

This thesis project has the following specific objectives: (i) Determine pathogenicity of *Globodera ellingtonae* to potato utilizing two trials conducted over a 16 week period, (ii) Elucidate the host range of *G. ellingtonae* using a variety of different *Solanum* weed species and crop species, and (iii) Characterize population decline of *G. ellingtonae* under field conditions at Powell Butte, Oregon over an 18 month period. Data collected is intended to be used to encourage, as warranted based on the data, the application of stronger quarantine measures for *G. ellingtonae* within the U.S. or to provide more robust support of the effectiveness of the existing management plan. In the pathogenicity study, *G. ellingtonae* caused minimal or no impact to the yield of potato compared to impacts reported in the literature for *G. pallida* and *G. rostochiensis*. The host range of *G. ellingtonae* was determined to be restricted to plants within the Solanaceae family. Lastly, reductions in population densities of *G. ellingtonae* were observed in areas with higher initial populations of *G. ellingtonae* while areas with lower initial densities showed little to no reduction.

The findings of this thesis project furthered the understanding of the pathogenicity to potato, the host range, and population decline of *Globodera ellingtonae*. The minimal impact of *G. ellingtonae* on the growth and yield of potato observed in this study is in contrast to what have been observed for the quarantine nematodes *G. pallida* and *G. rostochiensis*, a result which warrants additional research under different environmental conditions. The existing knowledge of the host range of *G. ellingtonae* was expanded to include more members of the Solanaceae family, demonstrating further similarities and differences between *G.*

ellingtonae, *G. pallida*, and *G. rostochiensis*. The population decline data supports a need for improved characterization of the population decline of *G. ellingtonae* over longer periods.

INTRODUCTION

Plant-parasitic nematodes are one of the primary factors of crop loss in the United States (López-Pérez 2010). Nematodes are economically important pests because of the wide range of species and of susceptible hosts they are able to parasitize. Nematodes inhibit the uptake of water and nutrients by decreasing the functionality of roots through feeding resulting in decreased plant vigor (Marks et al. 1998). They have many unique abilities that make them especially difficult to control. Some of the reasons they are so successful include their coevolution and long association with specific host plants; and their ability to rapidly reproduce, adapt to an ever-changing environment, and survive for lengthy periods of time in adverse conditions and in the absence of an acceptable host plant (Marks et al. 1998).

There are many different plant-parasitic nematode species and available data indicate that some have greater negative impacts on crop productivity than other species (Jones et al. 2013). One of the most important groups of plant-parasitic nematodes is the genus *Globodera* which includes the potato cyst nematodes (PCN; *Globodera pallida* and *G. rostochiensis*). Potato cyst nematodes are considered quarantine organisms in most countries because once established they can cause up to 80% loss in potato yield (CABI/EPPO). Even when the environment is not favorable to the survival of PCN, they are able to persist and have been reported to survive for

20 to 30 years (Marks et al. 1998). Additionally, the second-stage juveniles (J2) that have developed within the cyst can enter diapause. This stage is an extreme form of dormancy where they cannot be stimulated to hatch until the life stage is complete (Perry 1989). With suitable stimulation, the majority of the J2 will hatch. This allows PCN to adapt to the environment within 2 to 3 years of establishment (Marks et al. 1998). Diapause is one reason that limits the ability of farmers to use crop rotation to reduce population densities.

Since the 1940s, there has been an ongoing battle against *G. rostochiensis* in New York. Beginning in the 1970s, there has been success in containing and eradicating *G. rostochiensis* from the state (Jones 2016). Different potato varieties have been developed that have resistance to some of the *G. rostochiensis* biotypes (Jones 2016). More than 900,000 acres have been removed from regulation since 2010 as well (Jones 2016). *Globodera rostochiensis* poses a serious threat to domestic and international trade of potatoes and is a regulated organism in 60 countries worldwide (USDA-PCIT 2013). The other PCN, *G. pallida,* was first elevated to a species in 1973 once it was determined that it differed from *G. rostochiensis* (CABI/EPPO). *Globodera pallida* is regulated as a harmful organism in 81 countries worldwide (USDA-PCIT 2013) and poses a serious threat to international trade similar to *G. rostochiensis*. In Idaho, *G. pallida* was first detected in 2006, and efforts are underway to eradicate this nematode from infested fields. The symptoms of *G. pallida* infestation may resemble the symptoms caused by other plant-parasitic nematodes leading to growers overlooking the infestation. There have been several instances in history where trade between the United States and Canada has been

halted because of the presence of *G. rostochiensis* or *G. pallida*. The United States potato industry annually produces crops valued around $3.73 billion (Agricultural Marketing Resource Center 2014). With potatoes being the fourth most important food crop in the world and the leading vegetable crop in the U.S., additional information about the detrimental effects of nematodes needs to be obtained (Agricultural Marketing Resource Center 2014).

Both previously identified nematodes are significant potato pests and many different countries, including the U.S., have robust quarantine measures in place (Zasada et al. 2013). Any sample found in the U.S. and believed to contain PCN cysts are sent to Beltsville, Maryland to the U.S. Department of Agriculture – Agricultural Research Service Nematology Laboratory for analysis and confirmation (Skantar et al. 2011). Previously unknown and unusual populations of *Globodera* were found in 2008 in one field in Powell Butte, Oregon and two fields in Teton County, Idaho (Zasada et al. 2015). These locations all had a history of potato production. After they were analyzed using morphological and molecular characteristics, these unusual populations were described as a new species, *Globodera ellingtonae* (Handoo et al. 2012). *Globodera ellingtonae* has not been detected in any other location in the U.S. besides the initial detection sites in Oregon and Idaho. Studies using hatching assays, host range studies and phylogenetic analysis have indicated that *G. ellingtonae* is more closely related to *G. rostochiensis* than *G. pallida* (Phillips et al. 2015; Zasada et al. 2015). *Globodera ellingtonae* has also been shown to be able to survive in similar geographic ranges as *G. pallida* and *G. rostochiensis* (Phillips et al. 2015 and 2017). The phylogenetic similarity and the need for quarantine measures for the

existing PCN species have led to questions regarding the level of regulation warranted for *G. ellingtonae*. From these findings we believe that determining the host range of *G. ellingtonae* is crucial to give policy makers and regulators the necessary information to restrict PCN to its already known occurrences in North America (Skantar et al. 2011).

Understanding the interactions involved in the pathogenicity of PCN to potato is critical in understanding how to best counteract or prevent these interactions from occurring. To obtain nutrients, the J2 must damage root cells to establish their feeding sites (Trudgill 1986). The damage done to the roots by the J2 ultimately results in smaller root systems, continual nutrient deficiencies particularly in nitrogen (N), phosphorous (P), and potassium (K), stunted growth and loss in yield (Trudgill 1986). The impact of the J2 on the ability of the roots to uptake water is not evident while the host is in the early stages of growth (Trudgill 1986). However, the effects become more apparent later in the season when the plants demand for water increases due to higher temperatures and an increase in size. The damaged root system is incapable of supplying the necessary amounts of water to the plant resulting in decreased growth and wilting (Trudgill 1986). By gaining a better understanding of the pathogenicity of *G. ellingtonae* to potato better management strategies can be developed and implemented to control these populations and limit yield loss.

