A Predictive Risk Model Analysis of the Potato Cyst Nematode *Globodera pallida* in Idaho

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Abstract

Globodera pallida is a major nematode pest of potato (*Solanum tuberosum*) and is of great economic importance for the potato industry. Assessing potato yield loss caused by the Idaho *G. pallida* population under field conditions was not performed due to its quarantine status in Idaho, where it is prohibited by regulatory statutes to grow potato in any infested fields. The experimental data came from three trials that were conducted under greenhouse conditions. A predictive risk model analysis was performed to: (i) determine the effect of the Idaho population of *G. pallida* on potato yield; (ii) estimate reproduction rate from different initial nematode densities; and (iii) simulate potato yield losses in Idaho field conditions by integrating the coefficients of potato yield into the SUBSTOR-DSSAT crop simulation model. Experiments were conducted under greenhouse conditions using five initial *G. pallida* soil infestation levels (0, 10, 20, 40, and 80 eggs/g soil). The coefficients of potato yield achieved under each initial nematode density were integrated into the

SUBSTOR-DSSAT potato growth simulation model. The model showed that tuber weight reached a maximum yield of 96 ton/ha in noninfested soil. Based on the greenhouse trials, the model predicted a minimum yield of 12 and 58 ton/ha in trial 1 and trial 2/3 respectively, when initial nematode density was 80 eggs/g soil. In trial 1, tuber weight was significantly reduced by 44% at 40 eggs/g soil and by 87% at 80 eggs/g soil, and 20% at 40 eggs/g soil and by 39% at 80 eggs/g soil in trial 2/3. The outputs of this study should facilitate common understanding between regulators, policymakers, and potato growers on the challenges and opportunities for controlling this economically important pest in Idaho.

Keywords: *Globodera pallida*, potato cyst nematode, risk model analysis, *Solanum tuberosum*, SUBSTOR-DSSAT crop simulation model

The potato cyst nematode *Globodera pallida*, also known as the pale cyst nematode (Behrens 1975; Stone 1972), is a globally regulated and an economically important potato pest (CABI 2018; Hodda and Cook 2009). *G. pallida* and *Globodera rostochiensis* (the golden nematode) (Skarbilovich 1959; Wollenweber 1923), both potato cyst nematodes, coevolved with potato and other native *Solanum* species in the Andean Region of South America (Anthoine et al. 2010; Picard et al. 2004). Potato cyst nematodes were first observed on potato roots in Germany in 1881, before spreading worldwide (Anthoine et al. 2010; CABI 2018; Wollenweber 1923). According to recent survey data, *G. rostochiensis* has been detected in 68 countries and *G. pallida* in 48 (CABI 2018).

G. pallida is a specialized obligate sedentary endoparasite that can survive in the soil for up to 30 years in the absence of its potato host (Turner 1996). The major plant hosts of *Globodera* spp. are restricted to Solanaceae, in particular potato, tomato, and aubergine (Mai 1952; Stone and Roberts 1981). *G. pallida* is spread mainly through the movement of soil, tubers, or farm equipment contaminated with cysts (Evans and Stone 1977). In highly infested fields, *G. pallida* can reduce tuber yields up to 80% (Talavera et al. 1998; Vasyutin and Yakovleva 1998). In the U.K., potato cyst nematodes are the second most economically important potato pest after late blight, costing \$34 million per year in potato yield loss (Twining et al. 2009). In the U.K., following the widespread planting of potato cultivars resistant to only *G. rostochiensis*, an increase in *G. pallida* infestations was

observed (Minnis et al. 2002). Potato cyst nematodes are found in 64% of the potato fields in the U.K., with *G. pallida* found in over 90% of infestations (Minnis et al. 2002).

In the United States, *G. pallida* was found in southeastern Idaho in 2006 in two potato fields in Bingham County (Hafez et al. 2007; USDA-APHIS 2019). The U.S. Department of Agriculture's Animal and Plant Health Inspection Service (USDA-APHIS) and the Idaho State Department of Agriculture (ISDA) have listed *G. pallida* as a quarantine pest for Idaho under Title 7 CFR 301.86 Federal Regulation. The regulated area includes portions of northern Bingham and southern Bonneville counties and is, as of February 2019, limited to 3,057 hectares, of which 1,326 ha are fields infested with *G. pallida* (USDA-APHIS 2019). USDA-APHIS and ISDA have implemented a containment and eradication program to prevent *G. pallida* spread to other potato fields. In fields infested with *G. pallida*, the program outlines: (i) restrictions on the movement of soil and plant materials; (ii) prohibition of planting potato and other solanaceous crops; and (iii) sanitation procedures for farm equipment. Soil fumigation with the nematicide Telone II (1,3-dichloropropene, Dow AgroSciences, Indianapolis, IN) is being conducted in infested fields as part of the *G. pallida* eradication program, and *Solanum sisymbriifolium* 'litchi tomato' is under field scale trials in infested fields (USDA-APHIS 2019). *S. sisymbriifolium* is considered as a trap crop for both *G. pallida* and *G. rostochiensis* (Dias et al. 2012; Timmermans et al. 2006), and recent studies showed that *G. pallida* reproduction rate was significantly reduced by 99% in potato following *S. sisymbriifolium* compared with both the potato-following-fallow and the potato-following-potato treatments (Dandurand and Knudsen 2016).

Idaho is the largest producer, packer, and processor of potatoes in the United States, with a production value of \$1.19 billion in 2017 (USDA-NASS 2018). In 2017, the U.S. value of potato production is estimated to \$4.56 billion, and Japan, Canada, Mexico, and South Korea are the top customers of U.S. potatoes (USDA-NASS 2018). The presence of *G. pallida* in Idaho constitutes a considerable threat for the potato industry, and resistance to this nematode in russet-type potato cultivars is currently unavailable for the United States (Whitworth et al. 2018). However, the extent of *G. pallida* in Idaho

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is limited to a small area with low nematode population levels and represents less than 1% of annual potato production areas. Contina et al. (2018) showed that the fields infested with *G. pallida* in Idaho are spatially aggregated as an ellipsoidal-shaped cluster around a radius of 12 km. *G. pallida* spread followed a contagion effect scenario, where infested fields contributed to the infestation of nearby fields, probably through soil-contaminated agricultural equipment (Contina et al. 2018). The recent detection of *G. pallida* in Idaho is potentially associated with one introduction, and the nematode population growth in the area was maintained by local reproduction instead of continuous new introductions (Contina et al. 2018). The Idaho population of *G. pallida* showed a virulence pattern similar to other European populations in the Pa2/3 virulence group based on the examination of the mitochondrial cytochrome *b* gene (Blok and Phillips 2012). The ribosomal DNA of *G. pallida* population in Idaho population showed the greatest similarity to the European populations (99.9%) and the Clade 1c Peruvian population from southern Peru (Blok and Phillips 2012; Madani et al. 2010). USDA-APHIS quarantine and eradication programs are monitoring the presence of *G. pallida* in potato fields through intensive soil sampling and testing at regular time intervals. Research on the control of *G. pallida* in Idaho is focused on developing resistant potato varieties, trap crops, biofumigants, and biocontrol agents (Contina et al. 2017; Dandurand and Knudsen 2016; Dandurand et al. 2017; Whitworth et al. 2018).

