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Low-dose foliar treatments of the auxin analog 2,4-D reduce potato common scab and powdery scab for multiple potato cultivars and enhance root development

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ABSTRACT

Common scab and powdery scab are major soilborne diseases of potato (*Solanum tuberosum*). The agricultural cost of both diseases is due to discounting or rejection of infected seed tubers or the formation of lesions on the surface of the tubers that make them unmarketable or, for powdery scab, yield loss. There are no widely accessible and efficacious disease management options for either common scab or powdery scab. In prior work, low-dose foliar treatment with the auxin analog herbicide 2,4-D has been shown to reduce common scab severity of select *S. tuberosum* cultivars in field and greenhouse settings. In the present study, we address the broad applicability of 2,4-D in disease management by testing the efficacy of 2,4-D treatment across diverse potato cultivars and in suppressing multiple scab diseases of potato. Specifically, we tested whether low-dose 2,4-D treatment is broadly efficacious on multiple white potato cultivars used in Eastern United States potato production. Additionally, we sought to determine whether 2,4-D is efficacious for mitigating powdery scab for Russet Burbank potatoes in a commercial field setting. In two years of field trials, low-dose foliar 2,4-D treatment significantly reduced common scab of all tested potato cultivars with no impact on total tuber yield. In two years of field trials in Tasmania, Australia, low-dose foliar 2,4-D treatment also reduced powdery scab of Russet Burbank potato with no impact on total tuber yield while stimulating potato plant root growth. The ability of 2,4-D to suppress two major tuber diseases and stimulate potato root growth warrants further investigation and optimization for integration into commercial growing systems.

1. Introduction

Common scab is among the costliest soilborne diseases of potato and is present in all potato-growing locations in the world. The disease is caused by several pathogenic members of the genus *Streptomyces* and is manifest as raised or pitted lesions on the surface of tubers that can make them nonsalable (Braun et al., 2017). *Streptomyces* is a diverse genus with more than 800 named species, but only a small subset of *Streptomyces* species includes strains that cause common scab (Loria et al., 2006; Thapa et al., 2019). The primary pathogenicity determinant for *Streptomyces* strains that cause common scab is the phytotoxin thaxtomin A (Loria et al., 2008), which is involved in inhibition of cellulose synthesis (Scheible et al., 2003) and plant cell death (Duval et al., 2005; Thapa et al., 2019). Thaxtomin is demonstrably necessary for the formation of classic common scab lesions (Healy et al., 2000; Joshi et al., 2007).

Powdery scab is another globally significant soilborne disease of potato caused by the obligate Plasmodiophorid pathogen *Spongospora subterranea* f. sp. *subterranea* (Balendres et al., 2016) that also vectors the Potato mop-top virus (Jones and Harrison, 1969). *Spongospora* disease symptoms include zoosporangial infection of root hairs and root galling that impact root function and plant productivity (Falloon et al., 2016),

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and scab lesions on tubers that reduce marketability, and can result in seed crops failing seed certification standards (Wilson, 2016).

There are few disease management options available to growers for both common and powdery scab (Braun et al., 2017; Dees and Wanner, 2012; Falloon, 2008; Merz and Falloon, 2009). The only widely efficacious management option is planting of resistant cultivars. But resistant cultivars are often not the best choice for growers because of other agronomic considerations. Additionally for common scab, cultivars defined as resistant for growth in one area may not provide effective resistance in other areas due to pathologically meaningful distinctions in the local populations of pathogenic *Streptomyces* (Clarke et al., 2019). Cultural management options for common scab include maintaining high soil moisture (Lapwood et al., 1973; Wilson et al., 2001), altering soil pH (Lacey and Wilson, 2001; Waterer, 2002) or incorporating crop rotations that suppress the disease (Larkin et al., 2010). The efficacy and practicality of these approaches are limited and some control strategies such as maintaining high soil moisture are likely to exacerbate other diseases, including powdery scab (Merz and Falloon, 2009). Multiple classes of agro-chemicals have been considered for both common scab and powdery scab management. For both common and powdery scab, several seed or soil applied fungicides have been shown to have some impact on the severity of disease under certain treatment conditions (Al-Mughrabi et al., 2016; Braithwaite et al., 1994; Wilson et al., 1999), but control is never fully effective leading to failure to pursue registration in some countries. Some more efficacious materials are expensive, and some may also show phytotoxicity. As such, uptake by growers has been limited. The broad-spectrum soil fumigant chloropicrin can suppress common scab (Al-Mughrabi et al., 2016), likely through broad elimination of *Streptomyces* in the soil. Studies on this fumigant with powdery scab have produced contradictory results, some showing disease suppression (Tsror et al., 2016), others showing elevated levels of disease (Bittara et al., 2017), postulated to be caused by fumigant-induced changes to the soil microbial environment. Again, there are problematic limitations on the use and efficacy of these management options.

The herbicide 2,4-D, an auxin analog, has also been linked to suppression of common scab in potatoes treated at sub-lethal doses prior to tuber initiation (McIntosh et al., 1981, 1985; Thompson et al., 2013, 2014b), though this work has been limited to only a few potato cultivars. A minor effect of 2,4-D treatment on suppression of powdery scab has also been shown previously under experimental conditions (Thompson et al., 2014a). 2,4-D has long been known to cause changes to tuber physiology following herbicide drift including, for example, the darkening of red potatoes (Nylund, 1956). 2,4-D is translocated to the tubers (Burrell, 1982; Tegg et al., 2008) but does not lead to marked alterations in lenticel structure or periderm thickness (Tegg et al., 2008). The mode of action of 2,4-D in common scab resistance remains largely unknown, but it is potentially involved in alterations of plant hormone signaling pathways that alter the plant response to thaxtomin (Tegg et al., 2008, 2012) or other common scab pathogenicity factors.

In the present research, we investigated whether foliar low-dose 2,4-D treatment generally provides effective field management of common scab and if the treatment effect is dependent on the potato cultivar. Additionally, we tested whether 2,4-D treatment provides any protection against powdery scab in a commercial field setting and determined whether low-dose 2,4-D treatment affects root development and tuber production.

2. Methods

2.1. Field trial planting, cultivation, growth monitoring, and harvest

Field trials in the United States were conducted in 2017 at Aroostook Farms (USDA ARS) in Presque Isle, ME and in 2018 at Aroostook Farm and Weinreich Farm (Sterman Masser Inc.) in Sacramento, PA. These fields have a long history of common scab and no known history of high prevalence of other tuber blemish diseases. Common scab pressure in previous years at both sites was not evenly distributed throughout the field necessitating the need of a spatial covariate analysis (see below). No cultivation practices were used to promote development of common scab other than the planting of several common scab-susceptible cultivars. Potatoes were planted in an incomplete split plot design to separate the 2,4-D-treated from the mock-treated blocks with main plots being the treatment and subplots the genotype (potato cultivar). A barrier row of Chippewa potatoes was planted between each main plot. Each subplot was a five-hill planting of the appropriate genotype and there were eight subplots planted within each of eight main plots. The genotypes tested in ME in 2017 were Atlantic, Green Mountain, Russet Burbank, Ontario, Envol, Superior, Chippewa, and Elkton. The genotypes tested in ME and PA in 2018 were Atlantic, Green Mountain, Envol, Superior, Chippewa, and Elkton (one genotype was double planted in each main plot to be able to better assess the spatial trends discussed in section 2.7). These cultivars were selected because they represent a large range of susceptibility to common scab (Clarke et al., 2019; Wanner and Haynes, 2009). The 2017 ME trial was planted on 05/19/17 and harvested on 09/22/2017. The 2018 ME trial was planted on 05/31/2018 and harvested on 09/16/2018. The 2018 PA trial was planted on 05/08/2018 and harvested on 09/06/2018. Normal cultivation practices with no irrigation were applied throughout the growing season. In total, the ME and PA field trials each included 64 five-hill plots each.

