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Predicting potato tuber yield loss due to early blight severity in the Midwestern United States

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Abstract Although early blight is among the most damaging foliar diseases of potato, the information available on the disease-yield relationship is scarce. Twenty-three field trials were conducted from 2003 to 2016 across North Dakota and Minnesota potato growing regions to study the relationships among disease severity estimated from tuber initiation (TI) to early bulking (growth stage III to IV) and late bulking/tuber maturation (growth stage IV to V) and yield. The strength of the association and the functional relationships between crop and disease variables were assessed based on estimates of the Fisher's Z transformation of Pearson correlation r, the intercept (β_0) and slope(β_1) for each trial, which were combined and analyzed using meta-analytic models. At TI to early bulking stage, random-effect model estimated a slope of 0.20 mt/ha/$\%^{-1}$ for an expected yield (intercept) of 61.88 mt/ha. Each unit increase in percent severity at this growth stage would result in a 32 percentage point (pp) yield reduction. During late bulking/tuber maturation crop growth stage, the random-coefficients β_0 and β_1 were 65.89 mt/ha and 0.13 mt/ha/$\%^{-1}$, respectively. In relative terms, yield would be reduced by 19 pp. for each unitary percentage increase in early blight severity. Based on these meta-analysis results, growers are able to predict potential yield loss for each percentage increase of early blight severity at two growth stages, which can be useful for crop-loss assessments.

Keywords Early blight · Meta-analysis · Metafor · Heterogeneity

Introduction

Early blight, caused by Alternaria solani Sorauer, is a damaging foliar fungal disease in most potato growing regions of the United States (Harrison and Venette 1970). The pathogen can survive for extensive periods in the soil as mycelia and/or as conidia on infected plant debris (Runno-Paurson et al. 2015). Early blight epidemics are driven by temperature, leaf wetness duration, and the level of atmospheric relative humidity (Adams and Stevenson 1990; Harrison et al. 1965; Olanya et al. 2009; Vloutoglou and Kalogerakis 2000). Senescing plant foliage is usually affected first; therefore, primary infections typically occur at the base of the plant on the oldest leaves and move upward eventually affecting the upper plant canopy (Franc and Christ 2001; Secor and Gudmestad 2009). Leaf symptoms are characterized by small and dark concentric lesions, which may also emerge on stems and petioles (Franc and Christ 2001; Gudmestad et al. 2013). Severely affected potato foliage restricts photosynthetic activity limiting yield (Horsfield et al. 2010). During severe epidemics, yield losses of 20

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to 30% have been reported in the United States (Christ and Maczuga 1989; Shtienberg et al. 1990). Yield reductions of 5 to 40% have been reported in Israel (Rotem and Feldman 1965; Olanya et al. 2009). The lack of commercially acceptable resistant cultivars has compelled growers to continually rely on fungicides for early blight management to enhance tuber quality and yield (Franc and Christ 2001; Gudmestad et al. 2013).

Traditionally, the relationship between disease intensity and yield has been modelled using host- and pathogen-based measurements obtained from multiple greenhouse and/or field trials. Although, early blight is one of the important foliar diseases of potato, disease and yield relationship studies are seldom found in the literature, and only a limited number of studies modelling this relationship have been conducted. A general yield loss prediction model applicable for late blight and early blight of potato was developed based on tuber bulking growth stage of an infected crop compared to that of a non-infected crop (Shtienberg et al. 1990). A multiple regression model was designed to estimate yield loss based on early blight severity assessments at multiple points of crop growth from trials conducted over two years (Teng and Bissonnette 1985). Prior to this study, knowledge available was based on experiments conducted over a decade ago, several more than 25 years ago, and current production practices are substantially different as are the array of fungicides available for disease management. Moreover, the literature appears to be devoid of more recent studies addressing the relationship between early blight severity and potato yield in the United States under a range of environmental conditions spanning multiple years. The development of models that use early assessments of disease severity as predictor of yield loss can potentially assist potato growers in making economic decisions such as the optimal time to apply fungicides to maximize a return on their investment.

The objective of this study was to summarize the strength and the functional relationship between early blight severity estimated at the tuber initiation (TI) and early tuber bulking (growth stage III to IV) or at the late bulking-tuber maturation (late growth stage IV to V) with tuber yield at harvest, using meta-analytic models.