The host range for *G. pallida* and *G. rostochiensis* has previously been determined to be narrow and restricted to plant species within the Solanaceae family (Sullivan et al. 2007). Hairy nightshade (*Solanum sarrachoides*) is a common weed species in the Pacific Northwest that has been shown to be an excellent host to both

G. pallida and *G. rostochiensis* (Boydston et al 2010; Mimee et al 2014). Several varieties of potato as well as tomato are hosts for *G. ellingtonae* (Lax et al. 2014; Zasada et al. 2013). From this information, it can be concluded that a more extensive evaluation of the host range of *G. ellingtonae* needs to be conducted. Determining the host range of *G. ellingtonae* can provide critical information when trying to make more informed decisions about sustainable management strategies. Cover and rotation crops have the potential to be alternate hosts for PCN which could maintain populations against the intended purpose of eradication (Boydston et al. 2004; Boydston et al. 2010; Forge et al. 2000). Additionally, management of Solanceous weeds is paramount to ensure PCN populations do not unintentionally increase. Knowing which crops could potentially be used for these more sustainable management strategies is critical for these techniques to truly be successful. Therefore, a goal of this research was to expand the known host range of *G. ellingtonae* with greater focus on other potential Solanaceous host plant species.

Past studies have demonstrated that *G. pallida* and *G. rostochiensis* can survive in the soil for up to 30 years even in unfavorable conditions (Bird et al. 2018). Online tools exist that allow users to synthesize nematode population dynamics for *G. pallida* and *G. rostochiensis* and assist in making decisions about management strategies (Bird et al. 2018). However, *G. ellingtonae* has not been identified or been available to study in order to adequately use these tools to model their population dynamics. While *G. ellingtonae* appears to be phylogenetically similar to *G. pallida* and *G. rostochiensis* there is still more information that can be gathered regarding the natural decline in egg numbers over time. Using the population densities from May

2016 to July 2017 we hope to determine the population decline of *G. ellingtonae* in a field environment. The objective of this analysis of population density trends will provide policy makers with the information necessary to apply quarantine measures over longer periods of time.

The overall goal of this project is to expand knowledge of the biology of *G. ellingtonae*. This aim of providing information is critical in supporting (or not) the development of quarantine measures to protect the U.S. potato industry from the harmful effects of nematodes (Seinhorst 1971). The project has the following specific objectives: (i) Determine pathogenicity of *G. ellingtonae* to potato, (ii) Elucidate the host range of *G. ellingtonae*, (iii) Characterize population decline of *G. ellingtonae* under field conditions at Powell Butte, Oregon, and (iv) Use the resulting data to encourage (as warranted based on the data) the application of quarantine measures for *G. ellingtonae* within the U.S.

MATERIALS AND METHODS

Section 1 – Evaluation of the pathogenicity of *Globodera ellingtonae* to potato

Inoculum of *G. ellingtonae* was produced at Powell Butte, OR by planting potato 'Russet Burbank' into 22-liter pots buried in the soil containing *G. ellingtonae* cysts in May, 2015. Plants were allowed to grow for 4 months, receiving irrigation and fertilizer. The pots were collected and soil was emptied onto a tarp, dried, and passed through a 4-mm sieve. The soil was mixed and subsamples (100 g) collected to determine initial *G. ellingtonae* population densities. Cysts were extracted from ten 100 g soil subsamples using a USDA cyst extractor (Ayoub 1980), collected by hand,

and counted. The number of eggs/cysts was determined by crushing all the collected cysts within the subsample with a rubber stopper on a 60- over a 500-mesh sieve (Zasada et al. 2013). The eggs that were retained on the 500-mesh sieve were washed into a 50 ml polystyrene tube. Depending on the number of cysts crushed, the volumes of the tubes were adjusted to 10 ml for 0 - 25 cysts, 30 ml for 25-75 cysts, and 50 ml for greater than 75 cysts. Eggs were enumerated by counting two 1 ml aliquots using an inverted microscope (Zasada et al. 2013). The average cyst density of the soil was 0.663 (± 0.04) cysts/g soil and the average egg density was 169 (± 13.12) eggs/g soil. The average number of eggs/cyst was 254.9 (± 25.66) eggs/cyst. Soil without *G. ellingtonae*, was collected on a part of the farm at Powell Butte, OR where no *G. ellingtonae* had been found. Collected soil was dried and passed through a 4-mm sieve. Both the infested and uninfested soil was a Redmond ashy sandy loam.

The experimental unit was a 5-liter pot and pots were placed into constructed beds that were 2.44 x 1.22 x 0.305 m. The bed frames were constructed with wood and the beds were lined with pond liner. Four beds were constructed in total with two beds per trial. The experimental design was completely randomized for both trials with treatments replicated 6 times. Soil containing *G. ellingtonae* was mixed with non-cyst soil to achieve desired densities (Table 1). The total weight of soil in the posts was 4,800 g. During the process of mixing the soils, 450 ml of water was added to the mixture to create an initially moist environment. The pots were placed into the beds and the remaining area around the pots was filled with soil to help insulate the pots. A single-drop potato ‘Russet Burbank’ tuber was planted approximately 6 cm

deep in each pot. Two trials were conducted, with the second trial established a week after the first trial.

Table 1 – Attributes of treatments used in determining the pathogenicity to potato of *Globodera ellingtonae* on potato (*Solanum tuberosum*) 'Russet Burbank' in trial 1 and 2.

Treatment Number	Initial population density (eggs/g soil)	Amount of cyst soil required (g)	Amount of non-cyst soil required (g)
1	0	0	4,800
2	6	184	4,616
3	13	369	4,431
4	26	738	4,063
5	52	1,475	3,325
6	104	2,950	1,850
7	169	4,800	0

The pots were watered daily or as needed. Each plant was treated identically in terms of water, temperature, and light. The plants were fertilized with Osmocote Smart-Release Plant Food (Scotts Miracle-Gro; Marysville, OH) at planting and then one more time approximately 3 weeks after emergence with 20N-20P-20K fertilizer (Peters; Allentown, PA). Over the course of the experiments, any plant health issues (insect or pathogen damage, chlorosis, necrosis) present on a plant were noted. After the majority of the plants within an experiment had senesced, at approximate 16 and 15 weeks in experiment 1 and 2, respectively, the experiments were terminated. At this time, the tops of the plants were removed and placed into a 70°C dryer for a week and then weighed to obtain above ground biomass. Each pot was then lifted out of the ground and the contents of the pot emptied into a container. The contents of the pot were laid out to dry for a week in a greenhouse. The tubers were collected and the soil

was mixed within the container so that a 100 g subsample of soil could be collected for *G. ellingtonae* extraction. The number of tubers was counted and each tuber was weighed individually. *Globodera ellingtonae* was extracted from the 100 g soil subsample of soil as described above.

