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# Soybean Canopy Coverage, Population, and Yield Responses to Seed Treatment and Cultivar Resistance to *Phytophthora sojae* in Nebraska

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**Abstract**

Integrating disease control strategies has been the foundation for effective management of Phytophthora stem and root rot (PSRR; caused by *Phytophthora sojae*) in soybean (*Glycine max* [L.] Merr.). To determine the efficacy of seed treatment formulation (clothianidin + ethaboxam + ipconazole + metalaxyl) and host resistance (*Rps*1k or *Rps*1c and moderately resistant [MR] or moderately susceptible [MS]), five environments with disease history were evaluated in Nebraska during 2017 and 2018. Despite the use of resistant cultivars, PSRR developed in four out of five environments. Compared with the untreated control, seed treatment increased soybean emergence by 16,320 to 63,037 plants/ha and mid-season canopy coverage (CC) by 5.2 to 8.3%. Although management programs with MR cultivars had greater yields (538.9 to 747.5 kg/ha) than MS cultivars, there were negligible yield differences between *Rps*1k and *Rps*1c genotypes, except in one environment. A weak to moderate ($\rho = -0.32$ to $-0.45$; $P \leq 0.001$) association was observed between mid-season CC and the number of plants with *P. sojae* stem lesions. Outcomes from this study demonstrate the usefulness of integrating CC assessments to support disease severity evaluations in field settings and reinforce the benefits of combining host resistance and seed treatment to manage soybean seedling diseases in PSRR-conducive environments.

*Keywords*: integrated disease management, host resistance, seed treatment, canopy, *Glycine max*

Phytophthora stem and root rot (PSRR) is a yield-limiting disease in soybeans (*Glycine max* [L.] Merr.) caused by the soilborne oomycete *Phytophthora sojae* Kauffm. & Gerd. Annual soybean losses due to the disease are estimated at 9.4 million metric tons in North America (Allen et al. 2017). Disease symptoms include early-season damping-off and the development of stem lesions progressing from the soil line, culminating in premature plant death (Hartman et al. 2015). Stunting resulting from infection compromises yield and creates additional crop management problems, such as reduced soybean competitiveness for weed suppression.

Many factors including soil compaction and texture, tillage, drainage, and environmental conditions influence PSRR development (Dorrance et al. 2009; Duniway 1983; Gray and Pope 1986). Warm and saturated soil conditions increase PSRR occurrence by providing optimum conditions for propagule development and dispersal (Schmitthenner 1985; Schmitthenner and Bhat 1994). Even though infection can occur at any stage of plant development, most of the damage is believed to occur at emergence (Workneh et al. 1998), which may justify the use of oomycides (e.g., fungicides) at planting. Historically, metalaxyl and mefenoxam have been applied to seeds, banded in granular form, or sprayed in-furrow for *P. sojae* root rot and damping-off management (Anderson and Buzzell 1982; Ryley et al. 1989). More recently, ethaboxam was registered as a soybean seed treatment in the United States. Ethaboxam inhibits β-tubulin assembly during mitosis (FRAC group 22 [FRAC 2018]) and has demonstrated satisfactory in vitro efficacy against numerous oomycetes pathogenic to corn and soybean (Matthiesen et al. 2016; Radmer et al. 2017).

In addition to oomycides, PSRR has also been managed with host resistance (McBlain et al. 1991; Schmitthenner 1985). Host resistance occurs as two primary types: race-specific through *Rps* resistance genes and non-race-specific through polygenic resistance, commonly referred to as cultivar tolerance or partial resistance (Anderson and Buzzell 1992; McBlain et al. 1991). In the North Central United States, common resistance genes deployed in commercial soybean lines include *Rps*1a, 1b, 1c, 1k, and to a lesser extent *Rps*3a and *Rps*6 (Robertson et al. 2009; Slaminko et al. 2010). However, the continuous use of a few, single *Rps* genes has led to increased selection pressure on *P. sojae* populations (Dorrance et al. 2016; Schmitthenner et al. 1994), which combined with the natural in-field pathogen variability makes PSRR management complex (Stewart et al. 2016). Alternatively, cultivar tolerance is effective against multiple pathotypes by limiting the infection rate and lesion expansion (Mideros et al. 2007; Thomas et al. 2007) and preventing yield losses in conducive environments (Rehm and Stienstra 1993; Tooley and Grau 1984). Information about the presence or absence of *Rps* genes and PSRR tolerance levels in marketed soybean cultivars is available in seed company

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catalogs, which can assist growers to establish a disease management plan.

In the field, PSRR severity is assessed on the basis of early-season damping-off, incidence of plants with characteristic stem lesions, plant height, root lesion length, and yield reduction of susceptible cultivars compared with resistant lines (Dorrance et al. 2003; Gray and Pope 1986; Guy et al. 1989; Rehm and Stienstra 1993). However, because highly tolerant cultivars do not always develop stem lesions but may still exhibit permanent aboveground stunting (Meyer and Sinclair 1972; Schmitthenner 1985), additional screening approaches are needed to support severity assessments in field trials. Proximal remote sensing is an alternative method to nondestructively configure plant health status (Bock et al. 2010; Mahlein 2016). User-friendly, rapid data collection has been originated using handheld, open-source, phenotyping/phytopathometric mobile platforms (Patrignani and Ochsner 2015; Pethybridge and Nelson 2015, 2018), which may be used to quantify plant architectural changes associated with PSRR occurrence and aid in future disease management decisions.