Materials and methods

A total of 23 field trials were conducted in North Dakota and Minnesota from 2003 to 2016 under overhead irrigation (Table 1). These trials examined the efficacies of various existing and experimental fungicides for managing early blight on potato. All trials were planted in randomized complete block design with four replicates per treatment. Pathogen inoculation for disease development and fungicides were applied over the potato growing seasons as previously described (Pasche and Gudmestad 2008; Yellareddygari et al. 2016). Irrigation, fertilizer, herbicide and insecticide applications were made as applicable for potato agronomic practices used in North Dakota and Minnesota.

Approximately five weeks after planting, 11 weekly disease ratings (repeated measures) were obtained as previously described (Yellareddygari et al. 2016). For the purpose of this study, disease ratings for weeks 7 through 11 were included. The repeated measures of disease were averaged (for each trial) into two stages of potato development: tuber initiation to early bulking (growth stages III to IV, weeks 7 to 9) and late bulking-tuber maturation (late growth stage IV to V weeks 10 to11) (Miller and Hopkins 2008). These growth stages are similar to commonly referred crop development stages known as tuber development through to senescence. At the end of growing season, vines were mechanically killed and tuber yield was recorded from each experimental unit. For each trial, raw data for disease and yield were obtained at the experimental unit level. Although yield is the same for both disease variables (measured at two growth stages), two relationships (disease-yield) were studied to understand the effect of early blight severity on yield at each growth stage.

Effect-sizes and calculation

The statistical methodology applied for the current study is similar to that of previous phytopathological meta-analysis studies (Dalla Lana et al. 2015; Lehner et al. 2017; Paul et al. 2005; Paul et al. 2006). In meta-analysis, where common effects of interest are measured in different studies, the effect size is a statistical parameter used to compare the results from individual studies on a common scale (Rosenberg 2010). The common effects of interest for this study was the disease-yield relationship which was measured using various effect sizes. Fisher's Z transformation of Pearson correlation r and the slope and the intercept coefficients of linear regression were the three effect sizes estimated for this study (Dalla Lana et al. 2015). Within-study sampling variances for each study were estimated using all replication data. First, Pearson

Table 1 Attributes of 23 fungicide trials for managing potato early blight and summaries of the mean early blight severity (SEV) and maximum mean tuber yield (Max) in nontreated plots of the trial

Study	Year	Location-State	Cultivar	Early bulking SEV (%)	Late bulking SEV (%)	Max-Yield (mt/ha)
1	2003	Tappen, ND	Russet Burbank	97.25	100	55.34
2	2004	Browerville, MN	Russet Burbank	46.40	100	60.68
3	2004	Browerville, MN	Russet Burbank	43.12	100	62.44
4	2005	Browerville, MN	Russet Burbank	56.62	97.78	53.98
5	2005	Browerville, MN	Russet Burbank	71.62	98.34	48.79
6	2006	Browerville, MN	Russet Burbank	17.67	96.31	52.89
7	2006	Browerville, MN	Russet Burbank	62.06	99.65	49.97
8	2007	Tappen, ND	Russet Burbank	22.50	44.75	59.60
9	2007	Tappen, ND	Russet Burbank	13.47	30.06	64.07
10	2008	Tappen, ND	Ranger Russet	38.75	87.37	49.30
11	2008	Tappen, ND	Ranger Russet	58.44	86.56	53.83
12	2010	Inkster, ND	Ranger Russet	73.19	93.06	65.00
13	2010	Inkster, ND	Ranger Russet	41.31	69.28	85.28
14	2011	Inkster, ND	Ranger Russet	6.81	26.53	74.39
15	2011	Inkster, ND	Ranger Russet	14.94	48.16	61.86
16	2012	Inkster, ND	Ranger Russet	6.31	19.13	69.02
17	2013	Inkster, ND	Ranger Russet	10.33	62.56	54.01
18	2013	Inkster, ND	Ranger Russet	15.7	79.22	56.64
19	2014	Inkster, ND	Ranger Russet	63.94	98.47	51.99
20	2014	Inkster, ND	Ranger Russet	14.34	93.84	59.90
21	2015	Inkster, ND	Ranger Russet	13.40	70.37	58.45
22	2015	Inkster, ND	Ranger Russet	14.12	83.50	54.01
23	2016	Inkster, ND	Ranger Russet	25.37	84.47	55.25

correlation (PROC CORR of SAS) between early blight severity and tuber yield was estimated using all replication data for individual studies. Fisher's Z transformation of r value was applied to correct skewness of the data distribution and stabilizing variances across studies (Fisher 1921; Fisher 1928; Paul et al. 2005).