A one-way analysis of variance (ANOVA) was used to test for difference in mean yields, aboveground biomass, tuber number, individual tuber weight for each trail, followed by a Tukey's Honest Significant Difference (HSD) test for pairwise comparisons between trials. Means are provided followed by standard errors. To test for a relationship between initial population density (P_i)and tuber yield and P*i* and aboveground biomass, linear regression with $\log_{10}$ transformed P_i (with 1 added to P_i to adjust for zero values) was performed in concordance with the relationship between P_i and yield proposed by Oostenbrink (1966). Although various models have been proposed to describe the relationship between P_i and yield for PCN, the loglinear equation of Oostenbrink (1966) was used as it is simpler, does not require estimation of unknown parameters such as minimum yield and damage threshold, and has been determined to fit as well or better than other proposed relationships at mid-range P_i (Mulder et al. 1997). Linear regressions were performed separately for each trial. All analyses were performed using JMP 9.1 (SAS Institute Inc., Cary, NC).

Section 2 – Defining the host range of *Globodera ellingtonae*

Cysts of *G. ellingtonae* were reared on potato in the field at Powell Butte, OR in 2014 as described above. The initial cyst and egg densities of the inoculum used in the experiments were determined as described above. Several *Solanum* species were

tested for host status of *G. ellingtonae* including *S. dulcamara*, *S. nigrum*, *S. rostratum*, and *S. sisymbriifolium*. Seeds were obtained from the United States Department of Agriculture Germplasm Resources Information Network (USDA GRIN; https://www.ars-grin.gov/ in Beltsville, MD). Seeds were notched using a micro scalpel, placed on an 85 mm Grade 1 filter paper (Whatman; Buckinghamshire, UK), moistened with deionized water, and subsequently incubated in sealed 100 x 15 mm petri plates (VWR; Radnor, Pennsylvania) in complete darkness at 18°C for 3-5 days. Germinated seeds were then placed in 6-pack containers containing soilless media to continue to root. Potato 'Désirée' was included as a positive control and seedlings were produced by placing tubers in a 25 x 25 cm bin containing soilless media to germinate. Additional crop plants were also evaluated including oats, bell and jalapeño pepper, artichoke, alfalfa, tobacco, tomatillo, wheat, tomato, and eggplant. These were all direct seeded into 6-pack containers containing soilless media. When seedlings were approximately 5 to 7 cm tall, they were transplanted into 10.1 cm round clay pots containing approximately 500 g of 1:1 washed sand and Willamette loam mix. *Globodera ellingtonae* was inoculated onto plant roots either by pipetting ~2,500 eggs directly onto roots in 2-3 ml water or by placing 10 cysts containing eggs directly onto the root system prior to filling in the pots to achieve a density of approximately 5 eggs/g soil.

All experiments were arranged in a randomized complete block design with up to six replications per treatment. Pots containing plants were placed in 99 x 51 x 16.5 cm plastic bins with 25 pots per bin (Sterilite; Townsend, MA). Holes were drilled in the bottom of the bins and screens were secured to the 10 drilled holes.

Plants were watered with 9N-45P-15K fertilizer (Peters) immediately after transplanting. Plants were grown in a greenhouse under long-day conditions, 16-h photo period, with 23/18°C day/night temperatures and were fertilized twice each week with 20N-20P-20K fertilizer.

The plants were grown in the greenhouse for four months or until the plants naturally senesced. At harvest, the aboveground portion of the plant was removed and discarded. The soil from the pots, along with any tubers or roots, was spread out on trays to dry. Tubers and roots were removed and discarded from dry soil. The total amount of dry soil was weighed and 200 g subsamples were collected from each sample. Cysts were extracted, collected, counted, crushed, and the egg density determined as described above.

For each plant, the reproduction factor (RF) was calculated by dividing final egg density (*Pf)* by the initial egg density (*Pi)*. The RF values for host species tested were compared to the RF values of the positive control potato 'Désirée'. The relative susceptibility (RS) of the hosts was calculated by dividing the RF of the plant by the average RF for potato 'Désirée' (EPPO 2006). Each host was given a RS score with 1 indicating the highest level of susceptibility and a score of 9 being the highest level of resistance.

Section 3 – Decline of *Globodera ellingtonae* egg densities over time at Powell Butte, OR

Four areas within a field at Powell Butte, OR with different cropping histories (Table 2) were sampled. To collect samples, five transects approximately 30 m long

were established in each 13 x 30 m area. Along each transect, 20 2.5 x 15 cm-diam. cores were collected into a single composite sample. The collected soil was air dried for at least one week and subsamples of 500 g were collected and *G. ellingtonae* was extracted and quantified as described above. Samples were collected in May 2016, May 2017, and July 2017. For each sample, the average number of eggs/g soil was determined. Data were analyzed using a repeated measure mixed linear model ANOVA. Data were $\log_{10}(x+1)$ to correct for heterodscedasticity. Treatment means were separated using Tukey's honestly significant differences test ($P \leq 0.05$). All analyses were performed using JMP 9.1.

Table 2 – Cropping history of areas of a field at Powell Butte, OR used for *Globodera ellingtonae* research from 2012 to 2017.

Area	2012	2013	2014	2015	2016	2017
1	Potato	Field trial	Grass	Grass	Grass	Potato
2	Fallow	Potato	Field trial	Grass	Grass	Potato
3	Fallow	Grass	Potato	Field trial	Grass	Potato
4	Fallow	Grass	Grass	Potato	Grass	Potato

RESULTS

Section 1 – Evaluation of the pathogenicity of *Globodera ellingtonae* to potato

The trials were significantly different, therefore, the data are presented separately with trends between the two trials highlighted. Three parameters of nematode reproduction were considered, *Pf* (final eggs/g soil), eggs/cyst, and reproduction factor (RF) (Tables 3 and 4). In trial 1, no cysts were recovered from the

non-inoculated control. The lowest *Pf* was from the *Pi* 6 eggs/g soil treatment and this *Pf* was similar to that in the *Pi* 13 eggs/g soil treatment (Table 3). The highest *Pf* was in the *Pi* 104 eggs/g soil, however this *Pf* was not different from that of *Pf* 26, 52, and 169 eggs/g soil treatments. In trial 2, there was minimal contamination of the non-inoculated soil with 1 cyst recovered. There were no significant differences in *Pf* among the treatments in this trial, however, there was a nonsignificant trend of increasing *Pf* with increasing *Pi* (Table 4). In general, *G. ellingtonae* reproduction across *Pi* was higher in trial 1 compared to trial 2. When eggs/cyst was considered, there was variation between the final eggs/cyst densities across the treatments for both trials (Tables 3 and 4). In trial 1, there was no difference among the treatments (Table 3). In trial 2, the largest number of eggs/cyst was produced in the *Pi* 13 eggs/g soil, but this was only different from the eggs/cyst in the *Pi* 104 and 169 eggs/g soil treatments (Table 4). In both trials RF values decreased with increasing *Pi*, with similar trends across trials (Tables 3 and 4). The lowest *Pi*, 6 eggs/g soil, always had the highest RF. In trial 1, this RF value was significantly different from the RF values for *Pi* 104 and 169 eggs/g soil (Table 3). In trial 2, the RF value for *Pi* 6 eggs/g soil was different from the RF values for *Pi* 52, 104, and 169 eggs/g soil (Table 4).