Despite the geographical expansion of PSRR in Nebraska (Schimelfenig et al. 2005; White et al. 1983), previous studies were inconclusive in determining the effects of seed treatments and genetic resistance as part of an integrated disease management program (Dorrance et al. 2009; Giesler and Gustafon 2009). Herein, we synthesize the field efficacy of a seed treatment formulation and quantitatively estimate the benefits associated with cultivar selection using commercially available soybean lines, simulating a producer's approach for disease management. More specifically, we quantified differences in soybean canopy coverage (CC), population density, and yield resulting from (i) the use of a seed treatment formulation with clothianidin + ethaboxam + ipconazole + metalaxyl versus an untreated control; (ii) the selection of PSRR moderately resistant (MR) versus moderately susceptible (MS) cultivars; and (iii) the selection of cultivars carrying *Rps*1k versus *Rps*1c resistance genes.

## Efficacy Trials

A total of five experiments were conducted in the eastern part of Nebraska during 2017 and 2018 growing seasons. In 2017, a single field trial was located near Tekamah (41.7079089, –96.1081753), and in 2018, field trials were established in four locations near Tekamah (41.755558, –96.176062), Arizona (41.792885, –96.139346), Mead (41.182523, –96.459948), and Bruno (41.293432, –96.916723) in collaboration with local producers. All experiments were established in fields with PSRR history and corn (*Zea mays* L.) as the previous crop. Site-specific and research activities information is presented in Table 1.

The experimental design consisted of a split-plot arranged in a randomized complete block design with four replications. Experimental units were four-row plots, 5.18 m long by 3.04 m wide, planted at 0.76-m row spacing, and sown at a density of 308,000 seeds/ha. Cultivars were randomly assigned to whole-plot units, and thereafter, seed treatments were randomly assigned to the subplot units (Mead 1990). Soybean cultivars of maturity groups II and III with commonly deployed *Rps* genes were obtained from private soybean seed companies operating in the region (Supplementary Table S1). Although genotypes varied across years, at least two with the same *Rps* gene but distinct PSRR tolerance scores were selected to represent MR or MS classes, based on company-supplied disease susceptibility information. At the subplot level, treatments consisted of (i) untreated control and (ii) clothianidin + ethaboxam + ipconazole + metalaxyl (Intego Suite Soybeans, Valent U.S.A., Walnut Creek, CA) applied at 0.081 mg + 0.012 mg + 0.004 mg + 0.0032 mg of active ingredient per seed, respectively. Seed treatment was applied by adding 1.76 ml of fungicide to water for a total mix volume of 2.6 ml, poured into a plastic bag with 800 g of seeds, and mixed until seeds were treated uniformly. Soybean production practices related to nutrient management and pre- and post-emergence herbicide applications followed the University of Nebraska's extension service recommendations. Soil temperature at planting and cumulative monthly precipitation data were obtained from the weather service website (https://www.ncdc.noaa.gov/cdo-web/). In addition to natural precipitation, irrigation was supplemented through overhead irrigation delivered by a center-pivot system at some locations (Supplementary Table S2).

Plots were examined periodically to determine the number of plants with *P. sojae* stem lesions. The total number of symptomatic plants (nPSR) was recorded from all four rows of each plot, and *P. sojae* was isolated and confirmed based on morphological characteristics and culture growth in potato dextrose agar (Dorrance et al. 2008). Plant population densities were recorded at the first to the second trifoliate stage (V1 to V2) (Fehr et al. 1971), sixth trifoliate to full bloom (V6 to R2), and at maturity (R8) prior to harvest. Plant population was assessed by counting the number of emerged plants in 3.05-m row segments of each of the center two rows for a total of two subsampling measurements per experimental unit.

Early- and mid-season CCs were estimated at V1 to V2 and V6 to R2 growth stages, respectively, using the smartphone application *Canopeo* (Oklahoma State University, Stillwater, OK). A PVC pipe frame with dimensions of 1.05 m long by 0.76 m wide was arbitrarily placed within each row to consistently delineate the section of 0.798 $m^2$ during image collection. Each harvestable row section was systematically photographed using an iPhone 7 with a 4.7-in

**TABLE 1**
**Description of environments and assessments performed in 2017 and 2018**

| | | Soil parameters[a] | | | | | | | Execution date | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | CC[b] | | Plant population | | | |
| Year | Environments | Sand (%) | Silt (%) | Clay (%) | O.M. (g/kg) | pH | Tillage | Planting | V1–V2 | V6–R2 | V1–V2 | V6–R2 | R8 | Harvest |
| 2017 | Tekamah, NE | 17 | 41 | 42 | 1.3 | 7.9 | No-till | 2 Jun | … | 5 Jul | 21 Jun | 5 Jul | 28 Oct | 6 Nov |
| 2018 | Tekamah, NE | 17 | 16 | 67 | 5.4 | 6.2 | Disked | 18 May | 5 Jun | 6 Jul | 5 Jun | 6 Jul | 12 Oct | 1 Nov |
| | Arizona, NE | 19 | 36 | 46 | 3.4 | 7.6 | No-till | 18 May | 5 Jun | 9 Jul | 5 Jun | 9 Jul | … | … |
| | Mead, NE | 17 | 48 | 35 | 4.7 | 6.8 | No-till | 6 Jun | 29 Jun | 16 Jul | 29 Jun | 16 Jul | 19 Oct | 29 Oct |
| | Bruno, NE | 14 | 53 | 33 | 3.2 | 6.8 | No-till | 6 Jun | 29 Jun | 16 Jul | 29 Jun | 16 Jul | 22 Oct | 29 Oct |

[a] Soil organic matter (O.M.) and texture were determined from soil tests conducted by Ward Laboratories, Kearney, NE.
[b] CC = canopy coverage.

screen size and 12 megapixel embedded camera with *f*/1.8 aperture positioned horizontally above the canopy and approximately 1.2 m from the soil line. No camera flash was used, and a minimally reflective dark velvet cloth was fixed in between rows and below the canopy prior to imaging. The procedure specified above was repeated for all environments, except in Tekamah in 2017, where no frame was used and a single CC assessment was collected for each experimental unit.