Since the linear regression study has both fixed (disease severity) and random (block) effects, a mixed model was fitted to the data (Dalla Lana et al. 2015). The mixed model was performed using PROC Mixed procedure in SAS. The linear regression model is written as

$$y_{ij} = \beta_0 + \beta_1 x_{ij} + \varepsilon_{ij}$$

Where β_0 is intercept, β_1 is slope, and *yij* is yield, *xij* is severity, is error for i^{th} treatment at *j* block. From the regression function, β_0 is the expected attainable tuber yield (mt/ha) at zero early blight severity and β_1 is the amount of yield increase or decrease for each early blight percent severity (mt/ha/%$^{-1}$).

Data availability The datasets generated during and/or analyzed during the current study are available from corresponding author on reasonable request.

Random-effect meta-analysis

The disease-yield relationships were summarized using meta-analytic models by fitting the three effect sizes (Z, β_0, and β_1) (Paul et al. 2005; Paul et al. 2006; Madden and Paul 2009; Dalla Lana et al. 2015; Lehner et al. 2017). A standard univariate meta-analysis (maximum likelihood) was performed for Fisher's Z using the RMA function of metafor R package. Bivariate random-effects model (using RMA.MV function in metafor R package via maximum likelihood method) was fitted for the estimated intercepts and slopes (effect sizes) (Lehner et al. 2017; Paul et al. 2006; Raudenbush 2009).

Heterogeneity analysis

The presence or absence of true heterogeneity among the studies is determined using Cochran's Q test and τ^2 test (absolute measure of heterogeneity). I^2 estimates the variability in the effect sizes among trials relative to the total variability which includes within-trial variation and between-trial variation (Higgins et al. 2003; Thorlund et al. 2012). I^2 statistic ranges from zero to 100, with high heterogeneity indicating higher I^2 value and vice versa (Groenwold et al. 2010).

Mixed-effects models

As a follow-up, sub group meta-analysis incorporating moderator variables as fixed effects that could account for at least part of the heterogeneity in the effect sizes was performed using mixed-effects models (Borenstein et al. 2009; Lehner et al. 2017). This model was also fitted using maximum likelihood methods. Subgroup meta-analysis was performed using categorical variables, cultivar (Russet Burbank and Ranger Russet), location, year (e.g. 2003–2016) and disease pressure (DP) based on early blight severity (e.g. low or high), respectively. Early blight DP classes (low or high) for early bulking and tuber maturation potato growth stages were <58% or ≥58% and <91% or ≥91%, respectively.

Relative yield loss

Relative tuber yield loss due to the early blight severity was estimated from mean estimates of intercept and slope of the random-effect model (Dalla Lana et al. 2015). Since yield losses are usually reported as percentage increase or decrease, the ratio of slope mean estimate (β_1) to that of intercept mean estimate (β_0) is multiplied by 100 to quantify the percentage yield loss for each percentage of disease severity increase (Dalla Lana et al. 2015; Madden and Paul 2009; Rosenberg and Garrett 2004; Shah and Dillard 2006). The percentage yield loss is written as $((\beta_1/\beta_0) \times 100)$.

Results

Early bulking crop growth stage

Among the studies, early blight severity ranged from 5.3 to 97.2% in the nontreated plots (Table 1). During early bulking, Pearson correlation (r) between early blight and tuber yield across studies were mostly negative and ranged from −0.72 to 0.1. The distribution of correlation observations were slightly skewed (Fig. 1). Fisher's Z transformation of *r* resulted in symmetry about the mean and the Z values for disease-yield association ranged from −1 to 0.2 (Fig. 1). Mixed model effect sizes intercept and slope varied among individual studies (Fig. 1). For individual studies the intercept, representing expected yield at zero severity, ranged from 50.28 to 75.7 mt/ha, and the slope parameter, representing magnitude of increase or decrease of expected yield per unit increase in severity, ranged from −1.25 to 0.25 mt/ha/%$^{-1}$.