Two field trials were conducted at Myalla (40°59′04.5"S 145°35′03.8"E), on the NW coast of Tasmania, Australia over two consecutive seasons (2016/17 and 2017/18). Trials were conducted on a ferrosol soil with a known high level of *Spongospora subterranea* using the cultivar, Russet Burbank. The trial was undertaken within a commercial paddock with treatment plots consisting of an entire treated strip (16 rows wide by 500 m long) with each individual treatment plot separated by adjoining five row buffer strips. In the 2016/17 trial, which was planted on 10/22/2016, we monitored pathogen and disease development in the roots on three separate dates (01/11/2017, 02/07/2017, 03/08/2017), carried out a root biomass assessment on the third sequential assessment date (03/08/2017) and a fourth root biomass assessment on 03/24/2017. We also took four replicates of 3 m plot samples at plant senescence (04/28/2017) for tuber yield and disease assessment. In the 2017/18 trial, which was planted 11/10/2017, we undertook a disease (gall) assessment of the roots on 03/27/2018 and we made a tuber yield and disease assessment (four replicates each of ten plants per plot) on 05/18/2018.

2.2. 2,4-D treatment of potatoes

The low-volatility amine formulation of 2,4-D was used in all trials to minimize the effect of herbicide drift on conflating the treatment effects. 2,4-D and mock treatments were applied during early tuber initiation and flower development. Edge barrier row potato plants were extracted throughout the early growing season to monitor for the first signs of tuber development. Commercially available Weedar64 (Nufarm) 2,4-D was used for treatments in the Maine field trials. The concentrate 2,4-D was diluted to a final concentration of 200 mg/L and 0.05% tween-80 (Sigma) surfactant was also included in the treatment spray which was applied plant-by-plant using a backpack sprayer with wide angle Teejet #110 nozzle until run-off. The mock-treated plants were sprayed with 0.05% tween-80 only. In 2017, the ME field trial was treated on 06/26/17, which corresponded to 38 days after planting. In 2018 the ME field trial was treated on 07/03/2018, which corresponded to 33 days after planting.

For the PA field trial Weed-Rhap A-4D (Helena Agri) commercial 2,4-D product was sprayed (diluted to 200 mg/L) with Induce non-ionic surfactant (Helena Agri) as the surfactant at 0.05% concentration using a backpack sprayer until runoff. Mock-treated plots were treated with only the surfactant. Spray treatments were performed on June 25, 2018, coinciding with early tuber initiation, similar to the ME trials.

For the two field trials in Tasmania, Australia, substantially lower doses of 2,4-D (Amicide 625, Nufarm Ltd, Victoria, Australia) were used. This was based on the outcomes of prior Australian studies that indicated there were significant disease-suppression benefits at low doses of 2,4-D (Thompson et al., 2014b) and the perceived risks of high doses of 2,4-D in large commercial field plots on potato yield and environmental spray drift. In the first field trial we tested two levels of sub-lethal 2,4-D (6.25 and 25 mg/L) while in the second trial only 6.25 mg/L 2,4-D was tested and compared to a mock control. Plots were treated using a conventional commercial tractor set-up (wide boom positioned at a maximum of 50 cm above the target surface, providing a coarse spray, with a.i. applied in 1000 L water/ha under very light winds <10 km/h). Applications were made 5–10 days after plant emergence in the first trial (11/30/2016) and 20 days after emergence in the second trial (12/15/2017).

2.3. Disease scoring of potato tubers

Potato tubers were scored in various approaches depending on the disease of focus (powdery scab or common scab) and the year of the field trial, due to updated methodology and differential disease severity. In all cases, individual tubers were the unit of observation, sub-sampled from the experimental unit of a block of individual five-hill plots. All tubers (approximately 50) were collected from each five-hill plot. For common scab scoring, individual tubers were scored on two parameters: predominant lesion type and percent of total lesion coverage. Three distinct lesion types are associated with common scab: superficial, raised, pitted (Clarke et al., 2019; Dees and Wanner, 2012), which we used for the disease scoring (Fig. 1a). In 2017, percent coverage was estimated by determining the percent of the tuber surface affected by common scab symptoms using a previously described scoring system (Haynes et al., 2010) based on the Horsfall-Barratt scale. For statistical analyses, the mid-point of each percent coverage was assigned as the percent coverage value. In 2018, we updated the scoring system to rate each tuber based on predominant lesion type (Fig. 1a) and a numeric percentage estimate of the lesion coverage (opposed to binning the percent coverage by the Horsfall-Barratt scale). While we recognize that the numeric estimates are not necessarily more accurate than estimates using the Horsfall-Barratt scale, we found that this approach allows more robust statistical analysis of the disease data. In addition, we propose that inaccurate assessments using the Horsfall-Barratt scale cause greater problems for the accuracy of the disease data than mis-estimates in the continuous scoring system because of the large jumps between categories in the Horsfall-Barratt scale.

In Tasmania, common and powdery scab were scored following the methodology of (Thompson et al., 2013). Only tubers >2 g were assessed. Disease severity was assessed by tuber surface cover score (0: no visible disease on tuber surface, 0.5: <1%, 1: 1–<5%, 2: 5–<10%, 3: 10–<30%, 4: 30–<50%, 5: 50–<70% and 6: 70–100% tuber surface affected) with a percentage tuber coverage estimated from the mid values of these score ranges. Disease incidence was assessed for powdery scab only as the proportion of tubers with visible lesions (Fig. 1b) present.

2.4. Soil sampling and measurements soil covariates

In 2018, soil cores were taken from the middle of the planting hill from each of the main plots (eight total samples) at a depth of 8 cm for both the ME and PA field sites. Soil samples from the ME field were shipped to University of Maine soil test lab and soil samples from PA field were shipped to the Pennsylvania State University Agricultural Analytics Services Laboratory for standard soil analysis. Soil metrics quantified and used in the below-described covariate analysis were pH, phosphorous lb/acre, potassium lb/acre, magnesium lb/acre, calcium lb/acre, zinc ppm, copper ppm, boron ppm, sulfur ppm, percent organic matter, acidity, cation exchange capacity (CEC) and percent saturation of CEC of potassium, magnesium, and calcium. Moisture readings were taken at the same spatial positions as the soil cores biweekly using a Lincoln soil moisture meter (Agricultural Solutions).