Prior to harvest, the subplot units were trimmed to 4.5 m in length, and the center two rows were harvested with a plot combine (Almaco SPC20, Almaco, Nevada, IA) equipped with a grain gauge and handheld computer for data recording. Seed weight and moisture were recorded for each plot, and yield was adjusted to 13% moisture.

Statistical analyses were performed in R (version 3.6.0, R Foundation for Statistical Computing, Vienna, Austria) using RStudio (version 1.2.1335, RStudio). A mixed linear model was fitted using the *lme4* package (version 1.1.17) with soybean cultivars and seed treatment as fixed effects and blocks, experimental error, and subsampling error as random effects. Analysis of variance was conducted for each environment individually using the *lmerTest* package (version 3.0.1). Degrees of freedom for the denominator were estimated with the Kenward–Roger method, and variance components were obtained with the restricted maximum likelihood method. Because CC was initially expressed in percentage, data were arcsine square-root transformed (arcCC) prior to analysis to improve variance homogeneity. Least-squares means were obtained using the *emmeans* package (version 1.3.1), and single-degree-of-freedom contrast statements were used to make treatment comparisons. Probability values were adjusted with the Benjamini–Hochberg procedure to control for false discovery rate owing to the lack of orthogonality in the cultivar contrasts. The arcCC means were back-transformed to a 0 to 100% scale to improve variable meaningfulness. Covariation between PSRR disease parameters and yield was determined using Spearman's rank correlation in a two-sided hypothesis test (Madden et al. 2007).

**Disease development.** *P. sojae* was isolated from symptomatic plants in four out of five environments. The number of PSRR-positive plots was roughly 12, 8, 17, and 14% of total subplots in Tekamah, Arizona, Mead, and Bruno in 2018, respectively. In addition to stem lesions, symptoms of oomycete seedling damping-off were observed in Tekamah in 2018. Poor crop establishment occurred in Arizona and contrasted trial conditions at Mead, where seedling damping-off incidence was low, despite the development of *P. sojae* stem lesions as the season progressed. In addition to cultivars in the experimental area, sentinel-border plots planted with PSRR-susceptible cultivar 'Sloan' also developed disease symptoms in all environments, except at Tekamah in 2017.

**Effect of treatments on plant population.** Seed treatment had a significant effect on V1 to V2 soybean population in three of the five environments, with population increases ranging from 16,320 to 63,036 plants/ha. MR cultivars had greater ($P \leq 0.10$) emergence than MS by 10.9 and 18.3% at Tekamah and Bruno in 2018, respectively. Although seed treatment improved early-season stand, negligible differences, less than 4,326 plants/ha, were quantified between MS and MR in Arizona. Although soybean cultivars significantly differed in V1 to V2 population densities at all environments in 2018, differences were not associated with the selection of *Rps*1c or *Rps*1k genes. At Tekamah in 2018, MS cultivars had fewer plants than MR among *Rps*1c cultivars, but no differences were observed between *Rps*1k cultivars (Table 2). In addition, significant cultivar-seed treatment interactions were detected in soybean plant population at Arizona and Tekamah in 2018, where seed treatment increased plant population by 10.3 to 21.5% among MR cultivars and between 24.3 to 46.1% among MS cultivars. No effects for the integration of seed treatment and host resistance were detected for V1 to V2 population densities in Tekamah in 2017 and Mead and Bruno in 2018.

In agreement with previous stand assessments, seed treatment effects were also identified during mid-season (V6 to R2) and final (R8) plant population evaluations. On average, final plant population increased by 29,998 plants/ha across environments in 2018. Despite considerable differences in plant population between soybean genotypes in three environments, effects were not clearly associated with the *Rps*1k or *Rps*1c genes (Table 3). Conversely, MR cultivars had ($P \leq 0.10$) greater (≥8.6%) final population densities than MS at Tekamah in 2017 and 2018. Exclusively among cultivars with the *Rps*1c gene, MR cultivars had 15.9% greater population densities than MS, but the opposite was observed between *Rps*1k cultivars at Tekamah in 2017 (Table 3). Contrasting early- and mid-season stand evaluations, no cultivar-seed treatment interaction effect was detected for the final plant population assessment in 2018. Relatively, the lowest and highest final population were observed in Bruno in 2018 and Tekamah in 2017, with an estimated 110,134 and 212,437 plants/ha, respectively.

**Seed treatment and cultivar resistance affected soybean canopy development.** In total, 992 unique CC sampling measurements were recorded during two distinct phenological stages. At subplot level, early- and mid-season CC ranged from 0.4 to 10.1% and 3.9 to 63.4%, respectively (Fig. 1). Seed treatment consistently increased CC in three environments, but not at Tekamah in 2017 or Mead in 2018. Increases in CC related to seed treatment use ranged from 0.7 to 1.2% during initial plant developmental stages and developed to greater discrepancies (5.2 to 8.3%) during late vegetative and reproductive stages (Fig. 2A and D). Additionally, MR cultivars had significantly greater CC compared with MS cultivars at Bruno and Tekamah in 2018, but differences were stage-dependent (Fig. 2B and E). Despite the lack of significant seed treatment effect, cultivars with *Rps*1c gene had on average 1.8% lower early-season CC than *Rps*1k genotypes at Mead. Negligible effects of *Rps* resistance were observed on mid-season CC (Fig. 2F).