Table 3 – Reproduction of *Globodera ellingtonae* on potato (*Solanum tuberosum*) 'Russet Burbank' inoculated with varying initial egg population densities (*Pi*) of *G. ellingtonae* in trial 1.

Pi[a]	*Pf*[b]	Eggs/Cyst	RF[c]
6	99.1 (± 27.1) c	160.3 (± 16.3)	16.5 (± 4.5) a
13	138.7 (± 34.8) bc	170.0 (± 24.8)	10.7 (± 2.7) ab
26	247.7 (± 20.1) ab	126.4 (± 14.9)	9.5 (± 0.8) ab
52	357.1 (± 50.5) a	146.9 (± 60.1)	6.9 (± 1.0) abc
104	509.8 (± 93.0) a	153.5 (± 45.3)	4.9 (± 0.9) bc
169	490.7 (± 105.2) a	173.3 (± 48.4)	2.9 (± 0.6) c
P-value	*< 0.0001*	*0.5511*	*0.0001*

[a] Initial population density (*Pi*) are eggs/g soil.
[b] Final population density (*Pf*) are eggs/g soil.
[c] RF = reproduction factor (*Pi/Pf*).
[d] Values are the means + standard error. Values followed by the same letter are not significantly different.

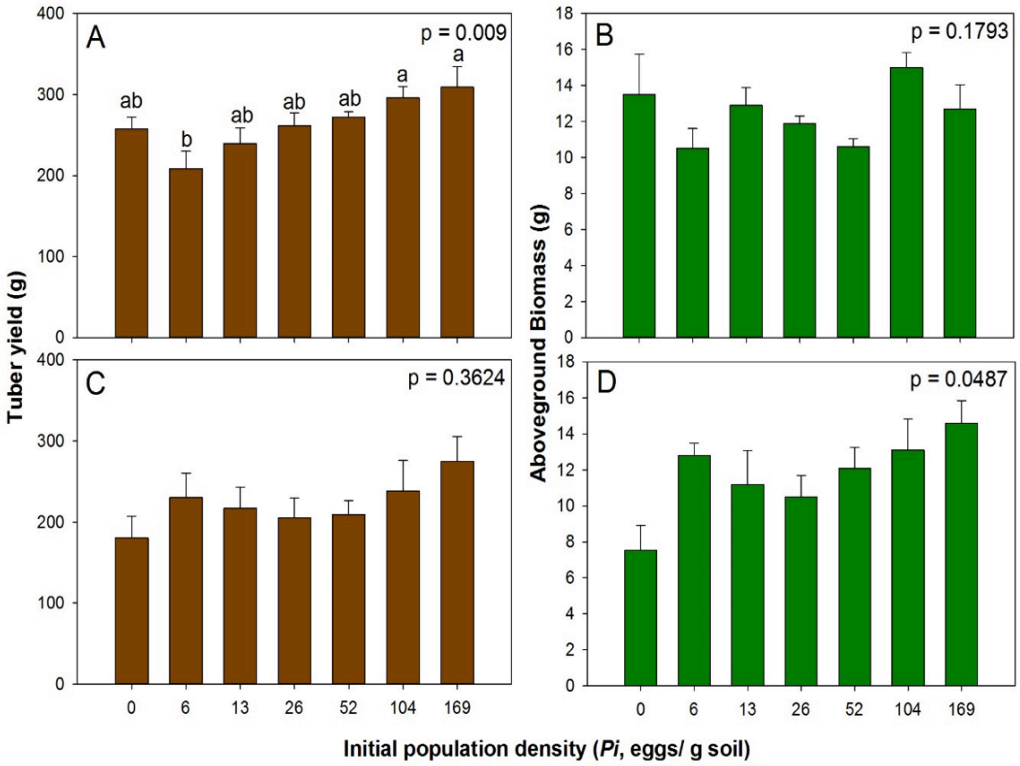
Table 4 – Reproduction of *Globodera ellingtonae* on potato (*Solanum tuberosum*) 'Russet Burbank' inoculated with varying initial egg population densities (*Pi*) of *G. ellingtonae* in trial 2.

Pi[a]	*Pf*[b]	Eggs/Cyst	RF[c]
6	120.0 (± 35.1)[d]	169.8 (± 20.2) ab	20.0 (± 5.9) a
13	238.3 (± 34.6)	231.0 (± 21.0) a	18.3 (± 2.7) a
26	290.3 (± 52.7)	196.9 (± 19.5) ab	11.2 (± 2.0) ab
52	258.7 (± 15.5)	132.6 (± 60.9) ab	5.0 (± 0.3) bc
104	241.5 (± 27.7)	113.8 (± 29.5) b	2.3 (± 0.3) c
169	328.3 (± 96.8)	115.1 (± 44.1) b	1.9 (± 0.6) c
P-value	*0.1814*	*0.0032*	*<0.0001*

[a] Initial population density (*Pi*) are eggs/g soil.
[b] Final population density (*Pf*) are eggs/g soil.
[c] RF = reproduction factor (*Pi/Pf*).
[d] Values are the means + standard error. Values followed by the same letter are not significantly different.

Parameters of plant growth that were considered included potato yield, aboveground biomass, tuber number, and average tuber weight. A significant difference in potato yield across *Pi* was only observed in trial 1. Differences among treatments were minimal with only the lowest yielding treatment, *Pi* 6 eggs/g soil, different from the highest yielding treatment, *Pi* 169 eggs/g soil (Fig. 1A). There was no difference in potato yield among the treatments in trial 2 (Fig. 1C). There were no differences observed among *Pi* treatments in aboveground biomass (Fig. 1B and 1D).

Figure 1. Yield and aboveground biomass of potato (*Solanum tuberosum*) inoculated with varying initial densities of *Globodera ellingtonae* in trial 1 (A and B) and trial 2 (C and D). Columns within a graph with the same letter is not significantly different ($P \leq 0.05$) based on Tukey's honest significant difference test. Column values are the means $\pm$ standard errors (n=6) of six replicates.