2.5. Principle component analysis to identify soil covariates putatively associated with common scab symptoms

Given the large number of candidate soil covariates, many of which

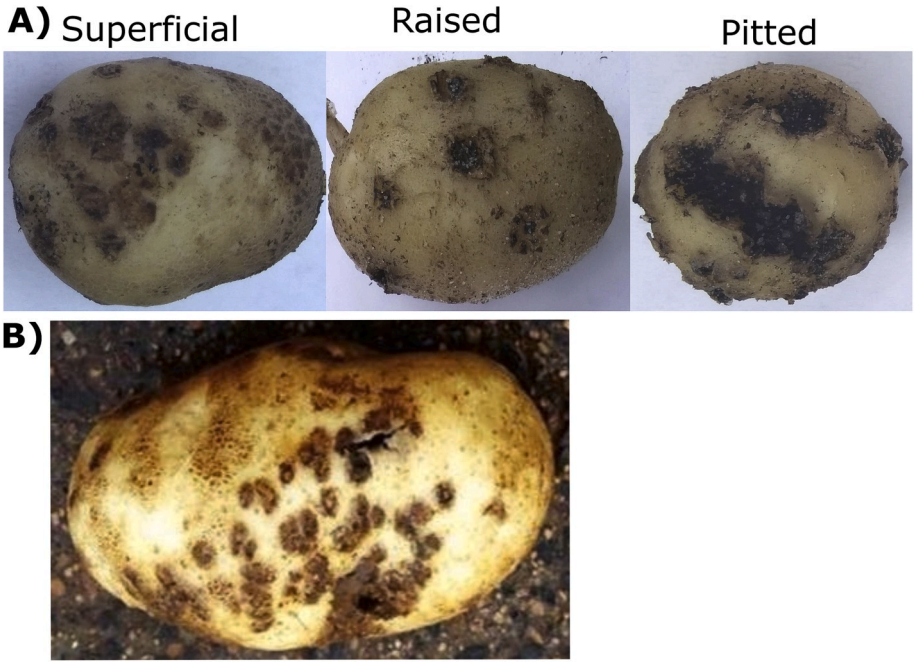

Fig. 1. Example lesion types used in disease scoring matrix. **A)** Superficial, raised, and pitted lesions caused by *S. scabiei* (common scab) from greenhouse-grown tubers of cvs. Green Mountain, Elkton, and Chippewa respectively. **B)** Powdery scab-infected tuber with typical lesions. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

were correlated, we reduced the dimensionality of these independent variables by extracting principal components using R software (R Core Team, 2019). Scree plots and cumulative sums of eigenvalues (variances) suggested that 2–4 principal component (PC) axes (dimensions) adequately captured the information in these variables. Since only one soil sample was taken from each main plot, we used kriging, a geostatistical interpolation method, to estimate the value of each PC at each five-hill location using the R package, geoR (Ribeiro and Diggle, 2018). We used an exponential model to describe the spatial autocorrelation. Estimated soil moisture for each five-hill plot also had to be estimated, and we used kriging, as described for the PC values above, to develop estimates for each five-hill plot at each time point.

2.6. Statistical analyses of disease and total tuber weight data

We modeled disease severity using R software (R Core Team, 2019), with tuber as the unit of observation using linear mixed models. Prior to analysis, for the 2018 data, the percentage estimate of the lesion coverage of each tuber was transformed using $Y = \log(X + 1)$, where X is the percent. This transformation yielded approximately normally distributed residuals when fitting models, so satisfying linear model assumptions. This is a commonly used transformation for percent data as long as most percentages are below 50%, as was our case, and yields a transformation similar to that obtained using logit, probit, or arcsine-square root for data in this range. The 2017 data, on the Horsfall-Barratt scale, did not satisfy linear model assumptions. There were two problems, one was that variances were a function of the mean, the second that the values were discontinuous (i.e. this scoring system does not produce a continuous range of values). We first transformed the data using a Box-Cox transformation (R MASS package (Venables and Ripley, 2002),), $Y = ((X + 1)^{\lambda} - 1)/\lambda$, where X is the score and the optimal $\lambda = -0.1$; this resulted in a transformed data set with homogeneous variances across the range of data. We then added a small amount of noise to the data, samples from a normal distribution with mean zero and standard deviation 0.75. This removed the discontinuities evident in the untransformed data, and model residuals were then normally distributed. While the 2017 data could then be used in analyses, we found that the estimated lesion coverage of each tuber (2018 data) produced a better dependent variable, requiring less manipulation to try satisfying assumptions of statistical models relying on normal distribution theory.

Modeling started using only a fixed effects model, that was reduced in a stepwise fashion (using an AIC criterion with the R function, step), starting with the independent variables treatment, genotype, and their interaction, all kriged PC's, all kriged soil moisture estimates, and the spatial variables (X, Y coordinates, as well as X^2, Y^2, and XY; the latter three allow for curvature in the spatial trend). Once a reduced model was developed, we allowed for correlation among the tubers within each five-hill by adding in random block effect for each five-hill position (lmerTest package (Kuznetsova et al., 2017),). Since plants and their tubers from the same five-hill position share the same micro-environment, we expected these tubers to be more similar to each other than to tubers taken elsewhere in the field, other effects being equal. Adding in this random block effect did not change any significance values on the fixed effects, and this random effect was always estimated as a positive variance (that is, there was non-zero positive correlation among the tubers within a five-hill plot). If the genotype, treatment, or their interaction were removed during the fixed model selection, we added them back to the model and tested for their significance using an F-test (in all cases the variables removed were not significant). We also checked the residuals for spatial autocorrelation and found none; the spatial trend variables and five-hill random effect (which allows for local spatial correlation) captured all the spatial effects of the data.

The quantitative (continuous) variables were treated differently for the variance decomposition, since that decomposition requires factors rather than continuous variables. Four categories or bins were created for each quantitative variable, with an approximately equal number of observations per bin (so ranges of values for each bin differed). Thus, the variance components capturing quantitative variables differ somewhat from one degree of freedom variables used in model selection/testing. However, a variance decomposition provided information not easily obtained from a typical ANOVA table, the percent of the total variability that can be ascribed to each model component.

Spatial data were not used for modelling the treatment effects in the two Tasmanian field trials because of a different experimental design and the unavailability of spatial covariates. Data for the two field trials were Box-Cox transformed ($\lambda = 0.19$ for the 2017 data and $\lambda = 0.57$ for the 2018 data) and then fitted with a mixed model with Rep (i.e. block) as a random effect, as described above, using the lmerTest R package. Pairwise contrasts (with adjusted p-values using Tukey's method) were calculated using the R emmeans package (Lenth, 2019). Data for total tuber weight exhibited large differences in variances among treatments unrelated to means. Therefore, a Box-Cox transformation would not be helpful. Instead, we used a copula transformation (essentially converting the data to ranks and applying a parametric analysis to the ranks, as residuals from this transformation are often close to normally distributed, as they were in our analysis). One effect of this transformation is that the comparison is then between medians, rather than means. Standard ANOVA methods were then used. The two sets (early and late) of root weight data did not require transformation and were analyzed using ANOVA. Since these were small data sets, *posteriori* pairwise means comparisons may not be meaningful as power is low; instead we did *a priori* contrasts between the control and the treatments.

2.7. Tuber necrosis assays

Tuber necrosis assays were performed following a previously described protocol (Loria et al., 1995) with a slight modification. Briefly, tubers of *S. tuberosum* cv. Chippewa were sliced into ≅0.8 cm cross sections and placed on slightly moist filter paper in Petri dishes. Whole tuber slices were collected to allow up to three toxin exposure spots on the same tuber slice. Three marker spots were added to the topside of each slice to indicate the toxin exposure site. Sterile filter discs were soaked in purified thaxtomin A (Sigma Aldrich), diluted 2,4-D (Nufarm), or appropriate solvent controls, air dried, and then placed over the marker spot. 30 μL of sterile water was then added onto the top of each filter disc and the Petri dishes were sealed with parafilm and placed in the dark at room temperature. Necrosis symptoms were observed underneath the filter disks after seven days.

3. Results

3.1. 2,4-D treatment has an overall positive effect on yield of marketable tubers

Spatial covariate analysis (see sections 2.5 and 2.6) of the 2017 field trial in Maine revealed that treating plants with low-dose 2,4-D (sprayed 38 days after planting) resulted in tubers with significantly lower levels of common scab (Table 1) with an overall reduction of approximately 25% disease severity due to the treatment. Additionally, there was no genotype by treatment interaction indicating that the treatment was efficacious for all of the tested genotypes (Table 1). This trial also confirmed that there were strong spatial trends of common scab pressure across the field site. Coefficients of the X, Y, and X^2 variables (which reference the geospatial distribution of the plants across the field) were significant effects for predicting the severity of common scab of the harvested tubers (Table 1). The raw tuber disease score data separated by treatment and potato genotype is shown as a boxplot in Fig. 2A.