The random effect model meta-analysis estimated the overall mean for the effect sizes (Z, β_0, β_1) (Table 2). The mean Fisher's Z, intercept and slope values were −0.41 (95% CI is −0.54 to −0.28), 61.88 mt/ha (95% CI is 59.08 to −64.67), and −0.20 (mt/ha/%$^{-1}$) (95% CI is −0.27 to −0.12). This indicates that when disease severity is zero, the mean tuber yield is 61.8 mt/ha and with each percentage increase of early blight severity the yield on average was decreased by 0.20 mt/ha. The variability among the intercepts and slope from individual studies and the mean estimates with 95% CI's from random effects model were plotted (Fig. 2). Heterogeneity across studies was high and supported by Q significance test and high τ^2 and I^2 values for all effect sizes (Table 2).

The moderator variable year showed significant ($P < 0.0001$) results on the Fisher's Z, slope and the intercept. However, cultivar, DP and location did not significantly affect Fisher's Z, the slope and the intercept.

Late bulking and tuber maturation crop growth stage

Among the studies (nontreated plots), substantial variation was observed in early blight severity (19.1 to 100%) and maximum yield (49.3 to 85.3) (Table 1). The correlation association between disease severity and tuber yield varied (r value ranged from −1.0 to 0.2) for individual studies and Fisher's Z value for disease-yield association ranged from −1.2 to 0 (Fig. 3). The mixed model results for the intercept and slope effect sizes were 37.7 to 101.4 mt/ha, and −0.35 to 0.15 mt/ha/%$^{-1}$, respectively.

The random effect meta-analysis estimated overall mean Fisher's Z association between severity and yield was −0.47 (95% confidence interval (CI) is −0.6 to −0.33). During tuber maturation stage the yield

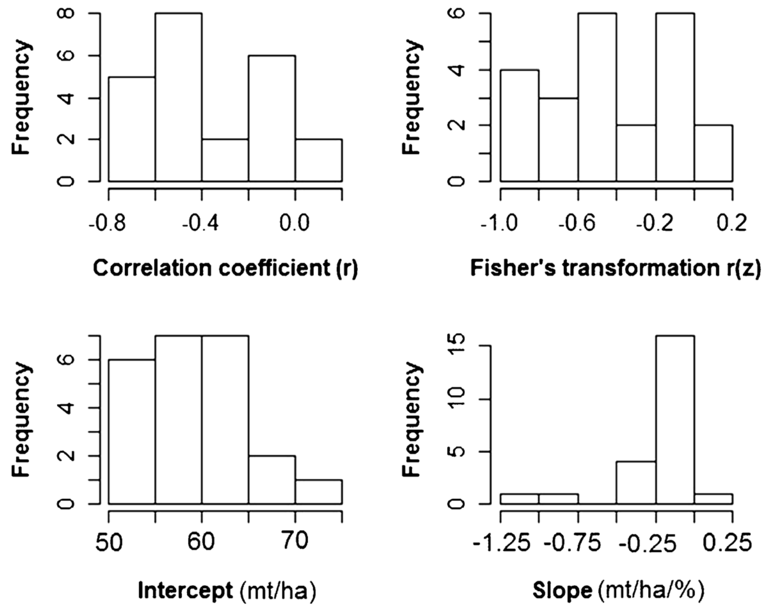


Fig. 1 Early bulking: Frequency distribution of Pearson correlation (r) coefficient and Fisher's Z transformation of r for 23 individual trials prior to meta-analysis. Intercept and slope are linear regression coefficients to study the relationship between early blight severity and yield for the individual studies

(intercept) at zero early blight severity was determined to be 65.8 mt/ha (associated 95% CI was 61.7 to 70). If early blight severity during this growth phase increases by 1 %, then the random effect model predicts that tuber yield would decrease by 0.13 mt/ha/%$^{-1}$ (Table 2). The mean estimates and the associated CI's and the variability among intercept and slope for individual studies were plotted (Fig. 4). Similar to early bulking growth stage, Cochran's Q significance test and high I^2 and τ^2values for all effect sizes indicate that the heterogeneity across studies was high (Table 2). The moderator variables cultivar, DP, and location, tested individually as categorical variables, did not significantly affect Fisher's Z, the slope, and the intercept. Moderator variable year showed significant ($P < 0.0001$) results on the Fisher's Z, slope and the intercept.