The relationships between *Pi* and aboveground biomass and potato yield are shown in Figures 2 and 3. Both trials had low R^2 values so the linear regression did

not fit the data well. In trial 1, there was no significant relationship between *Pi* and aboveground biomass (Figure 2). In trial 2, there was a significant relationship between *Pi* and the aboveground biomass, with increasing aboveground biomass as *Pi* increased (Figure 2). Similar to the relationship of *Pi* to aboveground biomass, low R^2 values were obtained in the analysis of *Pi* and potato yield (Figure 3). However, the *p*-values for both trials indicated that there was a significant relationship between *Pi* and tuber yield. In trial 1, an increase in tuber yield from *Pi* 6 to *Pi* 169 eggs/g soil was observed. In trial 2, a more symmetrical trend was observed with yield decreasing between *Pi* 6 and *Pi* 26 eggs/g soil, and then increasing through the remaining *Pi*.

Figure 2. Impact of initial egg density (log Pi) of *Globodera ellingtonae* on aboveground biomass of potato (*Solanum tuberosum)* 'Russet Burbank' grown in microplots in two trials.

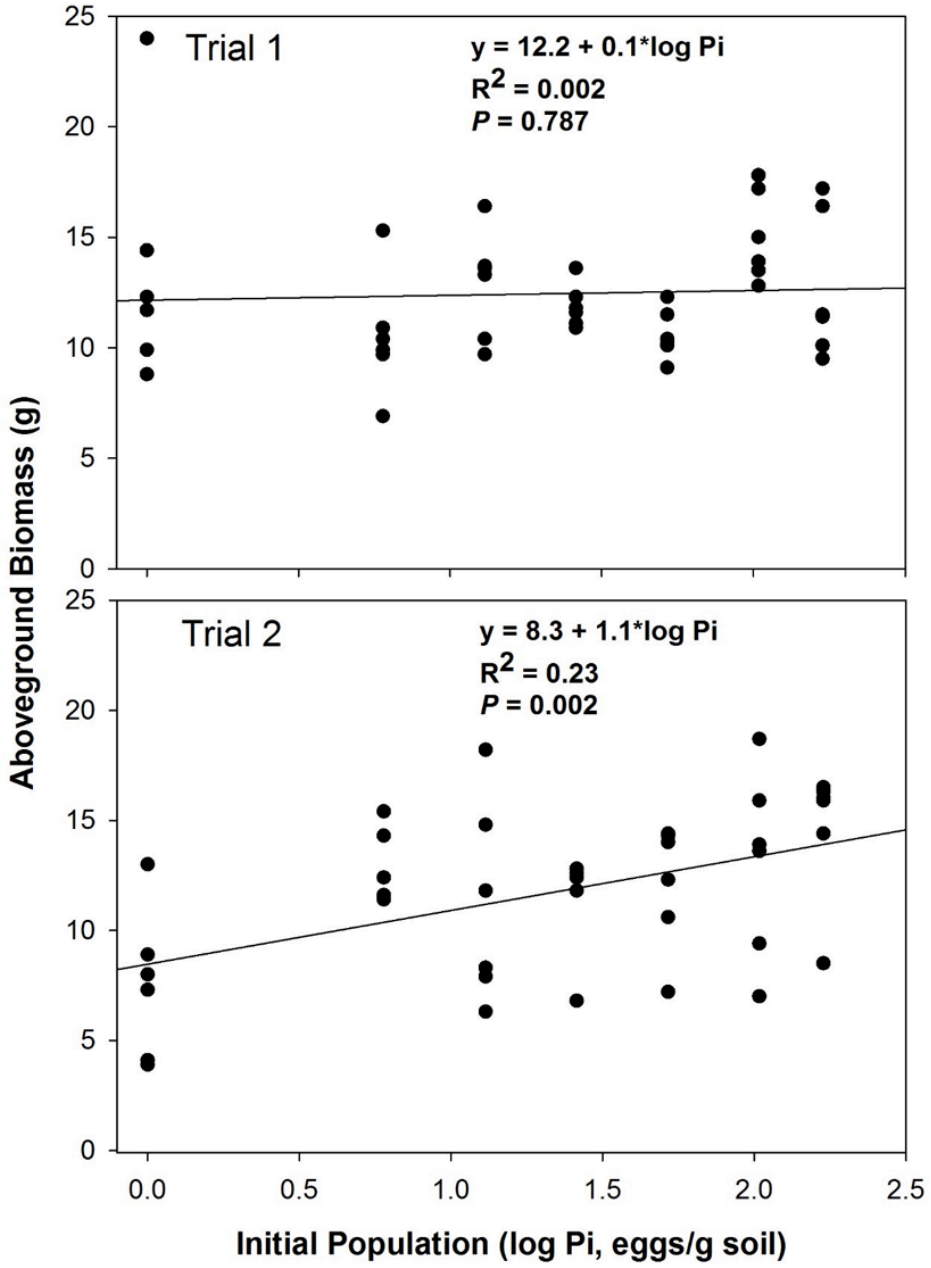
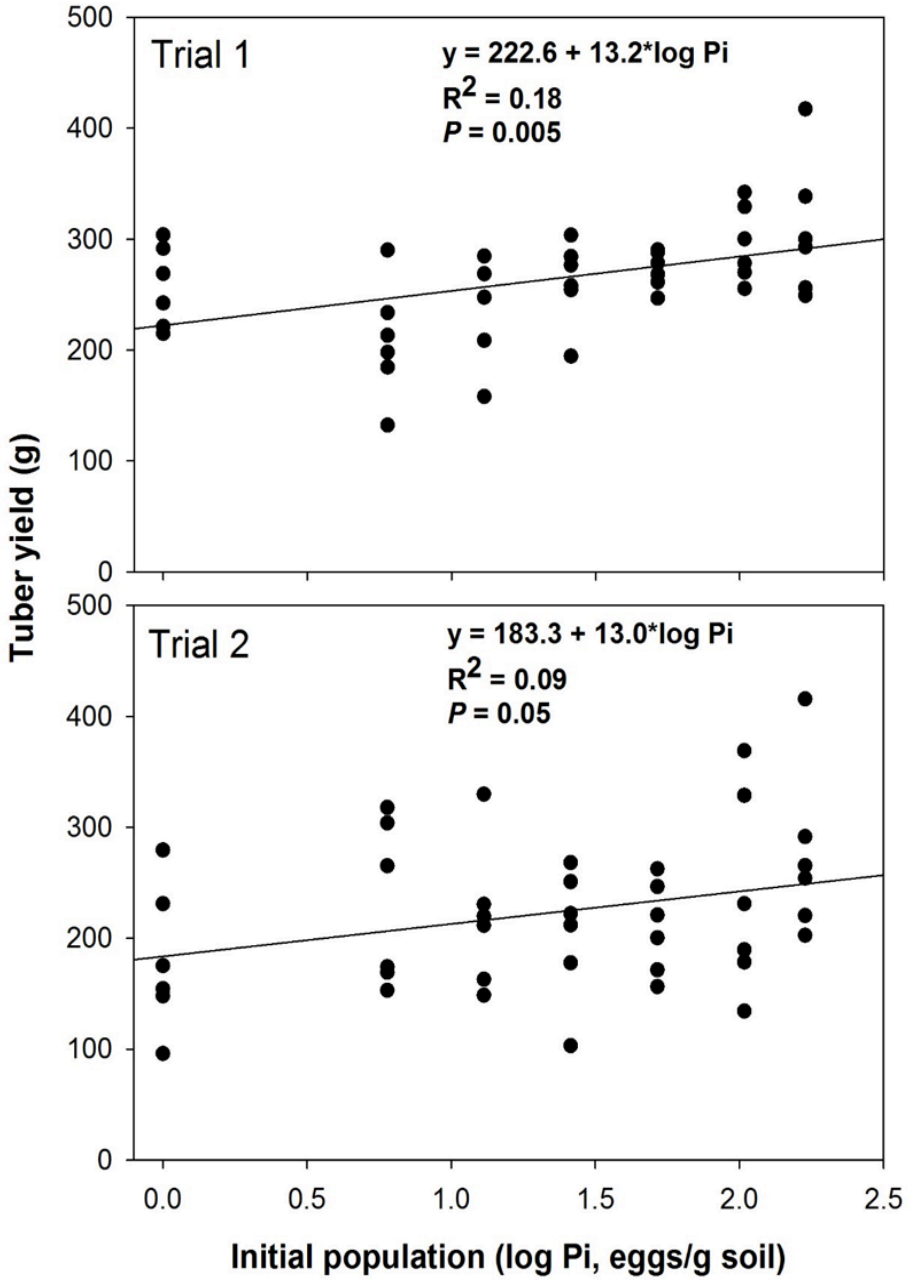