Table 1
Type III Analysis of Variance Table with Satterthwaite's DF method for disease severity for the 2017 field trial in Maine.

	Sum Sq	Mean Sq	mDF	DenDF	F value	Pr (>F)	
Genotype	235.14	33.592	7	48.034	14.713	4.59E-10	***
Treatment	46.035	46.035	1	49.19	20.163	4.31E-05	***
X position	29.105	29.105	1	44.345	12.747	0.00087	***
Y position	90.054	90.054	1	49.207	39.444	8.50E-08	***
X^2	22.609	22.609	1	45.575	9.9026	0.00290	**
Genotype:Treatment	16.513	2.359	7	48.122	1.0333	0.42068	

3.2. Identification of soil covariates that significantly affect common scab severity

Given the results from the 2017 trial, we modified the 2018 ME field trial. First, fewer genotypes were tested to allow more replicate plants of each genotype and some repeat subplot (genotype) replicates within each main plot (treatment) to better account for the spatial trends.

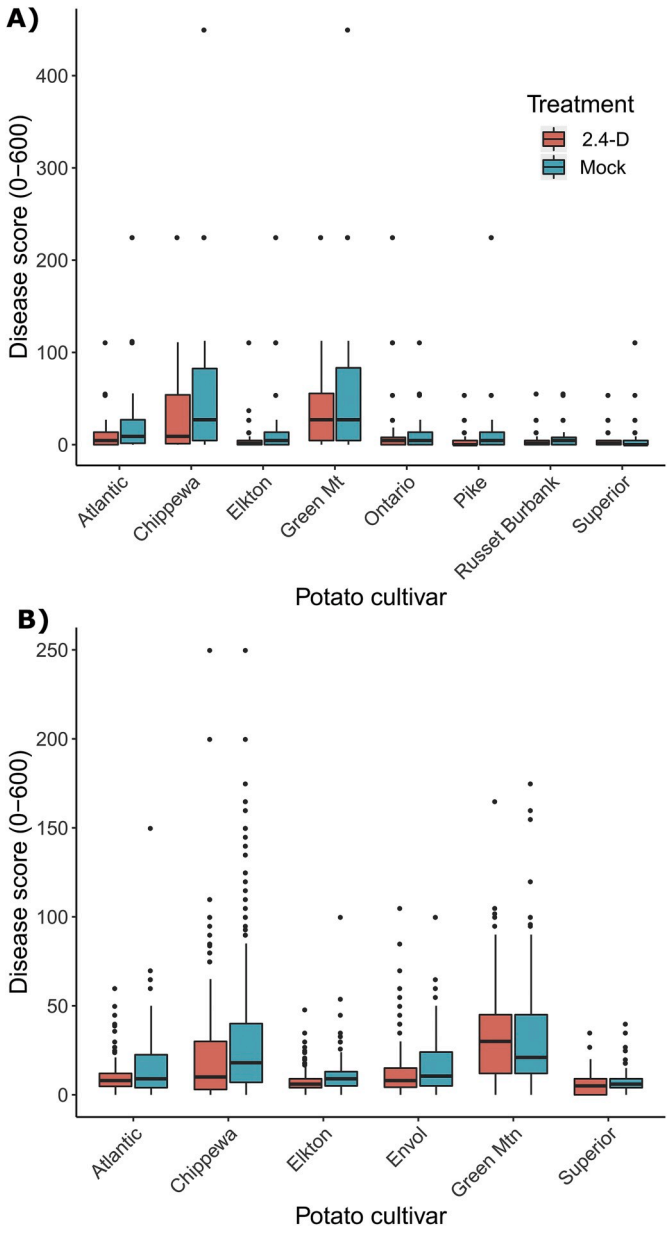

Fig. 2. Boxplot of raw disease score data of the 2017 (**A**) and 2018 (**B**) common scab trial separated by treatment and potato genotype.

Second, we collected soil nutrient data across the field site to be able to better model the spatial trends of common scab and better estimate the 2,4-D treatment effect. We collected eight soil samples (one from each main treatment plot) for analysis from both the ME and PA field sites in 2018. Principle component analysis reduced the ME soil data to two principle components that explained 85% of the variance of the soil nutrient conditions. PC1 explained 63.5% of the variance and PC2 explained 21.4% of the variance. The loadings of the ME soil data for each principal component are shown in Fig. 3. Kriged versions of both PC1 and PC2 were considered as parameters in model selection (see sections 2.5 and 2.6 of the methods) of the disease data. PC2 was identified as an important parameter for disease severity and significantly predicted disease severity (discussed below). Both PC1 and PC2 were also considered as parameters in the model fitting of the total tuber weight data but neither PC was included in the reduced model for the 2018 ME total tuber weight data. Additionally, we collected biweekly moisture readings from each subplot; the kriged moisture data were variables considered in the stepwise model fitting approach to model the disease and total tuber weight data. One of the moisture level readings was retained in the model (8/27) for tubers and two for weight (only one of which was statistically significant).

For the PA field site, principle component analysis reduced the soil data to four principle components explaining 95% of the variance of the soil nutrient conditions. PC1 explained 63.5% of the variance, PC2 explained 20.5%, PC3 explained 13.4%, and PC4 explained 8.3%. The loadings of the PA soil data for each principal component are shown in Table A.1. Kriged versions of all principle components were considered as candidate variables for stepwise model selection for disease severity and total tuber weight for the 2018 PA data. PC3 and PC4 were determined to be important predictors for modeling the disease severity data and PC1 for modeling the total tuber weight data (discussed below).

3.3. Analysis of spatial covariates confirms that low-dose treatment of 2,4-D significantly reduced severity of common scab

In 2018, we performed second year evaluations at the same ME field site with the slightly modified experimental design described above. For the second year, we observed a significant reduction in common scab severity due to low-dose treatment of 2,4-D early in the growing season (Table 2). The mean disease score data across all of the 2,4-D-treated plots was 15.92, and for the mock-treated plots was 21.6 suggesting an approximate 25% reduction in disease severity due to the treatment. As with the ME 2017 field data, there was no genotype by treatment interaction indicating that the treatment was efficacious for all tested genotypes (Table 2). The raw tuber disease score data separated by treatment and potato genotype is shown as a boxplot in Fig. 2B.

While most of the total variance was explained by the residual (this includes tuber-to-tuber variability and any other source of unaccounted for effects) (Table A.2), 7.4% of the explainable variance (variance components not including the residual) was attributed to the treatment while 62% of the explainable variance was attributed to the genotype (Table 3). Therefore, the effect of the low-dose 2,4-D treatment was smaller than the effect of the genotype on expressed tuber disease resistance.