Quantitative research on plant nematode disease epidemics is focused on: (i) modeling the relationship between initial (P_i) and final (P_f) egg densities; and (ii) evaluating the impacts of nematode infection on host growth (Brodie 1996; Ferris 1985; Jones and Kempton 1978; Jones et al. 1967; LaMondia and Brodie 1986; Seinhorst 1965; Seinhorst and Den Ouden 1971). Potato cyst nematodes produce only one infection cycle per crop cycle and cause the development of monocyclic disease. In monocyclic epidemics, the initial nematode inoculum represents a fundamental component of disease intensity over time (Seinhorst 1965). The early stages of monocyclic epidemics are characterized by a linear model, and a reduction in the initial inoculum or the rate of infection will result in a reduction of the disease level by the same proportion at any time throughout the epidemic (Madden et al. 2007). Pylypenko (1999) reported a linear relationship for *G. rostochiensis*; for a tolerant potato cultivar, 55 eggs per gram soil were associated with a 3.3% yield loss, whereas a 37.7% yield loss was observed for intolerant variety; and populations of 121 eggs per gram soil were associated with losses of 16.9% and 63.3%, respectively.

The main objective of crop disease modeling is to capture and understand the determinants of epidemic development in order to develop comprehensive disease management and control programs. The pathogen reproduction rate, considered as a measure of disease risk, provides quantitative information on the disease development and provides a basis for developing disease control programs that will reduce crop losses and disease incidence (Madden and Nutter 1995; Savary et al. 2006). The goals of disease management and control (Nutter 2001; Zadoks 1985) are to: (i) eliminate or reduce the initial pathogen inoculum; (ii) reduce the disease infection rate; and (iii) reduce the time of pathogen–host interactions to reduce disease intensity.

Risk in plant disease is considered as the probability of occurrence of a disease incidence or severity (Luo et al. 1998; Teng and Yuen 1991). The information can be obtained from the probability distribution where the mean and its deviation can be estimated (Luo et al. 1998), and from Monte Carlo simulation (Teng and Yuen 1991). Simulation modeling using crop growth models provides detailed analysis and prediction of risk of yield losses (Luo et al. 1998; Teng and Savary 1992). The Decision Support System for Agrotechnology Transfer (DSSAT) was developed by the International Benchmark Sites Network for Agrotechnology Transfer (IBSNAT) to facilitate the application of crop models into agronomic research (Jones et al. 1998, 2003). DSSAT integrates growth models for over 40 different crops and is supported by a cluster of applications for weather, soil, genetic, crop management, and observational experimental data with example data sets for all growth models (Hoogenboom et al.

2017). The Simulation of Underground Bulking Storage Organs (SUBSTOR) potato crop model, incorporated into DSSAT, has been tested and validated under a wide range of environmental conditions (Griffin et al. 1993; Raymundo et al. 2017).

There is a need to integrate crop pest into crop growth models for a comprehensive approach to disease management and control strategies. Jones et al. (1985) integrated the effects of soybean looper (*Pseudoplusia includens*), corn earworm (*Heliothis* spp.), and southern green stinkbug (*Nezara viridula* L.) in the Soybean Growth model (SOYGRO). Bourgeois (1989) developed a Cercospora late leaf spot model and combined it with the Peanut Growth model (PNUTGRO). Willocquet et al. (2002) coupled crop growth model simulating rice yield response to multiple pest injuries for tropical Asia. However, extensive research efforts are required to incorporate pest models into crop growth models. Collecting data on pest initial inoculum, infection rates, damage quantifications, and population genetics composition is a difficult task. Nevertheless, this approach for connecting pest models with crop models will extend the practical applications of crop models to wide-ranging problems (Batchelor et al. 1993; Boote et al. 1983; Donatelli et al. 2017).

This study is focused on investigating the risk of potato yield losses caused by *G. pallida* as a result of initial nematode densities in soil using the potato growth model in the SUBSTOR-DSSAT crop simulation system. Assessing potato yield loss caused by the Idaho *G. pallida* population under field conditions was not performed under field conditions due to its quarantine status in Idaho, where it is prohibited by regulatory statutes to grow potato in any infested fields. The experimental data came from three similar trials, using five different *G. pallida* initial nematode densities in soil (0, 10, 20, 40, and 80 eggs/g soil), that were conducted under greenhouse conditions over three time periods: trial 1 (September – November 2017), trial 2 (March – June 2018), and trial 3 (September – November 2018). We evaluated the potato growth in *G. pallida* infested and noninfested soils by measuring above- and belowground biomass, and we calculated the coefficients of achievable yield prior to coupling into the SUBSTOR-DSSAT simulation model outputs. We assessed *G. pallida* proliferation in soil for each initial nematode density, and we fitted a linear model to the experimental observations. Finally, we concluded our study by discussing the implications of understanding the impact of *G. pallida* on potato yield and the nematode population dynamics, and by comparing and exploring the strengths and limitations of our models. The objectives of this study were to: (i) determine the effect of *G. pallida* initial nematode densities on potato yield; (ii) determine the nematode reproduction rate; and (iii) simulate the risk of potato yield losses in Idaho field conditions by integrating the coefficients of potato yield obtained under different initial nematode densities in soil into the SUBSTOR-DSSAT simulation model outputs. The main goal of this study is to inform policymakers, stakeholders, potato growers, and the public in general of the threats posed by *G. pallida* for the U.S. potato industry.

Materials and Methods

Propagation of *G. pallida* and plant material culture. Cysts were obtained from infested potato fields in Shelley, ID, and were propagated on the susceptible potato cultivar ‘*Désirée*’ under greenhouse conditions of 18°C ± 2°C and 16:8-h light:dark period (Contina et al. 2017; Dandurand and Knudsen 2016; Dandurand et al. 2017; Kooliyottil et al. 2016). After 16 weeks of growth, cysts were recovered from soil using the USDA cyst extraction method (USDA-APHIS 2009) and picked by hand under a stereomicroscope (Leica Microsystems, Wetzlar, Germany). Before experimental use, all cysts were stored at 4°C for a minimum of 16 weeks. The identity of *G. pallida* was assessed and confirmed by morphological and molecular methods (Skantar et al. 2007). Cysts, with 50% hatching rate, 90% egg viability, and 300 eggs/cyst, were surfaced-sterilized in a solution of 0.3% NaOCl for 5 min and rinsed thoroughly with sterile distilled water. Hatching rate was determined by exposing *G. pallida* eggs to potato root diffusate, and the viability of eggs was assessed by using Meldola’s Blue staining assay (Thermo Fisher Scientific, Waltham, MA) (Ogiga and Estey 1974). Cysts were placed inside

a 2.54-cm² sterile nylon mesh bag (McMaster-Carr, Elmhurst, IL) with a 250 µm mesh opening. The nylon mesh was sealed along the edges with a hand sealer (Sealer 8" F-200, Sealer Sales Inc., Northridge, CA), and were placed in sterile distilled water for hydration for 3 days before adding to soil. Potato plants (*Solanum tuberosum*) 'Désirée', classified as certified disease free (from the Nuclear Potato Seed Program, University of Idaho), were grown from tissue culture plantlets in standard media (Murashige and Skoog 1962) for 4 weeks prior to transplanting.