**Yield responses.** Yield ranged from 1,384.4 to 5,767.6 kg/ha and averaged 3,568.8 kg/ha in the study. Lower quantile and upper quantile at 0.25 and 0.75 of the values were 2,930.2 and 4,436.9 kg/ha, respectively. Grain yield varied greatly across environments, and the efficacy of seed treatment averaged 259.9 kg/ha ($CI_L$, 151.3; and $CI_U$, 368.5 kg/ha) relative to the untreated control in 2018. Individually, seed treatment had a significant effect ($P \leq 0.05$) on yield in two of the four trials with yield data, with increments ranging from 257.9 kg/ha ($CI_L$, 118.2; and $CI_U$, 397.4 kg/ha) to 331.6 kg/ha ($CI_L$, 121.1; and $CI_U$, 542.2 kg/ha) depending on the environment. For host resistance, monogenic *Rps* resistance and PSRR tolerance effects were only detected in environments for which a significant seed treatment effect coexisted. MR cultivars yielded on average more, between 538.9 kg/ha ($CI_L$, 262.7; and $CI_U$, 815.3 kg/ha) and 747.5 kg/ha ($CI_L$, 361.7; and $CI_U$, 1,133.2 kg/ha), than MS cultivars in Bruno and Tekamah in 2018, respectively. In relative terms, cultivar resistance in the form of tolerance had a greater absolute yield size effect than seed treatment alone. In relation to *Rps* genes, an average yield increase of 12.5% was detected for *Rps*1c cultivars compared with *Rps*1k genotypes at Tekamah in 2018. No significant yield differences were detected between *Rps* genotypes elsewhere in the study (Table 4). Accounting for interactions, yield benefit resulting from seed treatment use seemed to be more dependent on environment than PSRR genetic resistance in commercial soybean lines.

**Association between PSRR disease components.** The association between PSRR disease components (nPSR, plant population, CC, and yield) varied across environments. Moderate Spearman's rank correlation coefficients (ρ) were observed between nPSR and yield (ρ = –0.50, $n$ = 60) at Tekamah in 2018 but not at all in Mead (ρ = –0.01, $n$ = 52) or Bruno (ρ = –0.02, $n$ = 58). No significant associations were observed between nPSR and final (R8) plant population using these field-specific data; however, significant correlations ($P \leq 0.005$) were found between nPSR and CC. Although early-season CC had a weak relationship, mid-season CC was moderately associated with nPSR in Tekamah (ρ = –0.45, $n$ = 56) and Arizona (ρ = –0.32, $n$ = 64) in 2018 (Table 5). Spearman's correlation between CC collected at V6 to R2 growth stages and yield was always positive and significant and ranged from 0.32 to 0.82. In certain instances, CC seemed to be equally or more closely associated to yield than final (R8) population density (Table 5). Correlation between yield and final plant population densities ranged from 0.23 to 0.79 across environments.

## Implications for Soybean Production in Fields with PSRR History

The present investigation examined the integration of host resistance and seed treatment in an effort to improve PSRR management in poorly drained, *P. sojae*-infested fields in Nebraska. The benefit of commercial seed treatment formulation containing ethaboxam and metalaxyl was variable across environments, despite PSRR field history. Host resistance (either *Rps* or PSRR tolerance) was most valuable in environments in which the seed treatment effect coexisted. However, the combination of these management strategies did not seem to be additive, indicating that both moderately susceptible and resistant cultivars benefited from seed treatment use in high disease pressure scenarios. Contrastingly, the selection of PSRR

**TABLE 2**
**Effect of seed treatment and host resistance to *Phytophthora sojae* on soybean population estimated at V1 to V2 growth stages at five Nebraska environments in 2017 and 2018[a]**

| | V1 to V2 population (1,000 plants/ha) | | | | |
|---|---|---|---|---|---|
| | 2017 | 2018 | | | |
| Parameter | Tekamah | Tekamah | Arizona | Mead | Bruno |
| Seed treatment[b] (ST) | | | | | |
| Treated | 246.7 | 257.0 | 178.0 | 157.3 | 115.1 |
| Untreated control | 243.4 | 193.9 | 152.1 | 158.6 | 98.8 |
| Diff. (%) | 1.4 | 32.5 | 17.0 | –0.8 | 16.5 |
| *P* > F | 0.5065 | **<0.0001** | **<0.0001** | 0.8253 | **0.0478** |
| Cultivars[c] (C) | | | | | |
| Tolerance | | | | | |
| MR | 241.5 | 237.1 | 166.9 | 155.8 | 115.9 |
| MS | 238.2 | 213.8 | 163.2 | 160.1 | 98.0 |
| Diff. (%) | 1.4 | 10.9 | 2.3 | –2.7 | 18.3 |
| *P* > F | 0.8481 | **0.0185** | 0.5428 | 0.7194 | 0.0735 |
| *Rps* resistance | | | | | |
| *Rps*1c | 249.9 | 223.0 | 168.2 | 153.9 | 107.0 |
| *Rps*1k | 236.6 | 232.8 | 155.8 | 170.2 | 106.9 |
| Diff. (%) | 5.6 | –4.2 | 8.0 | –9.6 | 0.0 |
| *P* > F | 0.2903 | 0.3754 | 0.1317 | 0.3277 | 0.9976 |
| Tolerance – *Rps* | | | | | |
| MR – *Rps*1c | 248.7 | 236.5 | 174.1 | 145.6 | 116.9 |
| MS – *Rps*1c | 251.2 | 209.6 | 162.2 | 162.2 | 97.0 |
| Diff. (%) | –1.0 | 12.8 | 7.4 | –10.2 | 20.5 |
| *P* > F | 0.8481 | **0.0185** | 0.1317 | 0.3277 | 0.0735 |
| MR – *Rps*1k | 222.6 | 239.1 | 145.3 | 186.4 | 112.9 |
| MS – *Rps*1k | 250.6 | 226.5 | 166.3 | 153.9 | 101.0 |
| Diff. (%) | –11.2 | 5.5 | –12.6 | 21.2 | 11.9 |
| *P* > F | 0.1393 | 0.4116 | 0.1317 | 0.3277 | 0.6060 |
| C × ST | | | | | |
| MR × treated | 243.4 | 260.1 | 175.1 | 157.3 | 127.0 |
| MR × untreated | 237.4 | 214.1 | 158.7 | 154.3 | 104.9 |
| Diff. (%) | 2.5 | 21.5 | 10.3 | 2.0 | 21.1 |
| *P* > F | 0.7487 | **0.0006** | **0.0203** | 0.6983 | 0.1129 |
| MS × treated | 200.7 | 253.8 | 180.9 | 157.4 | 103.3 |
| MS × untreated | 200.7 | 173.8 | 145.5 | 162.9 | 92.7 |
| Diff. (%) | 0 | 46.1 | 24.3 | –3.4 | 11.4 |
| *P* > F | >0.9999 | **<0.0001** | **<0.0001** | 0.6983 | 0.3443 |
| Mean | 245.1 | 224.4 | 165.1 | 158.1 | 107.2 |