A replicated field trial was also performed in PA in 2018 using an

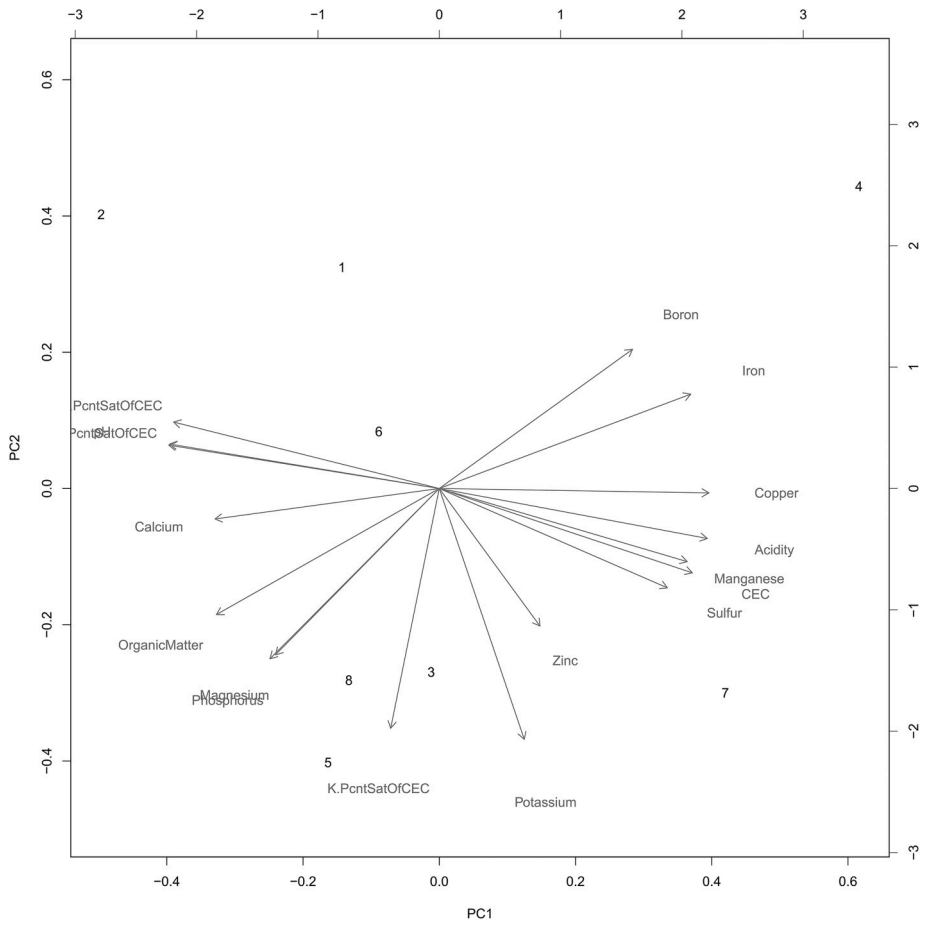

Fig. 3. PCA loading chart of Maine soil conditions in 2018. PC2 was significantly and negatively correlated with common scab severity in the 2018 Maine field trial.

Table 2
Type III Analysis of Variance Table with Satterthwaite's DF method for disease severity for the 2018 field trial in Maine.

	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr (>F)	
Genotype	144.6	28.9199	5	67.869	21.005	1.27E-12	***
Treatment	16.945	8.4724	2	62.57	6.1536	0.003633	**
PC2[a]	19.87	19.87	1	69.724	14.432	0.000307	***
Y position	17.753	17.7532	1	62.758	12.8945	0.000647	***
Moisture 8.27	12.447	12.4467	1	66.945	9.0403	0.003717	**
Genotype:Treatment	4.538	0.756	6	60.23	0.549	0.769	

[a] PC2 had a coefficient of −0.18 indicating a negative correlation between the soil conditions captured in PC2 and common scab severity.

Table 3
Variance decomposition analysis of factors affecting common scab severity from the 2018 field trial in Maine not including residual variance.

	variance	% total variation
plant	0.084688	20.5917
Genotype	0.255088	62.024
Moisture 8.27	0.001045	0.2542
Y position	0.008993	2.1865
PC2[a]	0.030831	7.4966
Treatment	0.030627	7.4469

[a] PC2 had a coefficient of −0.18 indicating a negative correlation between the soil conditions captured in PC2 and common scab severity.

identical experimental design including spatial covariates. At this site, only a small subset of the harvested tubers exhibited scab symptoms. We did not observe a significant treatment effect at the PA site ($p = 0.13$, Table A.3) in this low disease condition. However, genotype was still a significant factor for disease severity ($p < 0.001$, Table A.3) further indicating the greater influence of genotype over the treatment for explaining common scab severity. Additionally, there were strong spatial trends at the PA field site with multiple significant spatial variables and multiple significant soil nutrient principal components (Table A.3). However, the limited number of tubers that exhibited any notable common scab symptoms at the 2018 PA field site limits the ability to draw conclusions from this dataset.

3.4. Low-dose foliar spraying of S. tuberosum cv. Russet Burbank also provided management of powdery scab

In further trials, we tested whether low-dose treatment of 2,4-D can reduce the impact of the powdery scab pathogen, *S. subterranea* on Russet Burbank tubers in two years of field trials in Tasmania. Both 25

Table 4
Type III Analysis of Variance Table with Satterthwaite's DF method for disease severity for the 2016/17 and 2017/18 powdery scab trials in Tasmania.

Year	Factor	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr (>F)	
2017	Treatment	19.367	9.6834	2	909.08	10.833	2.24E-05	***
2018	Treatment	23.98	23.98	1	652.27	32.55	1.76E-08	***

mg/L and 6.25 mg/L treatments were tested in the 2016/17 growing season and both led to significant reductions in disease severity (Table 4, Table A.4). The 6.25 mg/L treatment reduced disease severity by approximately 27% and the 25 mg/L treatment reduced disease severity by approximately 54%. In the 2017/18 growing season, we only tested the 6.25 mg/L 2,4-D treatment level and observed significant reduction in powdery scab severity (Table 4, Table A.4). The disease score raw (untransformed) data are shown in Fig. 4. Disease incidence of powdery scab was also markedly reduced in both years of the trial (Table A.5). Therefore, we conclude that low-dose treatment of 2,4-D also protects tubers against powdery scab under the assessed trial conditions. Additionally, in both years we visually assessed *Spongospora*-induced galling from a number of plants in February and March. There was no obvious difference between controls and 2,4-D treatments with approximate