Effect of *G. pallida* initial inoculum densities on potato yield.

Three trials were conducted using Prosser fine sandy loam soil, which was air-dried and sieved through a 5-mm mesh. A 2:1 sand:soil mixture (56% sand, 35% silt, 8% clay, pH 7.0) was autoclaved twice for 90 min at 121°C prior to experimental use. Terra cotta clay pots (15 cm diameter, The Home Depot, Atlanta, GA) were used, and each clay pot contained 1.5 kg soil mix. There were five different levels of *G. pallida* initial nematode densities (0, 10, 20, 40, and 80 eggs/g soil) as treatments. The nylon mesh bags containing *G. pallida* cysts were placed in the pot above an 8-cm soil layer and covered with a 6-cm soil layer before placing one potato tissue culture plantlet on top. The initial *G. pallida* densities used in this study represent the upper-level of nematode densities associated with yield loss showed by the Seinhorst model for potato cyst nematodes (Seinhorst and Den Ouden 1971; Ward et al. 1985). Treatments included 10 replicates and were arranged in a completely randomized block design. Pots were maintained under greenhouse conditions of 18°C ± 2°C, 60% relative humidity, and 16:8-h light:dark period. Pots were watered twice daily in the amount of 100 ml of water and fertilized once a week using Jack's classic garden fertilizer 20-20-20 (JR Peters Inc., Allentown, PA) applied at a rate of 0.5 g/liter water.

Potato growth and nematode reproduction assessments. After 12 weeks, potato aboveground (top), roots, and tubers were weighed as fresh and dry in a scale, and were expressed in grams (Thermo Fisher Scientific, Waltham, MA). Cysts were extracted from soil using the USDA cyst extraction method (USDA-APHIS 2009). Extracted cysts were crushed in 100 µl of sterile distilled water, and eggs were counted under a dissecting microscope (Leica M80, Leica Microsystems, Wetzlar, Germany). Nematode reproduction rate (*Rf*) was calculated based on the ratio of the final egg population density (*Pf*) over the initial egg population density (*Pi*) per gram of soil.

SUBSTOR-DSSAT potato crop simulation models. The SUBSTOR-potato model inputs are daily weather data, soil profile parameters, cultivar parameters, and crop management information (Singh et al. 1998). The model simulates the daily dynamics of phenology, biomass, and yield accumulation. There are five phenological stages in the model (Griffin et al. 1993; Singh et al. 1998): (i) preplanting; (ii) planting to sprout germination; (iii) sprout germination to emergence; (iv) emergence to tuber initiation; and (v) tuber initiation to maturity. The SUBSTOR-potato models are designed to simulate growth and development under (Singh et al. 1998): (i) nonlimiting conditions; (ii) water limited conditions; or (iii) water and nitrogen limited conditions.

All growth stages are affected by temperature in root and tuber growth (*RTFSOIL*). Tuber initiation (*TI*) is a function of day length and temperature, and is also influenced by plant nitrogen level and soil water deficit (Griffin et al. 1993; Singh et al. 1998). The model uses potato cultivar coefficient (*P2*) and photoperiod (*PHPER*) to determine the relative day length factor for tuber initiation (*RDLFTI*), and is defined as:

$$RDLFTI = (1 - P2) + 0.00694 \times P2 \times (24 - PHPER)^2$$

The model estimates a tuber induction index (*TI*) at the beginning of emergence, and is defined as:

$$TI = (RTFTI \times RDLFTI) + 0.5 \times [1 - AMIN1(SWDF2, NDEF2)]$$

$$RTFTI = 1 - 0.0156 \times (TEMPM - TC)^2$$

where, *RTFTI* determines the relative temperature factor for tuber initiation calculated by a cultivar specific coefficient for critical

temperature (*TC*) and daily mean air temperature (*TEMPM*), and *AMIN1* (*SWDF2*, *NDEF2*) simulates water stress (*SWDF2*) or nitrogen deficiency (*NDEF2*).

Potato growth in the model is maintained by the carbohydrate resource from the seed piece (*SEEDAV*) during the pre-emergence phase, and continues to support postemergence growth up to a plant leaf area (*PLA*) of 400 cm² per plant (Griffin et al. 1993; Singh et al. 1998). In the postemergence vegetative growth stage, potential photosynthetic carbohydrate assimilation (*PCARB*) is defined as:

$$PCARB = RUE \times \frac{PAR}{PLANTS} \times \left(1 - e^{(-k \times LAI)}\right)$$

where *RUE* is the solar radiation, *PAR* is the percentage of incoming radiation intercepted by the canopy, *PLANTS* is the planting density (plants/m²), *k* is an extinction coefficient, and *LAI* is the leaf area index.

The actual daily carbohydrate accumulation (*CARBO*) is calculated as:

$$CARBO = PCARB \times AMIN1(PRFT, SWDF1, NDEF1) + 0.5 \times DDEADLF$$

where *PRFT* is the effects of nonoptimal temperature on *CARBO*, and *DDEADLF* is the carbohydrate translocation in senesced leaves prior to abscission.

The potential tuber growth (*PTUBGR*) is a function of maximum tuber growth rate (*G3*) and temperature, and is defined as:

$$PTUBGR = G3 \times \frac{RTFSOIL}{PLANTS}$$

The actual tuber growth (*GROTUB*) is influenced by water and nitrogen stress, and tuber sink strength (*TIND*) as:

$$GROTUB = PTUBGR \times AMIN1(SWDF2, NDEF2) \times TIND$$

The potential leaf expansion (*PLAG*) is estimated by the genetic coefficient for maximum leaf expansion (*G2*), a temperature factor (*RTFVINE*), water and nitrogen stress, and is expressed as:

$$PLAG = G2 \times \frac{RTFVINE}{PLANTS} \times AMIN1(SWDF2, NDEF2)$$

Weather data for southeastern Idaho was obtained from AgriMet Cooperative Agricultural Weather Network for the Pacific Northwest Region (AgriMet 2018). Ashton, ID weather station (AHTI) was used to generate the following weather parameters from 1988 to 2017: (i) minimum daily air temperature (°F); (ii) maximum daily air temperature (°F); (iii) daily precipitation (in); and (iv) daily global solar radiation (langley). AHTI weather data were saved as a text file, and WeatherMan, a DSSAT application, was used to import the data into DSSAT weather database. Prior to import, WeatherMan converted the units for temperature to Celsius (°C), rain to millimeters (mm), and solar radiation to megajoule per square meter (MJ/m²). We used a prebuilt simulation model in DSSAT based on validated data from a potato growth experiment conducted in Hermiston, OR (OSBO 8801) (Hoogenboom et al. 2017; Jones et al. 2003), which was modified to include the southeastern Idaho weather data (AHTI) and sandy loam soil data from Aberdeen, ID. The genetic coefficients for the potato cultivar 'Désirée' used in DSSAT included (Hoogenboom et al. 2017; Jones et al. 2003): (i) daily leaf expansion rate (*G2*) 2,000 cm²/m²; (ii) daily potential tuber growth rate (*G3*) 25.0 g/m²; (iii) index that suppresses tuber growth during the period that immediately follows tuber induction (*PD*) 0.9; (iv) tuber initiation sensitivity to photoperiods (*P2*) 0.6; and (v) temperature for tuber initiation 16°C.