[a] Bold indicates significant differences ($P \leq 0.05$).
[b] Seed treatment: clothianidin + ethaboxam + ipconazole + metalaxyl applied at 0.081 mg + 0.012 mg + 0.004 mg + 0.0032 mg of active ingredient per seed.
[c] *Rps* genes and tolerance information listed in Supplementary Table S2. MS and MR = moderately susceptible and moderately resistant cultivars to Phytophthora stem and root rot, respectively.

management tactics had negligible effects on soybean canopy, plant population, and yield in environments in which disease pressure, particularly at the seedling stage, was low.

Precipitation varied greatly across locations, but in general, soil temperatures were relatively warm (>20°C) during the planting, which occurred from mid-May through early June. In 2017, only 38.1 mm of precipitation was recorded during the first 2 weeks from planting, which may not have been favorable for the development of root rot and damping-off at emergence. In contrast, greater precipitation, ranging from 57.4 to 74.9 mm during 15 days from planting, were likely more favorable for epidemics in 2018. Under disease-conducive conditions, seed treatment increased soybean yields by 257.9 to 331.6 kg/ha on average. Based on quantitative synthesis of data from integrated disease management trials, similar to those established in this study, Dorrance et al. (2009) observed yield increases on the order of 215.0 to 416.6 kg/ha in Ohio and an average increase of 289.0 kg/ha in South Dakota from the addition of mefenoxam and metalaxyl as a seed treatment in *Phytophthora*-infested soils. These results corroborate with findings by Dorrance et al. (2012) and Scott (2018) for the use of ethaboxam combined with metalaxyl to manage seedling diseases in PSRR-endemic areas.

These results also indicate that besides chemical control, cultivar selection is an effective management strategy for PSRR control (Anderson and Buzzell 1982; Dorrance et al. 2003; Guy et al. 1989; Tooley and Grau 1984). Notably, company-supplied PSRR tolerance ratings were coherent with the level of disease suppression observed in the field, with MR cultivars having superior plant stand compared with MS cultivars from emergence to final population assessments. Also, in scenarios predisposed to damping-off and PSRR development, MR cultivars averaged around 538.9 to 747.5 kg/ha more than MS cultivars and experienced no yield penalty in environments with lower disease pressure. These findings substantiate Dorrance et al. (2003), which showed an additive yield effect of 669 kg/ha through the use of MR compared with MS cultivars, both with *Rps*1k resistance, under severe PSRR outbreaks in Ohio. Alternatively, results are not supportive of the hypothesis that *Rps*1c and *Rps*1k genes differ substantially in terms of field efficacy, particularly when a comprehensive characterization of in-field *P. sojae* virulence composition is lacking, as is the case here. It is worthy to note though that at Tekamah in 2018, where damping-off caused by oomycetes was the highest, comparable yield effects existed for *Rps*1c over *Rps*1k genotypes, even though such advantage was not accompanied by differences in stand or aboveground plant

**TABLE 3**
**Effect of seed treatment and host resistance to *Phytophthora sojae* on soybean population estimated at R8 growth stage at four Nebraska environments in 2017 and 2018[a]**

| | R8 population (1,000 plants/ha) | | | | |
|---|---|---|---|---|---|
| | 2017 | 2018 | | | |
| Parameter | Tekamah | Tekamah | Arizona | Mead | Bruno |
| Seed treatment[b] | | | | | |
| Treated | 214.3 | 215.9 | … | 148.2 | 125.6 |
| Untreated control | 210.4 | 162.0 | … | 143.5 | 95.2 |
| Diff. (%) | 1.8 | 33.3 | … | 3.2 | 31.9 |
| *P* > F | 0.3846 | **<0.0001** | | 0.5092 | **0.0002** |
| Cultivars[c] | | | | | |
| Tolerance | | | | | |
| MR | 216.8 | 202.0 | … | 140.9 | 117.5 |
| MS | 199.7 | 175.9 | … | 150.7 | 103.3 |
| Diff. (%) | 8.6 | 14.8 | … | –6.5 | 13.7 |
| *P* > F | **0.0158** | 0.0648 | | 0.4263 | 0.1928 |
| *Rps* resistance | | | | | |
| *Rps*1c | 207.8 | 192.6 | … | 144.5 | 110.5 |
| *Rps*1k | 212.0 | 178.0 | … | 149.7 | 110.1 |
| Diff. (%) | –2.0 | 8.2 | … | –3.4 | 0.3 |
| *P* > F | 0.4740 | 0.2117 | | 0.6389 | 0.9641 |
| Tolerance – *Rps* | | | | | |
| MR – *Rps*1c | 223.2 | 205.0 | … | 133.0 | 116.5 |
| MS – *Rps*1c | 192.5 | 180.2 | … | 156.1 | 104.4 |
| Diff. (%) | 15.9 | 13.7 | … | –14.7 | 11.6 |
| *P* > F | **0.0036** | 0.0878 | | 0.2180 | 0.2010 |
| MR – *Rps*1k | 202.6 | 192.9 | … | 164.6 | 120.3 |
| MS – *Rps*1k | 221.4 | 163.0 | … | 134.7 | 99.9 |
| Diff. (%) | –8.5 | 18.3 | … | 22.2 | 20.5 |
| *P* > F | **0.0387** | 0.1903 | | 0.2526 | 0.2010 |
| Mean | 212.4 | 188.8 | … | 145.5 | 110.1 |

[a] Bold indicates significant differences ($P \leq 0.05$).
[b] Seed treatment: clothianidin + ethaboxam + ipconazole + metalaxyl applied at 0.081 mg + 0.012 mg + 0.004 mg + 0.0032 mg of active ingredient per seed.
[c] *Rps* genes and tolerance information listed in Supplementary Table S2. MS and MR = moderately susceptible and moderately resistant cultivars to Phytophthora stem and root rot, respectively.