Figure 3. Impact of initial egg density (log Pi) of *Globodera ellingtonae* on tuber yield of potato (*Solanum tuberosum)* 'Russet Burbank' grown in microplots in two trials.



The number of tubers produced and the average individual tuber weight were also minimally affected by the different *Pi* (Table 5). In trial 1, the largest number of tubers was produced in *Pi* 52 eggs/g soil, but this was not significantly different from the other treatments (Table 5). In trial 2, there was also not a significant difference in the number of tubers produced between treatments. There were fewer tubers produced across treatments in trial 2 compared to trial 1. The average individual tuber weights in trial 1 and 2 were not significant different between the treatments (Table 5).

Table 5 – Attributes of harvested potato (*Solanum tuberosum*) 'Russet Burbank' inoculated with varying initial egg population densities of *Globodera ellingtonae*.

Pi[a]	Tuber Number		Average Individual Tuber Weight (g)	
	Trial 1	Trial 2	Trial 1	Trial 2
0	6.7 (± 0.7)[b]	6.8 (± 0.7)	43.6 (± 4.2)	38.9 (± 5.9)
6	6.8 (± 0.9)	6.5 (± 1.2)	33.1 (± 3.3)	48.7 (± 10.3)
13	7.7 (± 1.1)	6.3 (± 0.8)	33.7 (± 3.9)	39.7 (± 9.6)
26	8.8 (± 0.8)	5.5 (± 1.0)	31.3 (± 2.5)	34.9 (± 5.6)
52	9.2 (± 0.7)	6.0 (± 0.6)	34.0 (± 3.8)	33.4 (± 3.8)
104	7.7 (± 0.6)	6.3 (± 1.3)	32.3 (± 2.0)	31.0 (± 3.5)
169	8.0 (± 0.6)	8.0 (± 0.7)	39.0 (± 4.2)	37.6 (± 6.0)
P-value	*0.2534*	*0.6757*	*0.3718*	*0.7546*

[a] Initial population density (*Pi*) are eggs/g soil.
[b] Values are the means + standard error.

Section 2 – Defining the host range of *Globodera ellingtonae*

The Solanaceous plants that had RS scores closer to 1 had larger RF values reaching a maximum of 27.01 (±19.53), and those with scores closer to 9 had minimum RF values of 1.43 (±1.09) (Table 6). *Solanum sisymbriifolium* and *S. sisymbriifolium* II had RS scores of 9. The degree of resistance for the crop species tested was also determined. All crop species evaluated had RS scores of 9 except for tomato (*S. lycopersicum*) which had a RF value of 5.45 (±1.7) and an RS score of 1 (Table 7). The average RF value was 0 except for green pepper (*C. annuum*), tobacco (*N. tabacum*), and eggplant (*S. melongena*).

Table 6 - Solanaceous weed species degree of resistance[a]

***Solanum* species**	**Accession**	**RF (Std Dev)[a]**	***G. e* RS Score[b]**	***G. p* RS Score[c]**	***G. r* RS Score**
S. dulcamara	PI 643457	3.55 (±3.8)	2	7	4-9[d]
S. nigrum	PI 304600	27.01 (±19.53)	1	7	8
S. nigrum	PI 381289	14.32 (±16.73)	1	nt[e]	3-9[d]
S. rostratum	PI 420997	1.43 (±1.09)	5	nt	9
S. sisymbriifolium	-	0	9	nt	9
S. sisymbriifolium II	-	0	9	nt	nt
S. tuberosum	-	22.6 (±7.5)	-	-	-

[a] RF is the multiplication rate expressed as a ratio between final population (*Pf*) divided by the initial population (*Pi*) both expressed as a number of cysts

[b] Relative susceptibility (RS) Score equals *Pf* of test plant divided by the *Pf* of désirée potato multiplied by 100

[c] All scores for *G. pallida* were calculated from data available in the literature and are not associated with a specific accession of any species indicated here.

[d] Range of RS score was dependent on origin of isolate and accession of plant species

[e] Not tested

Table 7 - Crop species degree of resistance to *G. ellingtonae*

Crop species	**Common Name**	**RF (Std Dev)[a]**	**RS Score[b]**
Avena sativa (Oat)	Oat	0	9
Capsicum annuum	Green bell	0.02 (±0.03)	9
C. annuum	Jalapeño	0	9
Cynara scolymus	Artichoke	0	9
Medicago sativa	Alfalfa	0	9
Nicotiana tabacum	Tobacco	0.74 (±0.34)	9
Nicotiana tabacum cv. K326	Tobacco	0	9
Physalis philadelphica	Tomatillo	0	9
Solanum lycopersicum	Tomato	5.45 (±1.7)	1
S. melongena	Eggplant	9	9
Triticum sp.	Wheat	0	9
S. tuberosum	Désirée Potato	22.6 (±7.5)	-

[a] RF is the multiplication rate expressed as a ratio between final population (*Pf*) divided by the initial population (*Pi*) both expressed as a number of cysts