Integrating yield coefficients to SUBSTOR-DSSAT potato crop model. Potato yield coefficients for above- and belowground biomass were calculated by comparing yields in *G. pallida* noninfested with infested soil, and can be expressed by:

$$Y_{coeff} = 1 - \left[\frac{(Y_0 - Y_n)}{Y_0} \right]$$

where (Y_{coeff}) is the potato yield coefficient, (Y_0) is the yield in *G. pallida* noninfested soil, and (Y_n) is the yield in infested soil at different levels of P_i (n). The expression $\left[\frac{(Y_0 - Y_n)}{Y_0} \right] \times 100$ represents the percentage of yield loss.

The integration of the potato yield coefficients to the SUBSTOR-DSSAT simulation model outputs can be expressed by:

$$Y_{ij} = Y_i \times Y_{coeff}$$

where (Y_{ij}) is the potential potato yield for each level of P_i , and (Y_i) is the SUBSTOR-DSSAT simulated attainable potato yield outputs in the absence of plant disease stress.

The potato growth variables used as coupling points, as defined in the DSSAT v.4.7.0 software (Hoogenboom et al. 2017; Jones et al. 2003), were: (i) aboveground weight (*CWAD*), expressed as kilogram dry-matter per hectare (kg[dm]/ha); (ii) root weight (*RWAD*) (kg[dm]/ha); (iii) tuber dry weight (*UWAD*) (kg[dm]/ha) and fresh weight (*UYAD*) (ton[fm]/ha); and (iv) total plant weight (*TWAD*) (kg[dm]/ha).

Data analysis. Statistical data analyses were performed using R version 3.5.2 (R Core Team 2018). Analysis of variance and generalized linear models were performed to analyze the effect of P_i on potato growth variables with significant differences occurring at level of $P \leq 0.05$. Tukey's HSD test was performed to compare the mean differences for each level of P_i with significant differences occurring at level of $P \leq 0.05$. Linear regression analyses were performed to model the relationship between P_i (predictors) and potato growth variables (responses). Pearson correlation coefficient was used to assess the strength of the regression models with significant differences occurring at level of $P \leq 0.05$. A Bayesian analysis was performed to generate a sample from the posterior distribution of a linear regression model with Gaussian errors using Gibbs sampling in a random univariate Markov Chain Monte-Carlo simulation (MCMC) with 10,000 sampling size per chain (Martin et al. 2011). A generalized additive model (GAM) was performed to model the relationship between dry root weight and Rf using a nonlinear smooth function to model and capture the nonlinearities in the data (Hastie and Tibshirani 1990). The following R packages were used: (i) 'agricolae' for performing a Tukey's HSD comparison test; (ii) 'ggplot2' for plotting DSSAT simulation output; (iii) 'MCMCpack' for performing a Bayesian inference using posterior simulation; and (iv) 'mgcv' for fitting a GAM model to the data by using a Gauss-Seidel backfitting algorithm method.

Results

Potato growth assessment. For potato growth and *G. pallida* reproduction assessments, trial 1 was significantly different from trials 2 and 3 ($P \leq 0.05$), as determined by the analysis of variance and

model interactions, and was reported separately. No significant differences were detected between trial 2 and trial 3 ($P > 0.05$); therefore experimental data from both trials were combined and reported as trial 2/3. In trial 1, fresh and dry top weights were significantly reduced by 73 and 81%, respectively, when P_i was at 80 eggs/g soil compared with noninfested soil ($P \leq 0.05$) (Table 1). Dry root weight significantly decreased by 88% at 80 eggs/g soil compared with noninfested soil ($P \leq 0.05$) (Table 1). Fresh tuber weight was significantly reduced by 44% at 40 eggs/g soil and by 87% at 80 eggs/g soil, and dry tuber weight was significantly reduced by 34% at 40 eggs/g soil and by 86% at 80 eggs/g soil compared with noninfested soil ($P \leq 0.05$) (Table 1). Overall, total dry plant weight decreased significantly by 43% at 40 eggs/g soil and by 84% at 80 eggs/g soil compared with noninfested soil ($P \leq 0.05$) (Table 1). Tubers produced per plant showed a propensity to increase in number at 10, 20, and 40 eggs/g soil, with a significant 30% increase in the number of tubers at 20 eggs/g soil ($P \leq 0.05$); however the number of tubers was significantly reduced by 54% at 80 eggs/g soil compared with noninfested soil ($P \leq 0.05$) (Table 2). Furthermore, fresh tuber weight per unit was significantly reduced by 30% at 40 eggs/g soil and by 79% at 80 eggs/g soil, and dry tuber weights per unit were significantly reduced by 31% at 40 eggs/g soil and 82% at 80 eggs/g soil compared with noninfested soil ($P \leq 0.05$) (Table 2).

In trial 2/3, no significant weight reductions were observed for fresh and dry top at any level of P_i , and no significant dry root weight reduction was detected compared with noninfested soil ($P > 0.05$) (Table 1). However, fresh tuber weight was significantly reduced by 20% at 40 eggs/g soil and by 39% at 80 eggs/g soil, and dry tuber weight was significantly reduced by 20% at 40 eggs/g soil and by

Table 2. Potato tuber growth assessment for each level of *Globodera pallida* initial nematode densities (P_i) in soil

Pi (eggs/g soil)	# Tubers (unit)	Dry tuber	Fresh tuber
		Weight (g)/unit	
		Trial 1	
0	5.4 ± 0.7 ab ^z	1.99 ± 0.26 a	8.91 ± 1.00 a
10	6.4 ± 1.5 ab	2.30 ± 0.95 a	9.62 ± 3.80 a
20	7.0 ± 1.3 a	1.12 ± 0.17 ab	5.00 ± 0.67 b
40	6.2 ± 1.4 ab	1.37 ± 0.54 ab	6.23 ± 2.44 b
80	2.5 ± 0.6 b	0.36 ± 0.16 b	1.89 ± 0.76 c
Trial 2/3			
0	6.55 ± 0.64 a	2.81 ± 0.26 a	12.78 ± 1.24 a
10	7.45 ± 0.84 ab	2.74 ± 0.41 a	12.79 ± 1.99 a
20	7.80 ± 1.04 b	2.68 ± 0.31 ab	11.96 ± 1.33 a
40	7.00 ± 0.63 ab	2.01 ± 0.22 bc	8.93 ± 0.98 b
80	6.45 ± 0.80 a	1.62 ± 0.19 c	7.79 ± 0.95 b

^z Same letter indicates that the means (±standard error) are not significant $P > 0.05$.