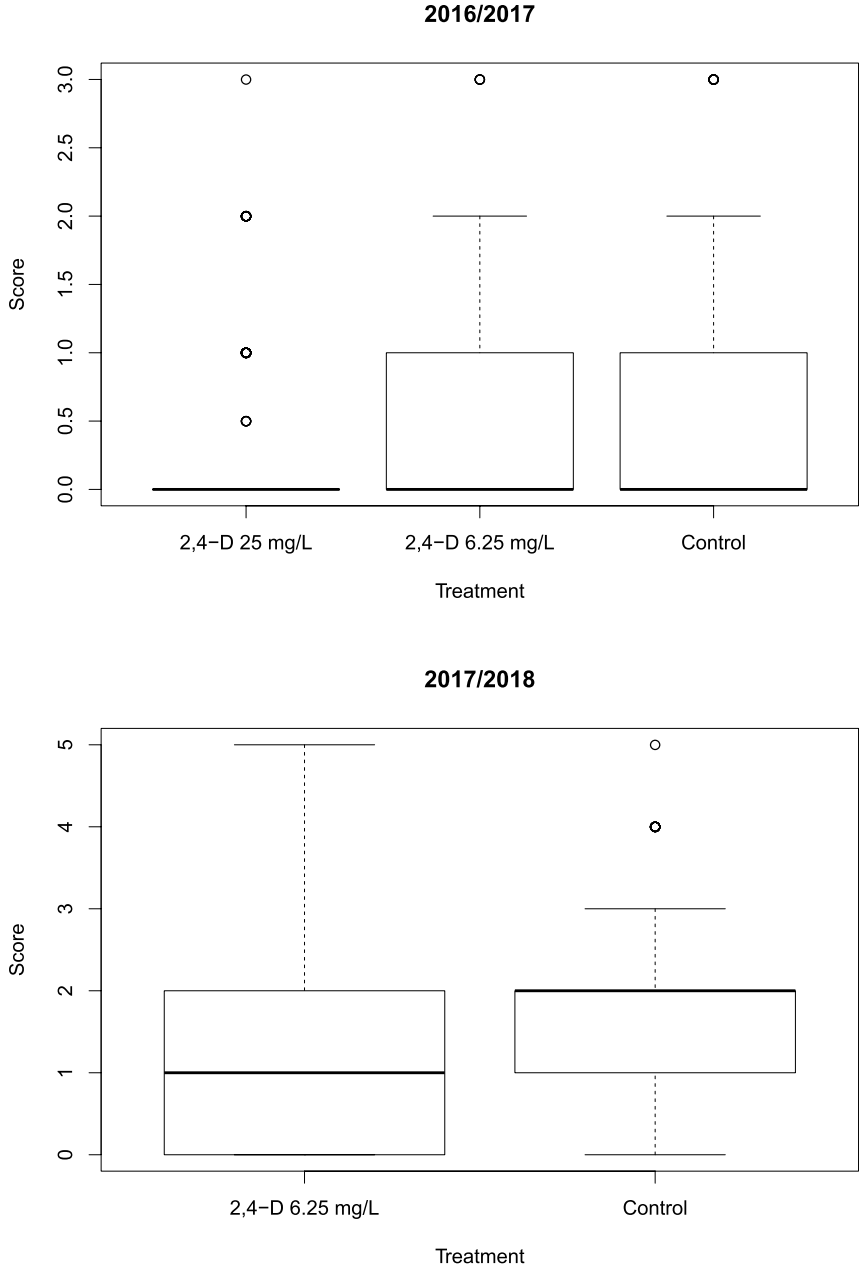

Fig. 4. Tuber disease scores of the raw data from the powdery scab field trials. Transformations of the data were required for statistical analyses shown in Table 4 (see section 2.7 of the methods).

galling scores of between 3 and 4. This represents a moderate-high gall count across all the plants assessed and suggests that 2,4-D only reduces powdery scab symptoms on tubers and not powdery scab-induced galling.

3.5. 2,4-D treatment did not reduce yield in any field trial and increased plant root growth

We also assessed whether the low-dose 2,4-D foliar sprays had a negative impact on tuber yield. The field trials in Maine and Pennsylvania were not large enough to be effective as true yield trials but total tuber weight for each five-hill plot was collected to preliminarily assess whether the treatment negatively impacted yield. In both the Maine and Pennsylvania 2018 field trials, the treatment group was not a significant factor in ANOVA analysis of the total tuber weights per five-hill plot (Table 5 and Table A.6).

The field trials in Tasmania in the 2016/17 and 2017/18 growing season were large plot trials (c. 32,000 plants per plot) with the crop grown under standard commercial production methods. Yield estimates from these trials should reflect likely impact under commercial practice. In both years, there was no significant difference in total harvested tuber weight following either of the tested 2,4-D treatment levels (Table A.7). Other tuber quality metrics were not formally assessed but there were no differences observed between the 2,4-D-treated and mock-treated plots. Taken together, these results demonstrate that the low-dose treatments of 2,4-D proposed for scab management did not have any negative impact on tuber yield across three geographically distinct field sites over two years.

As expected, genotype was a significant factor in total tuber weight at both the ME and PA field sites (Table 5 and Table A.6). PC1 of the PA soil data (Table A.1) was positively correlated with total tuber weight with a coefficient of 0.3342 at the 2018 PA field site, indicating that increased acidity and organic matter were positively associated with yield and levels of calcium and magnesium were negatively associated with yield. Only a single genotype was tested in the field trials in Tasmania.

We additionally assessed the impact of 2,4-D on plant root growth at the Tasmania field site in the 2016/17 growing season. Six to nine whole plants were removed from the soil at two assessment dates, 117 and 133 days after planting, for measurement of total root fresh and dry weights. At both assessment dates all concentrations of 2,4-D treatment led to an approximately 35% increase in potato root biomass (Table 6). Boxplots of the data are shown in Fig. 5.

3.6. The mechanism of 2,4-D control of common scab and powdery scab is unclear

Next, we tested the hypothesis that 2,4-D directly interferes with the effect of the phytotoxin thaxtomin through a chemical inhibition mechanism independent of the plant. Equal molar concentrations of 2,4-D and thaxtomin were applied to tuber slices individually or mixed together (Fig. 6). 30 μM thaxtomin induced marked cell death on tuber slices. 30 μM 2,4-D did not induce any cell death. However, 30 μM 2,4-D did not attenuate the necrotic induction of 30 μM thaxtomin, indicating that 2,4-D did not directly interfere with the phytotoxic effects of thaxtomin independent of the *in planta* inhibition previously demonstrated (Tegg et al., 2008, 2012).

Table 5
Type III Analysis of Variance Table with Satterthwaite's DF method for total tuber weight for the 2018 field trial in Maine.

	Df	Sum Sq	Mean Sq	F value	Pr (>F)	
Genotype	5	21.97	4.394	2.488	0.041	*
X position	1	3.572	3.572	2.023	0.16	
X^2	1	13.27	13.26	7.512	0.008	**
Y^2	1	1.311	1.311	0.742	0.392	
Moisture.7.16	1	7.838	7.838	4.439	0.039	*
Moisture.6.18	1	0.894	0.894	0.506	0.48	
Treatment	2	0.767	0.384	0.217	0.805	
Residuals	59	104.2	1.766			

Table 6
Effect of 2,4-D treatment on Russet Burbank root growth at the Tasmania field site in the 2016/2017 year.

	117 days after planting[a, b]		133 days after planting[a, b]	
Treatment	Fresh Weight (g)	Dry Weight (g)	Fresh Weight (g)	Dry Weight (g)
Control (No 2,4-D)	58.9 ± 4.7	5.2 ± 0.4 b	48.6 ± 2.0 b	7.3 ± 0.2 b
2,4-D (25 mg/L)	82.8 ± 6.0	7.4 ± 0.5 a	70.2 ± 4.5 a	9.0 ± 0.5 a
2,4-D (6.25 mg/L)	82.1 ± 12.2	7.3 ± 1.1 a	61.2 ± 5.7 a	8.9 ± 0.6 a
P[c]	0.051	0.048*	0.0004***	0.003**

[a] ±Represents the standard error.
[b] Different letters indicate means that are significantly different based on *a posteori* contrasts at 0.05 cutoff.
[c] Analysis of Variance for the treatment variable.

4. Discussion

In this work, we further explored the efficacy of low-dose 2,4-D treatments in potato disease management. The major project results were: 1) 2,4-D spray treatment suppressed common scab in white potato in field settings in the Eastern United States independent of the potato genotype (cultivar); 2) the distribution of common scab can be variable, even in a small field area, due to local environmental conditions; 3) 2,4-D at the proposed treatment levels did not attenuate total tuber yield; 4) foliar 2,4-D treatments may also provide limited suppression of powdery scab; 5) 2,4-D treatment led to enhanced potato root growth. Given these positive benefits obtained from a single spray treatment of a widely available chemical, there is potential for 2,4-D to be incorporated into integrated pest management plans for commercial potato production.

While the benefits of these tested 2,4-D treatments on potato production are clear and some studies have partly identified the most effective dose, timing, and frequency of 2,4-D treatment (Thompson et al., 2013, 2014b) further optimization is still required. Because 2,4-D is a broad-spectrum herbicide, increasing the dosage is not a viable mechanism for improving disease control due to the potential of severe plant injury. At the ME and PA field sites we observed delayed flower development and slightly altered leaf morphology with slight leaf curling in the 2,4-D-treated plots. Additionally, the observed increased root growth (Table 6) and neutral effect on yield (Table 5) are likely attenuated at higher 2,4-D treatment doses.