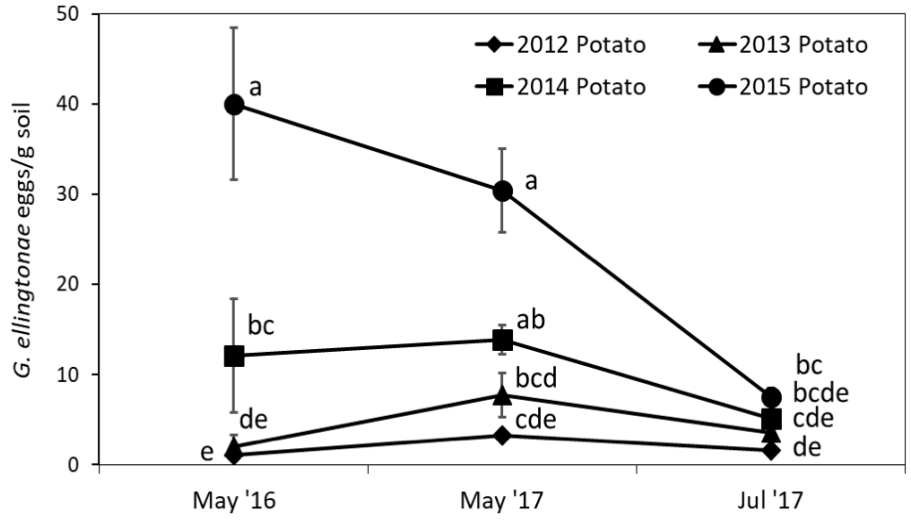
[b] Relative susceptibility (RS) Score equals *Pf* of test plant divided by the *Pf* of désirée potato multiplied by 100

Section 3 – Decline of *Globodera ellingtonae* egg densities over time at Powell Butte, OR

The longer that an area was out of growing potato the lower the population density (Figure 4). At the first sampling date, May 2016, there were significantly more *G. ellingtonae* eggs in the area most recently cropped to potato, in 2015, than the other areas. This was followed by the next highest egg density in the area cropped to potato in 2014, which was significantly greater than egg densities in the areas

cropped to potato in 2013 and 2012. The following spring, May 2017, a similar trend was observed with areas having potato most recently, 2014 and 2015, having the highest egg densities. Egg densities in the 2013 area were similar to that in areas planted to potato in 2014 and 2012. The final sampling date was in July 2017, which occurred after a potato trap crop had been planted. At this sampling date, egg densities were similar across areas with only the highest egg density in the 2015 area being different from the lowest egg density in the 2012 area. Across time within areas, there was no change in *G. ellingtonae* egg population densities in the areas planted to potato in 2012, 2013, and 2014 areas across the sampling dates. The only reduction in egg densities that was observed was in the 2015 area where egg densities significantly decreased after the planting of a potato trap crop in 2017 (Figure 4).

Figure 4. Population densities of *Globodera ellingtonae* encysted eggs at three sampling dates at Powell Butte, OR. Four areas within a field were sampled; these areas varied in when potato (*Solanum tuberosum*) was last cultivated (2012 to 2015). Data for each collection date represent the mean of 5 samples for each area. Error bars represent standard error. Data that share a letter are not significantly different ($P \leq 0.05$) based on Tukey's honest significant difference test.



DISCUSSION

Section 1 – Evaluation of the pathogenicity of *Globodera ellingtonae* to potato

A comparison of the *Pf* to the *Pi* demonstrated that each treatment had a significantly higher *Pf* than *Pi* indicating that both trials were successful and *G. ellingtonae* was able to reproduce in robust quantities. The RF scores also support this idea because the *Pf* for each treatment was significantly higher than the *Pi*. This trend demonstrates that with high *Pi* there is a limit to the amount of reproduction possible. This reduction in population growth with increasing *Pi* could be a result of many factors including competition for feeding sites and nutrients (Hajihassani et al. 2013).

The limited impact of *G. ellingtonae* on the growth and yield of potato observed in this study is contrary to previous studies characterizing yield loss caused by *G. rostochiensis* and *G. pallida*. In previous studies with increasing *Pi* of *G. rostochiensis* there was a significant reduction in yield reaching a maximum yield loss of over 50% (Hajihassani et al. 2013). This loss was experienced by potatoes grown with *Pi* between 32 and 64 eggs/g soil which is well within the *Pi* used in the current study. However, it has been found that different sites may have large variations in the level of yield loss caused by PCN (Trudgill 1986). While the effects of the yield loss are usually associated with the *Pi* at planting, a large proportion of the effects can be attributed to the effects that the J2 have on the root systems when developing (Hajihassani et al. 2013). With further research into the effect of *G. ellingtonae* on yield hopefully a better understanding of what the primary causes of this loss are and how they differ depending on environment can be obtained.

The regression analysis of *Pi* vs. tuber weight also supported the finding of minimal or no impact of *G. ellingtonae* on yield and productivity of potato. Previous research that analyzed the relationship between *Pi* and tuber yield using a regression analysis illustrated that the data cannot be accurately approximated by a straight line (Elston et al. 1991). Multiple equations have been used to attempt to model the data in more accurate ways. However, which model best predicts the impact of PCN on potato yield is still undecided (Elston et al. 1991). When utilizing linear regression methods, the asymptotic properties of the data result in the line generated being an approximation. Additionally, the commonly used equations to estimate the average yield loss can be misleading due to the amount of variation that can occur depending on many factors (Trudgill 1986). To obtain a more representative model for data regarding the effect of PCN on tuber yield, the models will need to include parameters such as the genotype of the potato and the attributes of the environment (soil type, climate, precipitation levels etc.) where the plants are to be grown (Elston et al. 1991).

The action threshold for *G. pallida* and *G. rostochiensis* varies depending on the geographic location, but the threshold most widely used is between 1.4 and 2.1 eggs/g soil (CABI 2018). The different *Pi* used in this study were all well above the action thresholds currently in place for either species. Difficulties encountered within this study may have influenced the outcomes observed. We believe that a few plants from *Pi* 0 were affected by a leaf curl disease. The full extent of its effect on the growth of the plant and yield of potato is not fully known. Additionally, the plant beds being outside resulted in the plants being exposed to natural changes in the

weather. During the growing period from mid-May until mid-August, high temperatures were experienced particularly during the first couple of weeks of growth. The average temperatures for May 2017 varied between 2.8°C and 32.8°C while the average temperatures for June 2017 were between 5.6°C and 37.8°C (Wunderground 2018). These changing conditions and hot weather may have affected the ability of the potatoes to establish and begin growth or may have stunted the growth of the new plantlet. Additionally, previous research documented that the hatch rates of *G. ellingtonae* decline after 30°C which may have affected the ability of the eggs to hatch (Phillips et al. 2015); however, considering that *G. ellingtonae* populations increased from 2 to 20 times over the course of the experiment, this is unlikely We were also unable to evaluate the pathogenicity of *G. ellingtonae* compared to *G. pallida* and *G. rostochiensis* because the latter two species are quarantine pests and only permitted facilities are able to conduct research on these nematodes. This unfortunately limited our ability to adequately compare the reproduction and damage potential of the different species under the same conditions.