Table 1. Potato growth assessment for each level of *Globodera pallida* initial nematode densities (P_i) in soil

	Fresh top	Dry top	Dry root	Dry tuber	Fresh tuber	Total dry plant
<i>Pi</i> (eggs/g soil)	Weight (g)					
Trial 1						
0	46.68 ± 4.20 a ^z	8.39 ± 1.05a	1.19 ± 0.11 a	9.22 ± 0.45 a	42.10 ± 2.53 a	18.80 ± 1.23 a
10	37.23 ± 3.94 a	5.74 ± 0.93 a	0.95 ± 0.15 a	8.30 ± 0.90 ab	35.93 ± 3.83 ab	15.00 ± 1.50 ab
20	38.79 ± 2.83 a	6.19 ± 0.85 a	0.93 ± 0.07 a	6.84 ± 0.86 ab	30.26 ± 3.36 ab	13.96 ± 1.52 ab
40	32.32 ± 5.47 a	4.76 ± 1.21 ab	0.78 ± 0.11 a	5.17 ± 0.86 b	23.51 ± 3.84 b	10.71 ± 1.88 b
80	12.41 ± 6.04 b	1.63 ± 0.80 b	0.14 ± 0.05 b	1.32 ± 0.53 c	5.58 ± 2.28 c	3.08 ± 1.32 c
Trial 2/3						
0	37.65 ± 3.94 a	5.17 ± 0.54 a	1.42 ± 0.16 a	16.34 ± 0.96 a	73.29 ± 3.97 a	22.93 ± 1.32 a
10	40.82 ± 3.58 a	5.93 ± 0.42 a	1.43 ± 0.11 a	16.21 ± 1.08 a	73.47 ± 4.52 a	23.57 ± 1.17 a
20	37.50 ± 3.06 a	5.68 ± 0.46 a	1.19 ± 0.11 a	15.75 ± 1.04 a	70.46 ± 4.42 a	22.62 ± 1.30 a
40	34.25 ± 3.50 a	4.79 ± 0.44 a	1.09 ± 0.10 a	13.10 ± 1.38 ab	58.35 ± 5.96 b	18.98 ± 1.77 ab
80	32.71 ± 3.75 a	4.33 ± 0.44 a	0.90 ± 0.13 a	9.51 ± 1.23 b	45.02 ± 5.45 b	14.74 ± 1.55 b

^z Same letter indicates that the means (±standard error) are not significant $P > 0.05$.

42% at 80 eggs/g soil compared with noninfested soil ($P \leq 0.05$) (Table 1). Overall, total dry plant weight decreased significantly by 36% at 80 eggs/g soil compared with noninfested soil ($P \leq 0.05$) (Table 1). Tubers produced per plant showed a propensity to increase in number at 10 and 20 eggs/g soil, with a significant 19% increase in the number of tubers at 20 eggs/g soil ($P \leq 0.05$), before dropping at 40 and 80 eggs/g soil (Table 2). Furthermore, fresh tuber weight per unit was significantly reduced by 30% at 40 eggs/g soil and by 39% at 80 eggs/g soil, and dry tuber weight per unit was significantly reduced by 28% at 40 eggs/g soil and by 42% at 80 eggs/g soil compared with noninfested soil ($P \leq 0.05$) (Table 2).

***G. pallida* reproduction assessment.** Trial 1 and trial 2/3 showed significant increased proliferation of *G. pallida* cysts in dry potato roots for each increasing level of *Pi* in soil ($P \leq 0.05$) (Table 3). Similar increased proliferation patterns of *G. pallida* cysts were observed in soil (Table 3). The number of eggs per cyst decreased significantly at each increasing level of *Pi* in soil ($P \leq 0.05$) (Table 3). *G. pallida* reproduction rate (*Rf*) decreased significantly at each increasing level of *Pi* in soil ($P \leq 0.05$) (Table 3).

Modeling the relationship between *Pi* and potato growth variables. Trial 1 showed strong and significant negative linear relationships between *Pi* in soil (predictors) and potato growth (response variables) ($P < 0.001$) (Table 4). Pearson correlation coefficient (R^2), a measure of strength in linear relationships, were for: fresh top (0.47), dry top (0.47), dry root (0.52), fresh tuber (0.61), dry tuber (0.60), and total dry plant (0.56). Bayesian regression analysis, a method to measure the posterior probability distributions in linear relationships, for total dry plant showed that the 97.5% confidence interval was for (Fig. 1; Table 5): (i) the intercept (15.96 and 19.80); (ii) *Pi* (−0.23 and −0.14); and (iii) the residual error variance σ^2 (15.15 and 34.13).

Trial 2/3 also showed a significant negative linear relationship between *Pi* in soil and potato growth variables ($P < 0.001$) (Table 4). Pearson correlation coefficient (R^2) were for: fresh top (0.03), dry top (0.05), dry root (0.10), fresh tuber (0.20), dry tuber (0.20), and total dry plant (0.20). Bayesian regression analysis for total dry plant showed that the 97.5% confidence interval was for (Fig. 2; Table 5): (i) the intercept (22.18 and 25.85); (ii) *Pi* (−0.16 and −0.07); and (iii) the residual error variance σ^2 (31.34 and 54.98).

Modeling the relationship between *Pi* and nematode reproduction. Trial 1 showed a strong and significant negative linear relationship between *Pi* and *Rf* ($R^2 = 0.60$, $P < 0.001$) (Table 6). Similar results were observed for trial 2/3 ($R^2 = 0.52$, $P < 0.001$) (Table 6). A generalized additive model (GAM) was performed to model the relationship between dry root weight and *Rf* using a non-linear smooth function to model and capture the nonlinearities in the data. Trial 1 showed a positive and significant nonlinear relationship between dry root weight and *Rf* with a correlation coefficient $r = 0.91$ ($P < 0.001$) (Fig. 3). Similar results were observed in trial 2/3 with a correlation coefficient $r = 0.34$ ($P = 0.01$) (Fig. 3).

SUBSTOR-DSSAT potato growth simulation and *G. pallida* impact assessment. The coefficients of potato yield achieved under each initial nematode density for each potato growth variable were integrated into the SUBSTOR-DSSAT simulation model outputs (Table 7). The model simulated the potential yield for potato dry top, dry root, fresh and dry tubers, and total dry plant for each *Pi* under Idaho weather and field conditions. In trial 1, 103 days after planting (DAP), potato dry top reached a maximum yield of 6,427 kg/ha under *G. pallida* noninfested soil and reached a minimum yield of 1,221 kg/ha at 80 eggs/g soil (Fig. 4A.). From 149 to 168 DAP, potato dry root reached a maximum yield of 1,804 kg/ha in noninfested soil and reached a minimum yield of 217 kg/ha at 80 eggs/g soil (Fig. 4B). At 149 DAP, potato dry and fresh tubers reached a maximum yield of 19,145 kg/ha and 96 ton/ha, respectively, in noninfested soil, and reached a minimum yield of 2,680 kg/ha and 12 ton/ha, respectively, at 80 eggs/g soil (Fig. 5A and B). At 148 DAP, potato total dry plant reached a maximum yield of 23,911 kg/ha in noninfested soil and reached a minimum of 3,826 kg/ha at 80 eggs/g soil (Fig. 6). In trial 2/3, similar potato yields are reported under *G. pallida* noninfested soil, corresponding to each potato growth variable. At *Pi* of 80 eggs/g soil, the following minimum potato yields were observed (Fig. 7A and B; Fig. 8A and B; Fig. 9): (i) dry top (5,399 kg/ha); (ii) dry root (1,137 kg/ha); (iii) dry tuber (11,104 kg/ha); (iv) fresh tuber (58 ton/ha); and (v) total dry plant (15,303 kg/ha).