There is some inconsistency in the efficacy of 2,4-D at improving common scab control in the field in past research (Thompson et al., 2013, 2014b) and the present study. For example, we did not observe a significant reduction due to 2,4-D treatment in common scab at the 2018 PA field site, a location with low observed disease pressure. This unexpectedly low level of disease was potentially due to the extremely wet 2018 summer for Pennsylvania given the previously observed negative correlation between high soil moisture and common scab (Lapwood et al., 1973; Wilson et al., 2001). Variable environmental conditions may also underpin the observed inconsistencies in 2,4-D efficacy for common scab control. Environmental factors that affect 2,4-D disease control efficacy are currently unknown.

Another major unknown is the breadth to which 2,4-D treatment can be effective for disease management in potato. This work provides the important finding that 2,4-D is effective for at least nine genotypes of potato, with no genotype by treatment interaction (Tables 1 and 2) suggesting that the plant cultivar will not determine 2,4-D efficacy. But the genotypes tested here only represent a small portion of the diversity

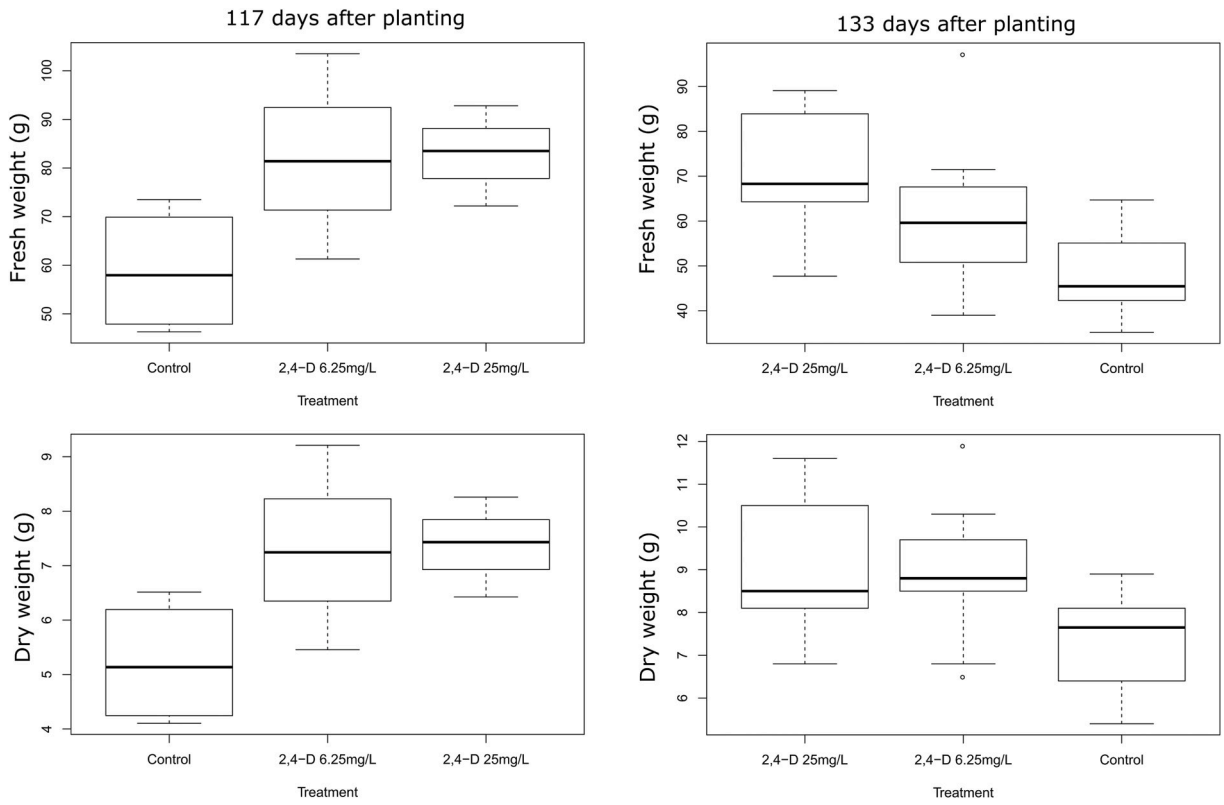

Fig. 5. Fresh and dry root mass weight following indicated 2,4-D treatments the indicated number of days after planting.

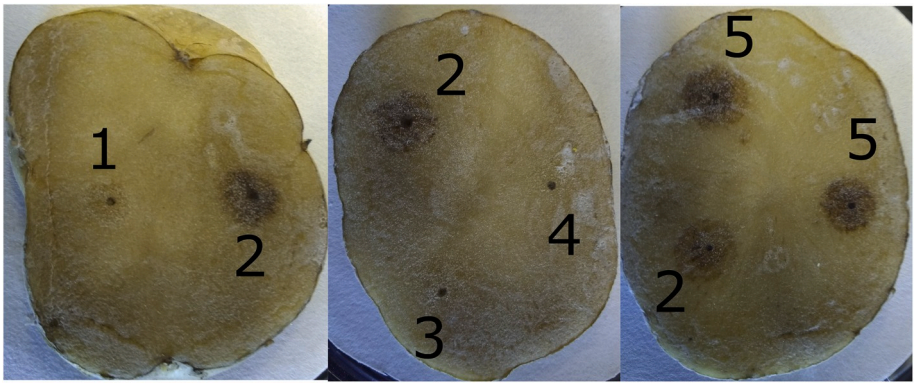

Figure 6. 2,4-D did not directly inhibit tuber necrosis induced by thaxtomin. 2,4-D and thaxtomin were applied to filter disks at the indicated concentrations and then placed on tubers of *S. tuberosum* cv. Chippewa for six days in the dark. 1: 3% methanol (mock); 2: 30 μM thaxtomin; 3: 10 μM thaxtomin; 4: 30 μM 2,4 d; 5: 30 μM thaxtomin +30 μM 2,4 d. Four tuber slices were tested in replicate. Very similar results were obtained in two independent experiments.

of potatoes, and we only tested for control of scab in a few select geographic locations. Likewise, whether 2,4-D provides the practical management of powdery scab indicated for Russet Burbank (Table 4) across other potato cultivars remains a major unknown.

Whether 2,4-D provides control against the myriad of diverse pathogenic *Streptomyces* (Wanner, 2006, 2009) also remains unknown. The ME field site contains several diverse lineages of pathogenic *Streptomyces* (Wanner, 2009), but specific determinations of whether the 2,4-D treatments are effective against specific pathogenic species cannot be determined from the available data. The present and previous studies indicate 2,4-D, and other auxin treatments, appear to ameliorate thaxtomin A toxicity in plant tissues (Tegg et al., 2008) by mechanisms yet to be elucidated. Given production of thaxtomin A appears central to disease induction across diverse pathogenic *Streptomyces* species, this suggests likely robust efficacy.

The uneven distribution of *Streptomyces* in any field also limits the ability to detect treatment effects in small-scale field studies. We employed moderate soil sampling and a spatial covariate analysis (described in the methods) at the U.S field sites to address this issue. The soil covariate data improves the estimate of treatment effect and enables identification of soil covariates associated with common scab. For example, PC2 of the ME soil data in Fig. 3 was significantly associated with common scab at the ME field site. However, identification of soil covariates associated with scab are only preliminary candidates for impactful soil factors at this time.