Future research should be conducted to continue to further our knowledge about the growth and development of *G. ellingtonae* and what factors contribute to the lack of pathogenicity of this nematode to potato. Conducting a study that allows for the comparison of *G. ellingtonae*, *G. pallida,* and *G. rostochiensis* under the same growing conditions could provide clearer evidence of the pathogenic differences between the species. Additionally, this study could be performed at a location outside of Oregon or in a different climate or environment to determine if *G. ellingtonae* is a pathogen of potato in a different growing environment. Finally, by understanding

how *G. ellingtonae* interacts with potato at a molecular level could also contribute to a better understanding of whether or not *G. ellingtonae* is a pathogen of potato. Technologies that could be used include RNA analysis of nematode effectors and corresponding gene expression in the potato host (Chen et al. 2005).

Section 2 – Defining the host range of *Globodera ellingtonae*

The findings of this study demonstrate additional similarities and differences between *G. ellingtonae* and the closely related species *G. pallida* and *G. rostochiensis*. *Globodera ellingtonae* has a narrow host range similar to that of *G. pallida* and *G. rostochiensis*. The host range appears to be restricted to species within the Solanaceae family, and more similar to the host range of *G. rostochiensis* than to that of *G. pallida*.

Multiple Solanaceous weed species were tested but not included in the results due to difficulty in obtaining enough viable seed to replicate the experiments sufficiently. These species include, *S. ptycanthum* (accession 64750068), *S. sarrachoides* (accession 954750073), *S. triflorum*, and *S. villosum* (accessions 804750186 and 884750018). Further work using these plant species could be valuable as each accession had an RS score of 1 with the exception of *S. ptycanthum* which had an RS score of 3 indicating that these species are either hosts or maintenance hosts for *G. ellingtonae*. Within the host ranges of *G. pallida* and *G. rostochiensis*, *S. ptycanthum* and *S. triflorum* are reported to be poor or non-hosts for *G. rostochiensis* (Rott et al. 2011). The host status of *S. sarrachoides* is particularly of interest because it has been reported as a non-host for *G. rostochiensis* but a suitable host for *G.*

pallida (Boydston et al. 2010; Rott et al. 2011). Field observations demonstrated that *S. sarrachoides* is an excellent host for *G. ellingtonae* (Zasada unpublished data).

The origin of a species (population) can impact the host status for a nematode. In previous research *S. nigrum* was a non-host for *G. rostochiensis* with an RS score of 9 (Sullivan et al. 2007). However, in another study it was determined that *S. nigrum* was susceptible to *G. rostochiensis*, and the susceptibility was dependent on where the plant was originally collected (Mimee et al. 2014; Rott et al. 2011). The relationship between *S. dulcamara* and *G. rostochiensis* appears to be variable, with the plant being a host in some experiments but not in another (Mimee et al. 2014).

The results show that there was more variation in the RS scores for *G. ellingtonae* on Solanaceous weed species than on the crop species evaluated. This indicates that the degree of resistance for crop species is more similar to each other while the Solanaceous weeds have more diversity in their resistance to *G. ellingtonae*. Due to the greater variation within the Solanaceous weed species, further exploration into the various degrees of susceptibility within this family to *G. ellingtonae* may prove to be advantageous for researchers seeking to develop plants with multi-gene resistance to *Globodera* spp.

This finding is significant for policy makers. Knowledge of the host range of *G. ellingtonae* provides information on the risk of the nematodes establishing in new areas on weed hosts. The knowledge of the narrow host range may be beneficial to growers as well. Many of the crop species tested had RF values of 0 indicating that they are non-hosts and could potentially be utilized as cover or alternate crops.

Section 3 – Decline of *Globodera ellingtonae* egg densities over time at Powell Butte, OR

A better understanding of the population dynamics of *G. ellingtonae* can provide insight into the natural decline of egg densities, and thereby how much time is needed to eliminate the nematode from infested fields. The data obtained from Powell Butte, Oregon for May 2016 to July 2017 show a clearer trend in how the population dynamics of *G. ellingtonae* changed over time. The areas that had potato planted in 2012 and 2013 had similarly low densities for both May 2016 and July 2017 sampling dates. In general, the areas of the field with lower egg population densities, did not exhibit significant reductions in egg densities over the course of the experiment. *Globodera* tend to have patch distributions within fields (Been and Schomaker 2000). The inability to detect changes in *G. ellingtonae* egg densities in areas with lower population densities may have been due to error associated with sampling. In the area planted to potato in 2015, we did not see the reduction in egg population densities that were previously observed within a growing season at Powell Butte, OR (Phillips et al. 2017). In a previous study, there was a 50% reduction in the number of *G. ellingtonae* eggs/cyst over a 10-week period (Phillips et al. 2017). This population reduction is similar to values reported for *G. pallida* and *G. rostochiensis* populations (Phillips et al. 2017). Reductions of up to 30 and 20% have been reported for *G. pallida* and *G. rostochiensis*, respectively (Back 2016).

This study demonstrated the power of utilizing potato as a trap crop to reduce population densities of *G. ellingtonae*. There was an approximately 60% reduction in egg densities in the area planted to potato in 2015 after potato was grown as a trap

crop in 2017. Growing potato as a trap crop has been suggested as potential management strategy for *Globodera* spp. (LaMondia and Brodie 1986). In this practice, the plant is grown for an adequate period of time to allow the nematode to invade the root but not complete its life cycle prior to destruction of the crop (Trivedi and Barker 1986). The risk of this practice is that if the potato crop is not destroyed at the right time there is the potential for the nematode population to increase instead of decrease. In the field where these samples were collected, the potato trap crop was successful in reducing *G. ellingtonae* egg densities.

Further research should be conducted to expand on our knowledge of *G. ellingtonae* and to get a greater understanding of how these populations decline over a much longer period of time. This would allow for population decline of *G. ellingtonae* being characterized in a similar manner to that of *G. pallida* and *G. rostochiensis*. Previous research has suggested that regular cultivation of the nematode infested land may assist in faster population decline (Turner 1996).

CONCLUSION

The findings of this study furthered the understanding of the pathogenicity to potato, the host range, and population decline of *Globodera ellingtonae*. The minimal impact on the growth and yield of potato by *G. ellingtonae* is in contrast to what have been observed for the quarantine nematodes *G. pallida* and *G. rostochiensis*, warranting additional research under different environmental conditions. The knowledge of the host range of *G. ellingtonae* was expanded to include more members of the Solanaceae family, demonstrating further similarities and differences

between *G. ellingtonae*, *G. pallida* and *G. rostochiensis*. The population decline data also supports the need for a better characterization of the population decline over longer periods of time and further exploration into the management strategies that can be utilized to control *G. ellingtonae*.

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