Discussion

Soil infested with *G. pallida* caused significant potato yield loss in the susceptible cultivar ‘Désirée’ and severely hindered potato

Table 3. Impact of the initial nematode densities (*Pi*) of *Globodera pallida* in soil on final nematode densities (*Pf*) and reproduction rate (*Rf*)

<i>Pi</i> (eggs/g soil)	Cysts/g dry root	Cysts/g soil	Eggs/cyst	<i>Pf</i> (eggs/g soil)	<i>Rf</i> (<i>Pf/Pi</i>)
Trial 1					
10	1,903 ± 561 a ^z	0.80 ± 0.08 ab	588 ± 21 a	473 ± 52 a	47.25 ± 5.21 a
20	1,572 ± 150 b	0.95 ± 0.08 ab	535 ± 19 ab	510 ± 56 a	25.51 ± 2.79 b
40	2,699 ± 269 c	1.19 ± 0.18 a	465 ± 24 b	567 ± 94 a	14.18 ± 2.35 c
80	36,933 ± 16,328 d	0.56 ± 0.13 b	324 ± 22 c	196 ± 52 b	2.45 ± 0.65 d
Trial 2/3					
10	562 ± 62 a	0.48 ± 0.04 a	439 ± 18 a	199 ± 16 a	19.90 ± 1.57 a
20	1,090 ± 148 a	0.73 ± 0.07 ab	424 ± 20 ab	289 ± 24 ab	14.43 ± 1.22 b
40	1,263 ± 173 ab	0.79 ± 0.10 b	389 ± 17 ab	301 ± 36 ab	7.52 ± 0.89 c
80	2,292 ± 558 c	0.89 ± 0.07 b	368 ± 14 b	328 ± 33 b	4.10 ± 0.41 c

^z Same letter indicates that the means (±standard error) are not significant $P > 0.05$.

Table 4. Linear relationships between the initial nematode densities (*Pi*) of *Globodera pallida* in soil and potato growth variables

Regression parameters	Fresh top	Dry top	Dry root	Fresh tuber	Dry tuber	Total dry plant
	Response variable (y) in gram as predicted by <i>Pi</i> (x) in eggs/g soil					
	Trial 1					
Equation	$\log_{10}y = -0.01x + 1.74$	$\log_{10}y = -0.007x + 0.94$	$y = -0.01x + 1.17$	$y = -0.44x + 40.75$	$y = -0.10x + 9.12$	$y = -0.18x + 17.88$
<i>p</i> -value	2.03e-08	2.03e-08	1.98e-09	1.03e-11	2.65e-11	2.50e-10
Adjusted <i>R</i> ²	0.47	0.47	0.52	0.61	0.60	0.56
Trial 2/3						
Equation	$\log_{10}y = -0.002x + 1.56$	$\log_{10}y = -0.001x + 0.73$	$y = -0.006x + 1.41$	$y = -0.38x + 75.65$	$y = -0.09x + 16.92$	$y = -0.11x + 24.01$
<i>p</i> -value	0.04	0.01	7.90e-04	2.47e-06	1.73e-06	1.78e-06
Adjusted <i>R</i> ²	0.03	0.05	0.10	0.20	0.20	0.20

growth development. Our study showed that fresh tuber yield losses in 'Désirée' reached between 87 and 39% when Pi was 80 eggs/g soil and between 44 and 20% at 40 eggs/g soil, compared with noninfested soil. Our greenhouse results coincided within the range of potato yield losses observed in other studies conducted in highly infested field plots planted with susceptible potato cultivars (Brown and Sykes 1983; Schomaker and Been 2006; Talavera et al. 1998; Trudgill et al. 1996, 2014; Vasyutin and Yakovleva 1998). We observed severe stunting, limited root development, and chlorosis in potato plants when Pi was 80 eggs/g soil, coinciding with similar phenotypic observations recorded by other studies conducted in highly infested soils (Evans 1982; Trudgill and Cotes 1983). In the second/third trial of our study, we observed a slight increase of potato biomass at Pi of 10 eggs/g soil; however at 40 and 80 eggs/g soil we observed significant biomass reductions. We observed a slight increase in the number of tubers at 20 and 40 eggs/g soil; however

the size of the tubers was considerably smaller compared with noninfested soil. Seinhorst and Den Ouden (1971) indicated that if potato

Table 5. Bayesian confidence interval for the linear relationship between total dry plant weight and *Globodera pallida* initial nematode densities (Pi) in soil

Parameters ^z	Trial	Confidence interval				
		2.5%	25%	50%	75%	97.5%
Intercept	1	15.96	17.24	17.90	18.53	19.80
Pi		-0.23	-0.20	-0.19	-0.17	-0.14
σ^2		15.15	19.28	22.05	25.48	34.13
Intercept	2/3	22.18	23.39	24.02	24.64	25.85
Pi		-0.16	-0.13	-0.11	-0.01	-0.07
σ^2		31.34	37.31	41.00	45.32	54.98

^z σ^2 represents the residual error variance.

Fig. 1. Bayesian regression analysis for total dry plant weight in trial 1. The posterior probability distributions showed that the 97.5% confidence interval was for: (i) the intercept (15.96 and 19.80); (ii) the initial population densities (-0.23 and -0.14); and (iii) the residual error variance σ^2 (15.15 and 34.13).

Fig. 2. Bayesian regression analysis for total dry plant weight in trial 2/3. The posterior probability distributions showed that the 97.5% confidence interval was for: (i) the intercept (22.18 and 25.85); (ii) the initial nematode densities (–0.16 and –0.07); and (iii) the residual error variance σ^2 (31.34 and 54.98).

Table 6. Linear relationships between the initial nematode densities (P_i) of *Globodera pallida* in soil and nematode reproduction

Regression parameters	Cysts/g soil	Final population (P_f)	Reproduction rate (R_f)
	Response variable(y) as predicted by P_i (x) in eggs/g soil		
	Trial 1		
Equation	$\log_{10}y = -0.001x + 0.31$	$\log_{10}y = -0.008x + 2.84$	$y = -0.56x + 43.30$
p-value	0.04	5.81e–05	2.20e–09
Adjusted R^2	0.08	0.33	0.60
Regression parameters	Trial 2/3		
	Response variable(y) as predicted by P_i (x) in eggs/g soil		
	Trial 2/3		
	Response variable(y) as predicted by P_i (x) in eggs/g soil		
Equation	$\log_{10}y = 0.003x - 0.31$	$\log_{10}y = 0.002x + 2.31$	$y = -0.21x + 19.40$
p-value	4.70e–04	0.01	2.61e–14
Adjusted R^2	0.14	0.06	0.52

cyst nematodes stimulate the growth of the plant directly, the growth stimulation would be inversely proportional to the density of the nematode in soil and would only have an effect at low *Pi*, as observed in trial 2/3.

In our study, the relationship between *Pi* and potato yield showed a negative linear interaction, indicating significant yield losses as *Pi* increased in soil. Numerous linear models for explaining the interaction between *Pi* and yield have been developed for tolerant and nontolerant potato cultivars (Elston et al. 1991; Seinhorst and Den Ouden 1971; Ward et al. 1985). The linear models developed in this study represent the upper-level of *Pi* associated with considerable yield loss, as determined by the Seinhorst model for potato cyst nematodes (Greco et al. 1982; Seinhorst and Den Ouden 1971; Ward et al. 1985). To estimate tolerance limit and minimum yield parameters for a given cultivar, it has been suggested that a full range of gradually increasing *Pi*, from 0 to at least 250 eggs/g soil is essential (Seinhorst and Den Ouden 1971). Using the Seinhorst model, Greco et al. (1982) found that the tolerance limit for *G. pallida* (pathotype Pa3) was 1.7 eggs/g soil in the intolerant cultivar 'Sieglinde'. Trudgill et al. (1996) found that the relationship between potato cyst nematodes *Pi* and yield in field trials was influenced by environmental factors, including soil type, and by differences in cultivar damage tolerance. Although the influence of soil texture or cultivar damage tolerance on the relationship between *Pi* and yield was not assessed in this study, yield loss was influenced by the initial infestation rate.