Relative yield loss

Relative yield loss due to early blight severity at two growth stages was calculated from the estimated intercept and slope of random effect meta-analysis. Relative

Table 2 Meta-analysis statistics and heterogeneity measures of three effects sizes used to estimate the disease-loss relationship at two growth stages of potato

Effect size	Statistics[a]							*Heterogeneity*[b]		
	K	Estimate	SE	CI_L	CI_U	PI_L	PI_U	τ^2	*P-value*	I^2
Early bulking										
Fisher's Z	23	−0.41	0.07	−0.54	−0.28	−1.05	0.23	0.09	<0.0001	89.33
Intercept (β0)	23	61.88	1.43	59.08	64.68	−49.77	173.53	2879.26	<0.0001	98.57
Slope (β1)	23	−0.20	0.04	−0.28	−0.12	−3.23	2.83	2.12	<0.0001	98.57
Tuber maturation										
Fisher's Z	23	−0.47	0.07	−0.61	−0.34	−1.14	0.20	0.10	<0.0001	89.83
Intercept (β0)	23	65.89	2.10	61.78	70.01	−91.58	223.36	5727.28	<0.0001	98.59
Slope (β1)	23	−0.13	0.02	−0.17	−0.09	−1.51	1.25	0.44	<0.0001	98.59

[a] Table characteristics representation (left to right): Number of studies (*K*), mean estimate, Standard error (SE), Lower and upper confidence intervals (CI), Lower and upper prediction intervals (PI),between-studies variance estimates (τ^2), Cochran Q test *P* value, and I^2 statistic

[b] Heterogeneity among studies were estimated by τ^2 , Cochran Q test *P* value, and I^2 statistic

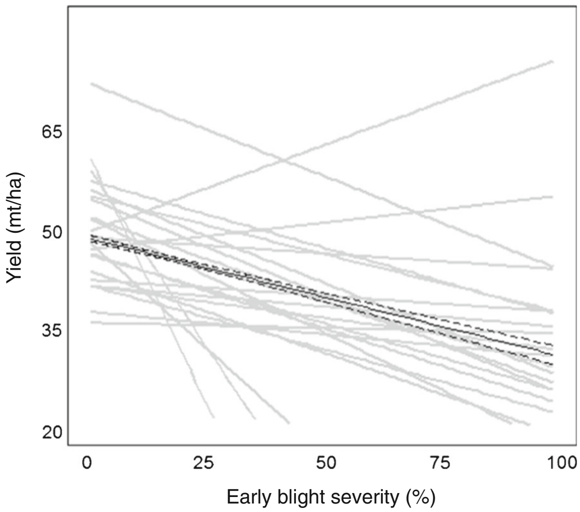


Fig. 2 Early bulking: The linear regression relationship between early blight severity and yield prior to meta-analysis. Gray lines represent each of 23 study trials, black solid line is the estimated mean and black dashed lines are associated 95% confidence interval. The 95% confidence interval for the estimated *X* is given by the points where the horizontal line intersects the lower and upper confidence bands of the regression line

yield loss due to early blight at early bulking growth stage was estimated to be 0.32 pp./%$^{-1}$. This indicates that the maximum (100%) early blight severity would decrease yield by 32 pp. Similarly, the relative yield loss associated with early blight severity at late bulking and tuber maturation growth stage of potato would be 0.19 pp./%$^{-1}$ (reduction of yield by 19 pp).