Importantly, this work indicates that the low-dose foliar treatments

of 2,4-D do not attenuate tuber yield. Assessment of potato yield under experimental systems can be compromised by limited plot size and compromised production systems, for example with limiting water to maximize disease. It is important to note that the present study included two trials with large treatment plots on crops grown under full commercial practice in which the low dosage foliar applied 2,4-D had no significant impact on yield, and indeed a trend for improvement in tuber yields was suggested.

Further optimization of 2,4-D treatment may depend on precise characterization of the mode-of-action. Previous work demonstrated that 2,4-D does not directly kill or interfere with the growth of the pathogenic *Streptomyces* sp. (Burrell, 1982; Tegg et al., 2008). Therefore, the mechanism of 2,4-D control of common scab is distinct from the mode-of-action of most crop pesticides. 2,4-D is translocated to the potato tubers (Tegg et al., 2008), but the effect of 2,4-D in the tubers is not fully understood. Previously, 2,4-D treated potatoes were shown to be significantly less susceptible to thaxtomin-induced necrosis (Tegg et al., 2008, 2012). Therefore, the mode-of-action is likely related to nullifying the virulence determinants of the common scab pathogen, such as the toxin thaxtomin (Tegg et al., 2008, 2012). Given the large-scale plant hormone signaling changes that occur following 2,4-D treatment, we hypothesize that specific alterations to plant hormone signaling pathways may be responsible for this phenotype. The precise plant signaling pathways 2,4-D alters to attenuate common scab development remain unknown. Determination of these 2,4-D-induced changes may enable further optimization of treatment conditions or identification of alternative chemistries to further improve scab control.

5. Conclusion

Low-dose foliar spray of 2,4-D near the timing of tuber initiation is sufficient to substantially reduce the severity of common scab in all tested cultivars of field-grown potatoes. Additionally, this work demonstrates that 2,4-D foliar treatment leads to a reduction in powdery scab on tubers and to an increase in potato root weight. The mechanisms through which 2,4-D acts on plants to attenuate the development of common scab and powdery scab and increase production of belowground biomass remain unknown. Given the observed benefits, the usage of 2,4-D for enhancing tuber disease resistance and stimulating root growth warrants further investigation for potential commercialization. We propose that future research optimizing the timing and dosage of 2,4D treatment will further improve the efficacy of common scab and powdery scab management.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

CRediT authorship contribution statement

Christopher R. Clarke: Conceptualization, Methodology, Formal analysis, Data curation, Investigation, Writing - original draft. **Robert S. Tegg:** Conceptualization, Methodology, Investigation, Writing - review & editing. **Hannah K. Thompson:** Investigation. **Curtis Frederick:** Investigation. **Kathleen G. Haynes:** Investigation, Writing - review & editing. **Matthew Kramer:** Methodology, Software, Formal analysis, Data curation, Writing - review & editing. **Calum R. Wilson:** Conceptualization, Methodology, Investigation, Writing - review & editing.

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Appendix B. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cropro.2020.105208.

Appendix A. Supplementary tables

Table A1
Loadings of the four considered principle components of soil nutrient data from the 2018 field trial in Pennsylvania.

	PC1	PC2	PC3	PC4
pH	−0.33798	0.081098	0.153322	−0.16911
Phosphorus	0.205583	0.034318	−0.57492	−0.18123
Potassium	0.040857	0.521243	0.047815	0.298941
Magnesium	−0.35617	0.017203	−0.11842	0.053324
Calcium	−0.34052	0.028715	−0.19425	0.188268
Acidity	0.3594	−0.00241	−0.01061	0.071083
CEC	−0.31011	0.058695	−0.27897	0.305798
K.%SatOfCEC	0.266854	0.302508	0.267585	−0.09324
Mg.%SatOfCEC	−0.23065	−0.08639	0.321838	−0.55955
OrganicMatter	0.26897	−0.21472	−0.3198	−0.26154
Zinc	0.215647	−0.23506	0.217248	0.53847
Copper	−0.05094	−0.45988	0.377232	0.15676
Sulfur	−0.01872	−0.55104	−0.19397	0.065907
Ca.%SatOfCEC	−0.35705	−0.02264	−0.09696	0.057293

Table A2
Variance decomposition analysis of factors affecting common scab severity from the 2018 field trial in Maine including residual variance.

	variance	% total variation
plant	0.0846883	4.7358
Genotype	0.2550883	14.2645
Moisture	0.0010455	0.0585
Y position	0.0089927	0.5029
PC2[1]	0.0308314	1.7241
Treatment	0.0306273	1.7127
Residual	1.3769996	77.0016

[1]PC2 had a coefficient of −0.18 indicating a negative correlation between the soil conditions captured in PC2 and common scab severity.

Table A3
Type III Analysis of Variance Table with Satterthwaite's DF method for disease severity for the 2018 field trial in Pennsylvania.

	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr (>F)	
Genotype	138.328	19.7612	7	43.506	19.2223	2.01E-11	***
Treatment	2.463	2.4629	1	42.361	2.3957	0.129107	
PC3[1]	5.04	5.0398	1	44.128	4.9023	0.032033	*
PC4[1]	16.884	16.8836	1	44.564	16.4232	0.0002	***
Y position	21.374	21.3738	1	46.102	20.791	3.77E-05	***
XY	10.068	10.0676	1	45.207	9.7931	0.003065	**
Genotype:Treatment	3.831	0.6386	6	43.347	0.6212	0.71224	

[1] PC3 had a coefficient of −0.08 and PC4 had a coefficient of −0.21 in the fitted model, indicating a negative correlation between the soil conditions captured in PC3 and PC4 and common scab severity.

Table A4
a posteori contrasts of treatment by treatment pairs in the powdery scab treatment trials.

Year	contrast	estimate	SE	df	t.ratio	p.value	
2017	25 mg/L - 6.25 mg/L	−0.155	0.078	909	−1.99	0.1152	
	25 mg/L - control	−0.358	0.0774	909	−4.619	<.0001	***
	6.25 mg/L - control	−0.203	0.0749	909	−2.704	0.0191	*
2018	6.25 mg/L - control	−0.386	0.0676	652	−5.704	<.0001	***

Table A5
Disease incidence of powdery scab in the 2016/17 and 2017/18 Tasmania 2,4-D field trial.

Treatment	Disease incidence (%)[1]	
	2017	2018
Control (No 2,4-D)	42.2 ± 6.4	90.4 ± 3.76
2,4-D (25 mg/L)	19.6 ± 7.7	not tested
2,4-D (6.25 mg/L)	30.8 ± 10.8	73.0 ± 15.0

[1]± indicates the standard error.

Table A6
Analysis of Variance Table for total tuber weight for the 2018 field trial in Pennsylvania.

	Df	Sum Sq	Mean Sq	F value	Pr (>F)	
Genotype	7	277.7	39.66	8.041	1.35e-06	***
PC1[1]	1	44.35	44.35	8.991	0.004	**
Y[2]	1	18.33	18.33	3.716	0.059	.
Treatment	1	0.745	0.745	0.151	0.699	
Residuals	52	256.5	4.933			

[1]PC1 had a coefficient of 0.3342 in the fitted model indicating a positive correlation between the soil conditions captured in PC1 and total tuber harvest weight.

Table A7
Type III Analysis of Variance Table with Satterthwaite's DF method for total tuber weight for the 2016/17 and 2017/18 field trials in Tasmania.

		Df	Sum Sq	Mean Sq	F value	Pr (>F)
2017	**Treatment**	2	0.10317	0.051587	1.0805	0.3797
	Residuals	9	0.42971	0.047745		
2018	**Treatment**	1	0.0102	0.010204	0.0683	0.8026
	Residuals	6	0.89683	0.149471		

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