We observed a significant increase in *Rf*, reaching almost 50 times the amount of eggs initially applied in soil. Whitehead (1991) showed a *G. pallida* *Rf* of 21.7 in the susceptible 'Désirée' in infested fields. Phillips et al. (1991) reported the maximum *G. pallida* *Rf* for

the following potato cultivars: (i) 'Maris Piper' (nonresistant) 44.4; (ii) 'Morag' (moderate resistance) 44.3; (iii) 'Fiona' (low level of resistance) 29.1; (iv) '11233' (moderate resistance) 26.2; (v) 'Vantage' (high resistance) 9.6; and (vi) '12243' (low level of resistance) 12.4. Greco et al. (1982) reported *G. pallida* *Rf* of 128, 58, and 65 in the susceptible 'Sieglinde' *Pi* of 6,856 eggs/g soil in three separate microplot experiments. Whitehead (1977) estimated that if each gram of soil contains one *G. pallida* egg, then the number of nematodes could reach 3.30×10^9 eggs/g soil per hectare, in the top 40 cm of the soil profile. The reproduction rate of *G. pallida* decreased, as *Pi* increased in soil, due to the reduction of the root system and infection court, leading to a density-dependent population dynamic, as observed in our trials (Phillips et al. 1991; Seinhorst and Den Ouden 1971; Trudgill et al. 1996). Jones and Kempton (1978) showed that the nematode sex ratio, the number of eggs produced by the female, and the host crop growth limitations were the main mechanisms for the density-dependent regulation of *G. rostochiensis* population growth. In trial 1, we observed that *Pf* increased slightly at increasing *Pi*; however at *Pi* of 80 eggs/g soil *Pf* significantly decreased, as nematode proliferation in root is limited by competition and the total amount of food that the root can supply. In trial 2/3, we observed a continuous increase of *Pf* at increasing *Pi* because potato plants were able to grow significantly at higher biomass than plants in trial 1, thus providing more food supply for the nematode. In both trials, we observed a continuous reduction of the number of eggs per cyst at increasing *Pi*, as a consequence of the root infection court being overcrowded by the nematode and a limited food source for the juveniles.

The integration of crop growth simulation models to crop pest disease models provides valuable predictions of potential crop yields under disease and real farm conditions, and represents a tool to assess potential pest risks for agricultural production and food security (Batchelor et al. 1993; Boote et al. 1983; Bourgeois 1989; Donatelli

Fig. 3. A generalized additive model (GAM) was performed to model the relationship between dry root weight and *Globodera pallida* reproduction rate using a nonlinear smooth function to model and capture the nonlinearities in the data. Trial 1 showed a positive and significant nonlinear relationship between dry root weight and *G. pallida* reproduction rate with a correlation coefficient $r = 0.91$ ($P < 0.001$). Similar results were observed in trial 2/3 with a correlation coefficient $r = 0.34$ ($P = 0.01$).

Table 7. Coefficients of potato yields for each *Globodera pallida* initial nematode densities (*Pi*) in soil

<i>Pi</i> (eggs/g soil)	Dry top	Dry root	Dry tuber	Fresh tuber	Total dry plant
Trial 1					
0	1.00	1.00	1.00	1.00	1.00
10	0.68	0.80	0.90	0.85	0.80
20	0.74	0.78	0.74	0.72	0.74
40	0.57	0.66	0.56	0.56	0.57
80	0.19	0.12	0.14	0.13	0.16
Trial 2/3					
0	1.00	1.00	1.00	1.00	1.00
10	1.15	1.01	0.99	1.01	1.03
20	1.10	0.84	0.96	0.96	0.99
40	0.93	0.77	0.80	0.80	0.83
80	0.84	0.63	0.58	0.61	0.64

Fig. 4. SUBSTOR-DSSAT potato growth simulation coupled with the impact of *Globodera pallida* initial nematode densities in soil for trial 1. **A.** After 103 days after planting (DAP), dry top reached a maximum yield of 6,427 kg/ha in noninfested soil and reached a minimum yield of 1,221 kg/ha at 80 eggs/g soil. **B.** From 149 to 168 DAP, dry root reached a maximum yield of 1,804 kg/ha in noninfested soil and reached a minimum yield of 217 kg/ha at 80 eggs/g soil.

et al. 2017; Jones et al. 1985). The DSSAT software application program includes database management programs for soil, weather, crop management, and experimental data, and the databases are used for precision management, gene-based modeling and breeding selection, water use, greenhouse gas emissions, and long-term sustainability through the soil organic carbon and nitrogen balances. However, DSSAT database programs for assessing the direct impact of crop pests on yields, estimating the economic impact of yield losses and predicting the level of pathogen populations in soil sampling remain unavailable. To remediate for the lack of crop disease components in DSSAT, we generated coefficients of potato yields under different *G.*

pallida *Pi* in soil from greenhouse trials, and integrated them into the SUBSTOR-DSSAT crop growth model outputs to simulate the impact of *G. pallida* under Idaho potato field conditions. From the simulation, we were able to estimate significant fresh tuber yield losses between 84 and 38 ton/ha in the susceptible 'Désirée' when *Pi* was 80 eggs/g soil and to evaluate the overall potato plant growth. To our knowledge, this is the first time that DSSAT was used to simulate the impact of *G. pallida* on potato yield. Numerous potato cyst nematode models and simulation platforms, based on many years of field trials, were directly developed to evaluate the impact on yields, determine the economic threshold, estimating soil sampling methods and nematode probability detection, and to assess the effectiveness of nematicides, trap crops, and resistant cultivars on nematode population dynamics in the field (Been et al. 2005; Jones and Kempton 1980; Moxnes and Hausken 2007; Schomaker and Been 2006; Ward et al. 1985). Been et al. (2005) developed NemaDecide, a decision support system for the management of potato cyst nematodes, based on the results from 50 years of Dutch quantitative nematological research that had been structured into stochastic models and integrated in a software package. NemaDecide was used as a quantitative information system to enable growers to estimate risks of yield losses, to determine population development, to estimate the probability of detection of nematode foci by soil sampling, to calculate the cost/benefit of control measures, and to provide adequate advice for growers to optimize financial returns.

In this study, we observed significant differences in potato growth and *G. pallida* reproduction between trial 1 and trial 2/3. Trial 1 was conducted in Fall (September – November 2017), trial 2 in Spring (March – June 2018), and trial 3 in Fall (September – November 2018). In trial 1, we observed a high *G. pallida* reproduction coinciding with a high potato growth reduction; however in trial 2/3, *G. pallida* reproduction was reduced, and a low potato growth was

Fig. 5. SUBSTOR-DSSAT potato growth simulation coupled with the impact of *Globodera pallida* initial nematode densities in soil for trial 1. **A.** At 149 days after planting, fresh tuber reached a maximum yield of 96 ton/ha in noninfested soil and reached a minimum of 12 ton/ha at 80 eggs/g soil. **B.** At 149 days after planting, dry tuber reached a maximum yield of 19,145 kg/ha in noninfested soil and reached a minimum yield of 2,680 kg/ha at 80 eggs/g soil.