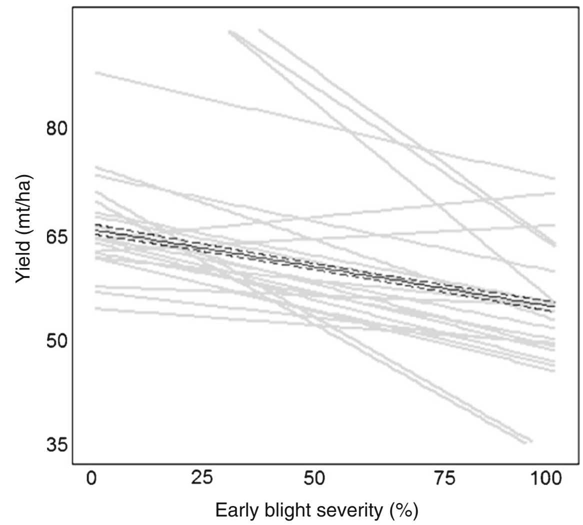
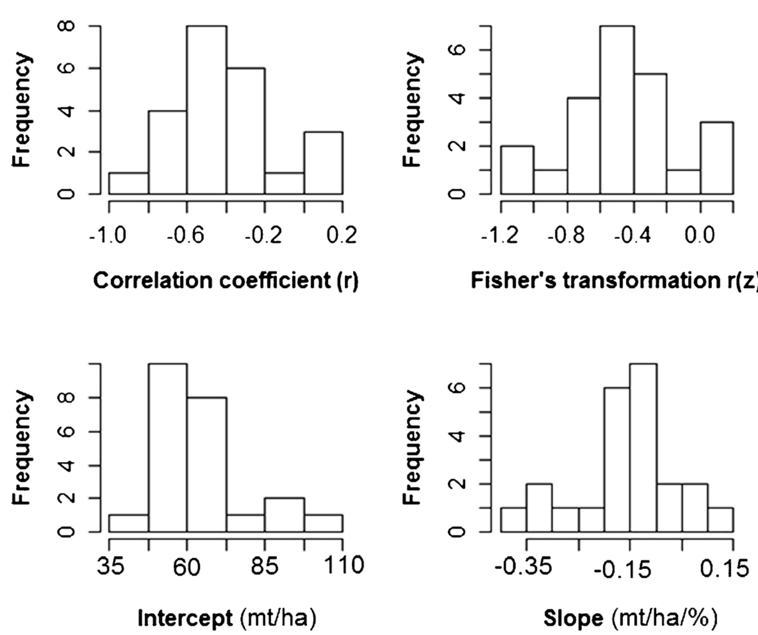


Fig. 4 The linear regression relationship between early blight severity (at late bulking-tuber maturation) and yield prior to meta-analysis. Gray lines represent each of 23 study trials, black solid line is the estimated mean and black dashed lines are associated 95% confidence interval

Discussion

To our understanding, this study represents the first meta-analysis for the relationship between early blight severity and tuber yield. This study assessed large amounts of empirical data obtained from field trials (involving two potato cultivars) conducted over several years and multiple locations across Minnesota and North Dakota. The

Fig. 3 Late bulking and tuber maturation: Frequency distribution of Pearson correlation (r) coefficient and Fisher's Z transformation of r for 23 individual trials prior to meta-analysis. Intercept and slope are linear regression coefficients to study the relationship between early blight severity and yield for the individual studies



predicted relationship between disease and tuber yield information is relevant to growers in the these Midwestern states because estimations were made from studies implementing current agronomic and management strategies for potatoes grown under irrigation in these production areas. Additionally, this study estimated the relationship between early blight severity and tuber yield at two different growth stage periods of potato.

The first step was to determine if any relationship between early blight severity and crop yield existed. Both correlation coefficient and linear regression were used to quantify the strength of the relationship between early blight severity and yield. For this study, Pearson correlation for both crop growth phases showed mostly negative correlations between early blight severity and tuber yield. Also, the linear regression results demonstrated mostly negative linear relationship between severity and yield. This indicates that increasing severity results in decreasing yields among individual studies selected for meta-analysis, on average. Previous research work also has demonstrated an inverse correlation between foliar symptoms and yield in individual studies (Teng and Shane 1984; Lim and Gaunt 1986; Shah et al. 2004b). Most recent disease and yield loss relationship studies examined the role of specific crop or disease variables affecting the tuber yield (Shah et al. 2004a; Shtienberg et al. 1996). For example, these studies quantified the percentage yield loss association to early blight severity based on magnitude of correlation (r) and linear regression (R^2). However, research directed at predicting the relationship between disease intensity due to a percentage increase in early blight severity and tuber yield at different growth stages cannot rely on these types of statistical measures. Therefore, we felt it was important to estimate actual disease and yield relationships at two different growth stages of potato.