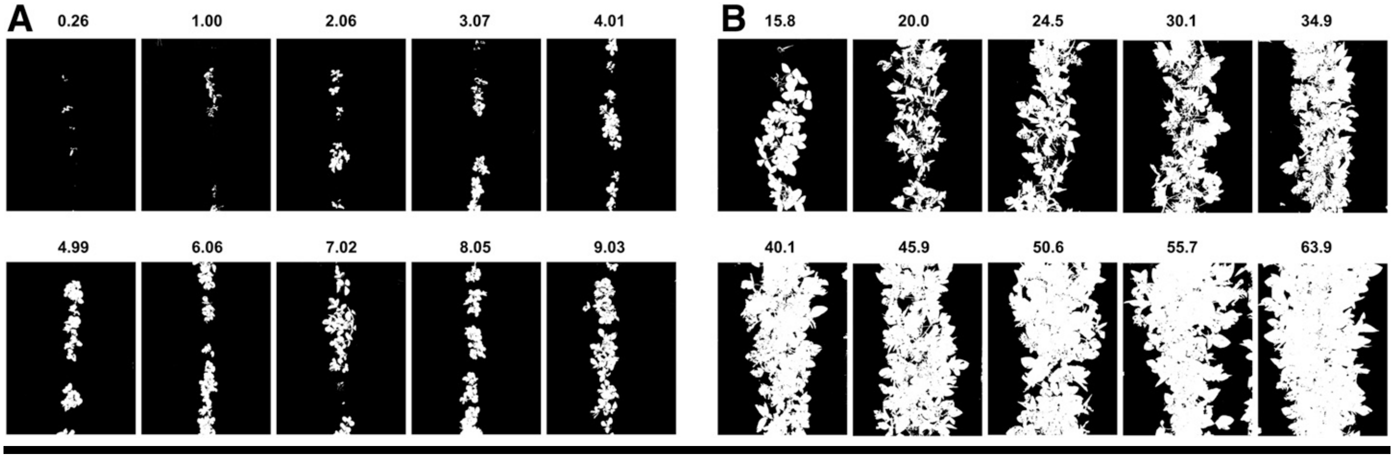


**FIGURE 1**

Representative soybean canopy coverage values (%) estimated with *Canopeo* smartphone application (Oklahoma State University, Stillwater, OK) at **A,** V1 to V2 and **B,** V6 to R2 growth stages in Nebraska in 2018.