Fig. 6. SUBSTOR-DSSAT potato growth simulation coupled with the impact of *Globodera pallida* initial nematode densities in soil for trial 1. At 148 days after planting, total dry plant reached a maximum yield of 23,911 kg/ha in noninfested soil and reached a minimum of 3,826 kg/ha at 80 eggs/g soil.

Fig. 7. SUBSTOR-DSSAT potato growth simulation coupled with the impact of *Globodera pallida* initial nematode densities in soil for trial 2/3. **A.** After 103 days after planting (DAP), dry top reached a maximum yield of 6,427 kg/ha in noninfested soil and reached a minimum yield of 5,399 kg/ha at 80 eggs/g soil. **B.** From 149 to 168 DAP, dry root reached a maximum yield of 1,804 kg/ha in noninfested soil and reached a minimum yield of 1,137 kg/ha at 80 eggs/g soil.

observed. Although greenhouse conditions were kept constant for the trials, we concluded that temporal difference between the trials might be the source of variation in the results obtained. Temporal differences might affect the potato plant photoperiod experienced during *G. pallida* development, and also might influence nematode breaking of diapause. Evans (1987) showed that *Globodera* spp. undergo a diapause stage in which juvenile development within egg remains dormant until favorable hatching conditions are reached. Ellenby (1958) found that *G. rostochiensis* produced fewer females on potato roots in short days than in long days. De Scurrah et al. (1975) reported that *G. rostochiensis* and *G. pallida* distinct distributions in the

Andes were related to the effects of day length on the hosts. Franco and Evans (1979) observed that *Globodera* spp. from Europe tended to produce more cysts on plants grown in 16-h days; however *G. rostochiensis* from Peru produced more cysts on plants grown in 12-h days. Hominick (1986) showed that the breaking of nematode diapause was attributed to photoperiod signals passed to the developing *G. rostochiensis* females and eggs by the plant. Evans et al. (1985) observed diapause in *G. rostochiensis* and recorded a low rate of hatch in the fall and winter after harvest, and a faster rate of hatch the following spring and summer. Temporal temperature conditions might also explain the variations in the results obtained. Franco (1979) reported that *G. pallida* is better adapted to temperatures between 10°C and 18°C, and more cysts and eggs per plant were produced at lower temperatures. Similar temperature conditions and nematode reproduction were also reported for *Globodera* spp. (Martin 1965; Oostenbrink 1967).

Due to *G. pallida* high reproduction rate and considerable impact on potato yield, this pest can rapidly spread via contaminated farm equipment or plant materials in the absence of an effective biosecurity regulation (Hodda and Cook 2009). *G. pallida* produces only one infection cycle per crop cycle and causes the development of monocyclic disease. The early stages of monocyclic epidemics are characterized by a linear model, and a reduction in the initial inoculum or the rate of infection will result in a reduction of the disease level (Madden et al. 2007). The enforcement of quarantine regulation in Idaho greatly contributed in restricting *G. pallida* infested fields to a small area of 1,326 ha (USDA-APHIS 2019). The benefits of excluding these nematodes from potato growing areas in the United States are estimated to be \$300 million annually (Dwinell and Lehman 2004; Hockland et al. 2006). Hodda and Cook (2009) estimated, in the absence of potato cyst nematodes regulation, the economic losses for Australian agriculture could exceed \$370 million. Schomaker and Been (2006) estimated that the mortality rate of *G. rostochiensis* and *G. pallida*, in the absence of the host, was greater in the first year after potato crop (69%) than in subsequent years (20 to 30%), and the population decline was independent of nematode population density. When nonhost crops were cultivated for 2 or 3 years consecutively, potato yield increased by 2.7 and 3.4 times, and *G. pallida* populations declined by 54 and 91%, respectively (Samaliev 1998). In the absence of potato crop, *G. pallida* rapid reproduction rate will stop and control measures will achieve better results in the eradication of the remaining viable nematode eggs in the fields. The use of nematicides contributes to the reduction of initial nematode densities in soil, however the high cost, inherent toxicity, and potential environmental damage of many nematicides have limited or prohibited their use (Haydock et al. 2006; Schneider et al. 2003). One of the most important environmental problems associated with nematicide usage is groundwater contamination (Cohen 1996). Furthermore, models showed that sufficient *G. pallida* eggs are likely to survive in the soil after nematicide applications, leading to a resurgence of large nematode populations in subsequent potato crop cycle (Trudgill et al. 2003). Resistance in potato russet-type varieties suitable for U.S. producers is currently unavailable (Whitworth et al. 2018). Breeding resistance for *G. pallida*, with integration into a crop rotation scheme (nonhost and trap crops), can provide a viable alternative to nematicides and will favor a long-term sustainable control of *G. pallida* in the field (Dandurand and Knudsen 2016; Dandurand et al. 2017; Whitworth et al. 2018). Gurr (1992) reported that resistance may offer more effective control of *G. pallida* than chemical treatment.

We acknowledge some limitations in our risk simulation model in terms of its evaluation and validation using real field data. Because of the quarantine status of *G. pallida* in Idaho, this study could not be performed in potato field conditions. Furthermore, there are no recorded field data on *G. pallida* associated potato yield losses for Idaho, which in most cases are used to establish the robustness of a risk model by comparing observed data with the simulated model. However, the simulation model in this study provides important information on the potential risk of significant potato yield losses caused by *G. pallida* for the potato industry. This study provides valuable simulation data for agricultural economists to model the

Fig. 8. SUBSTOR-DSSAT potato growth simulation coupled with the impact of *Globodera pallida* initial nematode densities in soil for trial 2/3. **A**, At 149 days after planting, fresh tuber reached a maximum yield of 96 ton/ha in noninfested soil and reached a minimum yield of 58 ton/ha at 80 eggs/g soil. **B**, At 149 days after planting, dry tubers reached a maximum yield of 19,145 kg/ha in noninfested soil and reached a minimum yield of 11,104 kg/ha at 80 eggs/g soil.

Fig. 9. SUBSTOR-DSSAT potato growth simulation coupled with the impact of *Globodera pallida* initial nematode densities in soil for trial 2/3. At 148 days after planting, total dry plant reached a maximum yield of 23,911 kg/ha in noninfested soil and reached a minimum of 15,303 kg/ha at 80 eggs/g soil.

economic impact of this pest for Idaho potato production, and contributes to the growing demands by decision-makers for the integration of disease model into crop growth simulation platform. This study is especially oriented toward potato growers affected by the presence of this nematode in their fields. The tools and methods used in this study can be expanded to include the impact of various control methods on *G. pallida* population dynamics and potato growth, as well as to estimate the risk impact of climate change for potato production. The outputs of this study should facilitate common understandings between regulators, policymakers, and potato growers on the challenges and opportunities for controlling this economically important potato pest in Idaho.

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