The results for both crop growth phases demonstrated that large variability exists among individual studies. Differences among the studies is expected and could be due to high variability in fungicide efficacies or other epidemiological factors. Specialty and traditionally applied fungicides have shown varying efficacy levels for early blight control (Yellareddygari et al. 2016). Such variability/ heterogeneity is often not accounted for when studies are based on individual trials performed in the same location over a few seasons or years (Rouse 1988). Therefore, moderator analysis is used to explain unknown variability in meta-analysis. Moderator variable year significantly explained heterogeneity of the correlation coefficient, slope and the intercept for relationships between early blight severity and yield (for both growth stages). This could be due to varying environmental conditions across the years affecting the crop and disease and thereby affecting the relationship. Environmental factors such as temperature, rainfall, relative humidity, alternate wet and dry conditions influence early blight development and outbreaks (Olanya et al. 2009; Yellareddygari et al. 2016). Other moderator variables tested (cultivar, DP, and location) did not significantly affect the Fisher's Z, slope and the intercept. Other crop, environmental and edaphic factors not quantified in this study may be contributing to the variability and potentially affecting the strength and magnitude of the relationship between early blight severity and yield.

Overall, mean (random-effects meta-analytic model) slope effect size increased from early bulking to late bulking-tuber maturation growth stages of potato. This suggests that each percentage unit increase in early blight severity at both growth stages result in gradual yield loss. Our results clearly indicate that for each percentage point increase in severity at the early bulking stage results in higher yield loss compared to that of unitary increase in severity at late bulking-tuber maturation. The results reported here agree with previous research that early blight disease development after tuber initiation results in rapid foliage damage and yield loss (Horsfield et al. 2010). High early blight severity at early to mid-tuber bulking stage results in yield reductions due to lower dry matter content in tubers (Stevenson et al. 2008). However, our results contradict previous research findings that late applications of fungicide results in higher tuber yield compared to early applications (Davidson et al. 2016). This emphasizes the need for early blight control during the initial stages of bulking, because of the greater yield loss potential at this growth stage. Although, there are two assessments of disease and only one assessment of the yield, the random effect model intercept (yield at zero early blight severity) for two growth stages differ slightly. In the current study, the difference between intercepts is likely due to variation in general.

This study estimated the relative yield loss at two growth stages of potato due to highest (100%) early blight severity. Early blight severity at early bulking and tuber maturation-late bulking growth stages would result in relative yield losses of 32 percentage point (pp) and 19 pp., respectively. Yield reductions due to the early blight disease at both growth stages indicate that fungicide management is essential for the duration of the growing season. Continuous application of fungicides from early in the growing season to vine kill is recommended as the most effective management practice (Curwen et al. 1984; Douglas and Groskopp 1974; Harrison et al. 1965; Harrison and Venette 1970; Horsfield et al. 2010; Pscheidt and Stevenson 1986). Additionally, previous research has demonstrated that specialty fungicides possessing a higher degree of efficacy on early blight could be used effectively during the entire growing season while standard protectant fungicides were less useful late in the growing season (Yellareddygari et al. 2016). It is also important to note, however, that pathogen-induced foliar damage at the early bulking stages results in greater yield loss than during tuber maturation and late bulking. This suggests that fungicide disease management at early bulking growth stage is critical for increasing tuber yield. These results agree with the previous research work demonstrating that early bulking was most critical for early blight management (Horsfield et al. 2010; Yellareddygari et al. 2016) and that prolonged maintenance of the green canopy extends the tuber bulking period thereby increasing the crop yield (Horsfield et al. 2010).

The results from this study represent a first step towards clarifying the relationship between tuber yield and early blight severity at different crop growth stages. Further meta-analysis research is needed to determine other underlying mechanisms that may influence the disease and yield relationship. For example, a study to determine if other disease level moderators such as relative humidity and rainfall can have an influence on crop yield. The information provided here should prove useful to potato growers as they develop and implement strategies to successfully manage early blight.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Human and animals rights No human and/or animal participants were involved in this research.

Informed consent All authors consent to this submission.

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