2019

Cover crop rotation effects on growth and development, seedling disease and yield of corn and soybean

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Disciplines

Agriculture | Agronomy and Crop Sciences | Plant Pathology

Comments

This is a manuscript of an article published as Acharya, Jyotsna, Thomas B. Moorman, Thomas C. Kaspar, Andrew W. Lenssen, and Alison E. Robertson. "Cover crop rotation effects on growth and development, seedling disease and yield of corn and soybean." *Plant Disease* (2019). doi: 10.1094/PDIS-09-19-1904-RE.

Cover crop rotation effects on growth and development, seedling disease and yield of corn and soybean

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Abstract

The effects of winter cover crops on root disease and growth of corn and soybeans is poorly understood. A three-year field experiment investigated the effect of winter cereal rye (*Secale cereal* L.) and winter camelina [*Camelina sativa* (L.) Crantz] used either in all three years or in rotation with each other, on corn (*Zea mays* L.*)* and soybean [*Glycine max.* (L.) Merr.] growth, root disease, and yield. Corn following a cover crop of camelina had reduced root disease, a lower *Pythium* population in seedling roots and greater growth and yields compared to corn following a rye cover crop. Camelina and rye cover crops before soybean had either a positive or no effect on soybean growth and development, root disease and yield. Moreover, *Pythium* Clade B populations were greater in corn seedlings after a rye cover crop compared to those following a camelina cover crop, while Clade F populations were greater on soybean seedlings following a camelina cover crop compared to seedlings following a rye cover crop. Winter camelina cover crop grown before corn had less negative effects on corn seedling growth, root disease, and final yield than a winter rye cover crop before corn. Neither cover crop had negative effects on soybean and the cover crop in the preceding spring had no measurable effects on either corn or soybean.

Introduction

Cover cropping of agricultural land is gaining popularity and interest because of benefits to long-term soil health and environmental sustainability. In 2017 Iowa farmers planted cover crops on 393,797 ha compared with 152,621 ha in 2012 (Census of Ag, 2019). Cover crops increase the diversity of soil microbial community, help build soil organic matter, protect soil from erosion, suppress weeds, reduce nitrate leaching, recycle nitrogen and other nutrients for next subsequent crops, and improve soil structure and water infiltration (Basche et al. 2016; Kaspar et al. 2007; Larkin et al. 2010; Moore et al. 2014; Sarrantonio and Gallandt 2003; Sturz et al. 1998; Villamil et al. 2006)

Additionally, cover crops have become an important component of state and regional scale initiatives to meet critical environmental challenges associated with large-scale agriculture. In the upper Midwest, incorporating winter cereal rye (*Secale cereale* L.) into the corn and soybean farming system is highly encouraged and has been promoted as one viable option for reaching water quality goals set in the Midwest (e.g. Iowa Nutrient Reduction Strategy; Iowa Department of Agriculture and Land Stewardship, 2013). Winter cereal rye is the most widely used cover crop in the upper Midwest because it is relatively easily to establish in the fall, has superior winter hardiness and documented environmental benefits, and has been used successfully in corn-soybean rotations (Kaspar and Bakker 2015; Snapp et al. 2005). Nevertheless, reduced corn yields have been reported following winter rye cover crops (Acharya et al. 2017; Kaspar and Bakker 2015; Miguez and Bollero 2005). This is puzzling because a winter cereal rye cover crop improves soil health (Ding et al. 2006; Moore et al. 2014), which should in theory, increase corn yield.

A number of mechanisms have been proposed for corn yield decrease following a cereal rye cover crop, including water stress (Munawar et al. 1990), limited nitrogen availability (Karlen and Doran 1991; Tollenaar et al. 1993; Wagger and Mengel 1993), impaired planter performance (Duiker and Curran 2005), and allelopathy (Kessavalou and Walters 1997; Tollenaar et al. 1993). The effect, however, has been difficult to study because it does not occur every year, does not seem to occur in some fields, or does not occur for some farmers. Another possible cause of the corn yield decrease that may fit this pattern of variable occurrence is increased seedling disease. A cereal rye cover crop can provide a “green bridge” or living host for pathogens over winter that then can infect corn seedlings in spring (Bakker et al. 2016; Smiley et al. 1992). These pathogens can cause seed rot, lesions on roots and mesocotyls, slow growth, and sometimes seedling death (Acharya et al. 2017; Bakker et al. 2016; Schenck et al. 2017). Obviously, reductions in plant stand can have a direct effect on corn yield (Munkvold 1999; Nafzinger et al. 1991). More often, however, seedling disease delays emergence and reduces plant vigor, which also can result in lower yields. Optimum corn yield often is dependent on uniform emergence, growth, and development (Nafzinger et al. 1991). When plants are uneven in size, as often occurs with seedling disease, the smaller plants produce smaller ears or no ears and thus, yields are reduced.