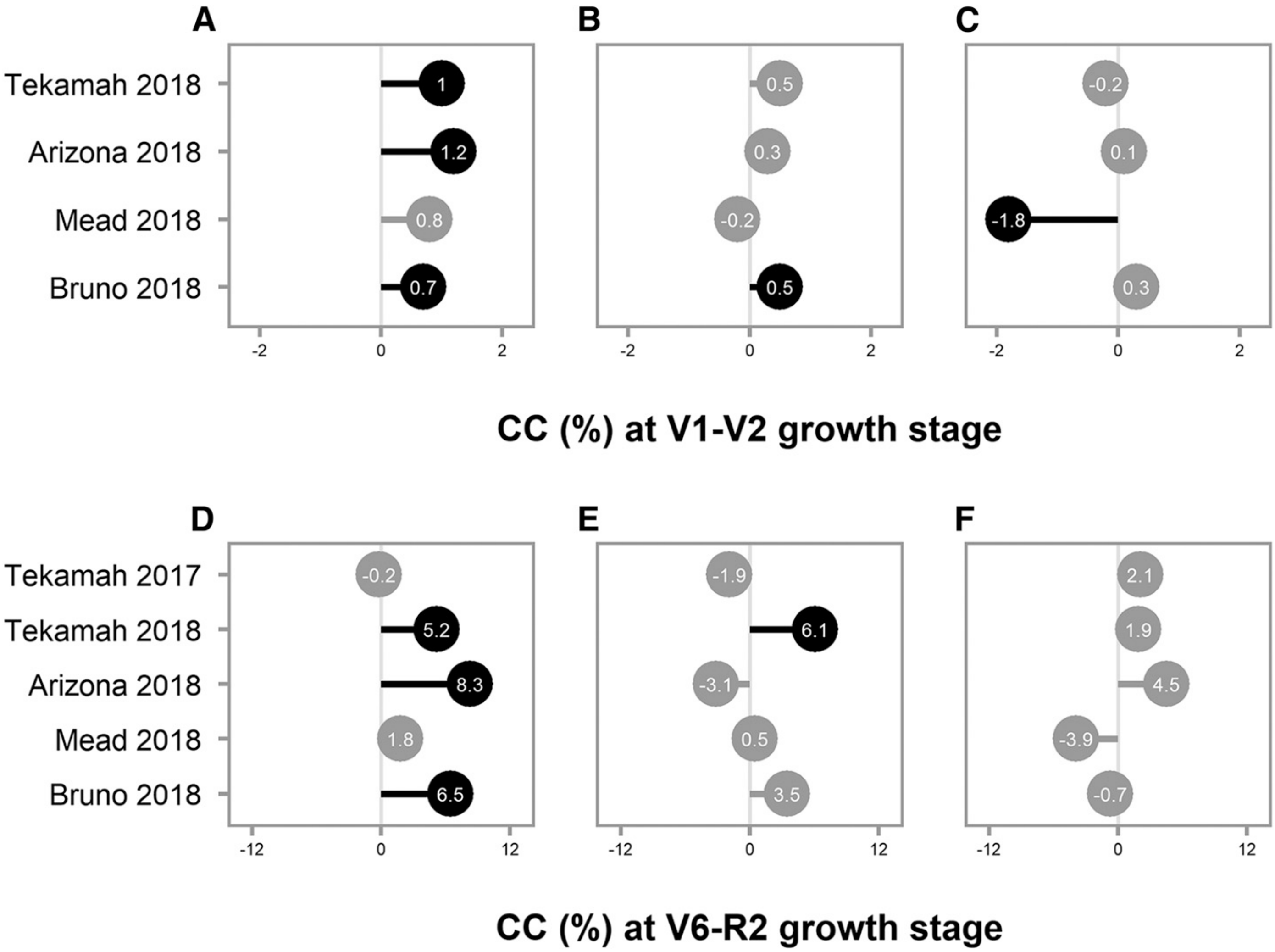


**FIGURE 2**

Soybean canopy coverage (CC) mean differences for seed treatment and cultivar resistance to *Phytophthora sojae* at early- (V1 to V2) and mid-season (V6 to R2). Positive, significant differences ($P \leq 0.05$, black circles) indicate increasing CC associated with **A and D,** seed treatment versus untreated control; **B and E,** moderately resistant versus moderately susceptible cultivars; and **C and F,** *Rps*1c versus *Rps*1k cultivars. Contrasts were performed on arcsine square-root-transformed data and mean differences displayed on the back-transformed scale.

development. Among the *Rps* resistance genes examined here, little disagreement between company-supplied and publicly evaluated resistance has been reported (Slaminko et al. 2010), which suggests that other factors, perhaps agronomic performance of cultivars, influenced *Rps* yield response in that environment. It also could be speculated that *P. sansomeana*, which is considered race non-specific (Reeser et al. 1991) and occurs in Nebraska (Alejandro Rojas et al. 2017), was active in Tekamah in 2018 and affected

**TABLE 4**
**Effect of seed treatment and host resistance to *Phytophthora sojae* on soybean yield at four Nebraska environments in 2017 and 2018[a]**

| | Yield (kg/ha) | | | | |
|---|---|---|---|---|---|
| | 2017 | 2018 | | | |
| Parameter | Tekamah | Tekamah | Arizona | Mead | Bruno |
| Seed treatment[b] | | | | | |
| Treated | 5,051.2 | 3,475.7 | … | 3,581.3 | 2,925.9 |
| Untreated control | 5,011.9 | 3,217.8 | … | 3,418.9 | 2,594.2 |
| Difference | 39.3 | 257.9 | … | 162.4 | 331.6 |
| *P* > F | 0.5818 | **0.0010** | | 0.1674 | **0.0036** |
| Cultivars[c] | | | | | |
| Tolerance | | | | | |
| MR | 5,030.3 | 3,720.5 | … | 3,484.1 | 3,029.5 |
| MS | 5,028.8 | 2,973.0 | … | 3,516.2 | 2,490.6 |
| Diff. | 1.5 | 747.5 | … | –32.1 | 538.9 |
| *P* > F | 0.9845 | **0.0001** | | 0.8411 | **0.0001** |
| *Rps* resistance | | | | | |
| *Rps*1c | 5,104.8 | 3,443.5 | … | 3,391.1 | 2,752.3 |
| *Rps*1k | 4,971.2 | 3,056.5 | … | 3,827.2 | 2,783.4 |
| Diff. | 133.6 | 387.0 | … | –436.1 | –31.0 |
| *P* > F | 0.3494 | **0.0263** | | 0.1042 | 0.7940 |
| Tolerance – *Rps* | | | | | |
| MR – *Rps*1c | 5,107.2 | 3,819.9 | … | 3,321.1 | 3,014.2 |
| MS – *Rps*1c | 5,102.5 | 3,067.1 | … | 3,461.2 | 2,490.3 |
| Diff. | 4.7 | 752.8 | … | –140.1 | 523.9 |
| *P* > F | 0.9845 | **0.0003** | | 0.6100 | **0.0004** |
| MR – *Rps*1k | 4,951.6 | 3,422.4 | … | 3,973.0 | 3,075.4 |
| MS – *Rps*1k | 4,990.7 | 2,690.6 | … | 3,681.3 | 2,491.3 |
| Diff. | –39.1 | 731.8 | … | 291.7 | 584.0 |
| *P* > F | 0.9845 | **0.0214** | | 0.6100 | **0.0131** |
| Mean | 5,031.6 | 3,346.8 | … | 3,500.1 | 2,760.1 |

[a] Bold indicates significant differences ($P \leq 0.05$).
[b] Seed treatment: clothianidin + ethaboxam + ipconazole + metalaxyl applied at 0.081 mg + 0.012 mg + 0.004 mg + 0.0032 mg of active ingredient per seed.
[c] *Rps* genes and tolerance information listed in Supplementary Table S2. MS and MR = moderately susceptible and moderately resistant cultivars to Phytophthora stem and root rot, respectively.

**TABLE 5**
**Spearman's rank correlation[a] coefficient (ρ) for the relationship between the number of plants with *Phytophthora sojae* stem lesions (nPSR), canopy coverage (CC) and plant population (Pop.) at different growth stages, and yield across environments in Nebraska**

| | 2017 | 2018 | | | |
|---|---|---|---|---|---|
| Association | Tekamah | Tekamah | Arizona | Mead | Bruno |
| nPSR – CC (V1–V2) | *[b] | –0.11 (0.3860) | –0.11 (0.3475) | –0.05 (0.6991) | 0.16 (0.2097) |
| nPSR – CC (V6–R2) | * | –0.45 (**0.0003**) | –0.32 (**0.0089**) | 0.08 (0.5691) | –0.03 (0.7900) |
| nPSR – Pop. (R8) | * | –0.24 (0.0524) | …[c] | –0.22 (0.1036) | –0.06 (0.6025) |
| nPSR – Yield | * | –0.50 (**<0.0001**) | … | –0.01 (0.9269) | –0.02 (0.8388) |
| Pop. (V6–R2) – CC (V6–R2) | 0.24 (0.0376) | 0.34 (**0.0096**) | 0.41 (**0.0006**) | 0.50 (**0.0001**) | 0.69 (**<0.0001**) |
| Yield – CC (V6–R2) | 0.32 (**0.0054**) | 0.82 (**<0.0001**) | … | 0.69 (**<0.0001**) | 0.63 (**<0.0001**) |
| Yield – Pop. (R8) | 0.23 (0.0514) | 0.43 (**0.0005**) | … | 0.24 (0.0856) | 0.79 (**<0.0001**) |

[a] *P* values in parentheses. Bold indicates a significant relationship ($P \leq 0.01$).
[b] Phytophthora stem and root rot not detected.
[c] At least one of the assessments was not performed.

emergence and CC of *Rps*1k and *Rps*1c cultivars equally. This may be a reasonable assumption given that MR cultivars outperformed MS cultivars for nearly all parameters evaluated in that particular environment. Considering that quantitative disease resistance is polygenic (Glover and Scott 1998; Schneider et al. 2016) and coordinates the expression of physical barriers in the plant (Thomas et al. 2007), it may be worth examining the effects of PSRR tolerance on *P. sansomeana* infection and colonization rate, because to date little is known about the host resistance mechanisms to this pathogen (Phibbs et al. 2014).

## PSRR Severity and Canopy Development

Acknowledging the numerous sources of variation that occur under natural conditions, including inoculum density (Miller et al. 1997), phenotypic diversity (Robertson et al. 2009; Stewart et al. 2016), and environmental conditions (Dorrance et al. 2009), results from this study were unconvincing for the efficacy of seed treatment at reducing the incidence of *P. sojae* stem lesions solely. The relatively low accumulated incidence of plants with *P. sojae* stem lesions and frequency of disease-positive plots generated poor estimates for hypothesis testing, despite attempts to fit the count data with zero-inflated generalized linear mixed models using Poisson and negative binomial distributions (Madden et al. 2017; Stroup 2015). It is possible that the incidence of *P. sojae* stem lesions was low in part owing to the higher levels of tolerance, even for MS lines, that are employed in commercial soybean germplasm. By contrast, studies evaluating treatment efficacy on the basis of the number of PSRR-symptomatic plants have traditionally used partially to highly susceptible materials (Dorrance et al. 2003).

Yield losses resulting from PSRR damage are not exclusively related to damping-off and premature plant death (Wilcox and St. Martin 1998). Results from this study indicate that CC is a valid criterion to determine plant health status and constitutes an important yield component for late-planted soybeans. Greater canopy development influences the plant's ability to intercept light and produce biomass (Board and Harville 1996; Purcell 2000), have adequate transpiration rates (Monteith 1977), increase crop competitiveness against weeds (Bussan et al. 1997), and counterbalance for plant productivity under suboptimal population densities (Gaspar and Conley 2015). These results confirm enhanced soybean canopy development upon oomycide use in *Phytophthora* spp. infested soils (Rehm and Stienstra 1993; Ryley et al. 1989) and present an innovative, standardized protocol to estimate aboveground plant growth using an open-source smartphone application, which potentially could replace traditional seedling vigor assessments performed in field trials. As far as the relationship between disease components, the association between CC and yield seemed to be slightly more robust in environments in which PSRR occurred than the opposite. Also, there was a noticeable improvement in the strength of the relationship between the number of *P. sojae* stem lesions and CC at readings performed during late-vegetative and early-reproductive stages than earlier in the season. This is likely because PSRR onset (wilting/stem lesions) usually manifests after the development of trifoliate leaves (V5 through reproductive stages), as noted by Dorrance et al. (2003). Variations of the remote sensing techniques have shown applicability in the study of root stress associated with biotic disorders in several crops (Reynolds et al. 2012; Steddom et al. 2003), including those caused by *Phytophthora* spp. in cranberry (Pozdnyakova et al. 2002) and avocado (Salgadoe et al. 2018), as well as to other soybean diseases (Wang et al. 2004; Yang et al. 2016). Here, proximal remote sensing was well-fitted for quantifying architectural changes in soybean CC associated with PSRR occurrence, most likely because MR cultivars do not always develop stem lesions but still exhibit permanent aboveground stunting as a result of oomycete infection (Meyer and Sinclair 1972; Schmitthenner 1985).

## Concluding Remarks

This study documents the usefulness of cultivar selection using commercial soybean lines and emphasizes the importance of adopting effective seed treatments as part of an integrated PSRR management program in Nebraska. Genetic resistance provided an overall better yield advantage than using seed treatment alone; however, seed treatment with multiple active ingredients was more consistent across environments, possibly because of the broad-spectrum activity of active ingredients in the commercial formulation. Producers should consider the selection of highly tolerant soybean cultivars carrying either *Rps*1k or *Rps*1c in areas where PSRR is endemic. Although not evaluated in this study, producers may also benefit by employing cultivars with *Rps*3a resistance and its pyramided forms (e.g., *Rps*3a+1c, *Rps*3a+1k), given its superior efficacy against populations of *P. sojae* in Nebraska and neighboring states (Dorrance et al. 2016; Schimelfenig et al. 2005; Yang et al. 1996). Overall, the information presented here may be valuable for producers and crop consultants wanting to make informed decisions about PSRR management in the North Central United States and also serves as a baseline for future studies regarding integrated PSRR management.


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