Our previous studies reported greater densities of *Pythium* spp. in the roots of corn seedlings following a winter cereal rye cover crop compared with the roots of corn seedlings grown following a winter fallow (Acharya et al. 2017). In a controlled environment study, Schenck et al. (2017) also reported greater Clade B *Pythium* populations than Clade F *Pythium* populations in radicle and mesocotyl tissues of corn seedlings following winter cereal rye, compared with those following a winter fallow, or non-grass cover crops of hairy vetch (*Vicia villosa* Roth) or canola (*Brassica napus* L.).

In contrast to corn, soybean yield is not usually reduced following a winter rye cover crop (Ruffo et al. 2004; Thelen and Leep 2002). This is somewhat surprising because soybeans are susceptible to some of the same *Pythium* and *Fusarium* spp. that a rye cover crop is known to host (Bakker et al. 2016, 2017; Matthiessen et al. 2016). Although seedling disease may reduce soybean stand like it does for corn, yield loss due to a reduction in soybean population is not as common (Bradley 2008). This is because soybean is planted at much higher seeding rates than corn and because soybean plants respond to random missing plants by producing new branches, pods, and seeds and often maintain adequate yields despite reductions in plant stand (Carpenter and Board 1997a, b; Cox and Cherney 2011).

Assuming that corn seedling disease is one of the primary causes of poor corn growth and reduced population following a cereal rye cover crop then the classical approach to many plant disease issues is to rotate or change the plant species that precedes the crop or plant affected by disease to a species that is not a host to those pathogens. In this case, that would mean using a different cover crop than rye preceding corn, which like corn is a grass species. Although, many plant species are used as cover crops, the species selected often depends on several factors including local climate conditions, the length and season of the interval between cash crops, potential to overwinter, and the cost and availability of seed. In the upper Midwest corn-soybean rotations, the cover crop growing season from late fall to early spring is short and cold. As a result, winter cereal grain cover crops such as winter cereal rye, winter wheat (*Triticum aestivum* L.), and winter triticale (*Triticale hexaploide* Lart.) (×*Triticosecale* Wittm. ex A. Camus [*Secale* × *Triticum*]) are often planted because they establish well in the fall, produce substantial biomass in late fall and early spring, usually overwinter, and are widely available (Singer et al. 2007; Snapp et al. 2005). Other popular cover crop species, such as hairy vetch (*Vicia villosa* R.) or oilseed radish (*Raphanus sativus* L.) either don't overwinter in the upper Midwest or don't produce much biomass by the time of corn planting in the spring when planted after soybean harvest. In recent years, winter camelina [*Camelina sativa* (L.) Crantz], a brassica species, has been reported to consistently overwinter in Minnesota and North Dakota (Berti et al. 2017; Gesch and Cermak 2011) and consequently it has drawn interest as a possible cover crop from upper Midwest researchers.

The goal of our research program is to develop best management practices to increase the adoption of cover crops by Iowa farmers in a corn-soybean production system. Although winter rye has been successfully managed as a cover crop by many farmers, adoption by additional farmers is limited by concerns of possible corn seedling disease and yield decreases following a winter rye cover crop. At this time, rotation of grass and broadleaf cover crop species have not been consistently used in the corn-soybean rotation in Iowa because of the difficulty of finding a broadleaf species that successfully overwinters and produces substantial biomass. Additionally, more work is also needed to determine the relationship of different cover crop species, like camelina, to soil borne diseases. We hypothesize that winter camelina grown as a broadleaf cover crop before corn could prevent the increased seedling disease and the reduced growth and yield sometimes seen following a winter rye cover crop. Additionally, we hypothesize that a cover crop rotation of winter camelina before corn and winter rye before soybean may be a good compromise between cover crop biomass production and limiting negative effects on corn and soybean yield than growing either winter camelina or winter rye cover crops every year without rotation. Thus, we established a field trial to evaluate the effect of winter rye and winter camelina cover crops grown every winter or in rotation with each other in a corn-soybean rotation, on cover crop biomass and on corn and soybean seedling disease, growth and yield.

Materials and Methods

Study location and experiment setup. Research plots were established at an Iowa State University Agricultural Engineering/Agronomy research farm in Boone County, IA (42°1’ 15 N, 93°46’26’’ W) in 2015, 2016, 2017, and 2018. The field used in this experiment was in a corn-soybean rotation, with both cash crops of the rotation present each year, and used a no-till management system. The soils series at the field site were Nicollet loam, Clarion loam, and Webster clay loam. Each plot was an experimental unit containing five rows with a 76-cm interrow spacing and 53.3 m long. The experimental design was a split plot within a randomized complete block design with five blocks or replications. Main plot treatments were the cash crop rotation sequence (corn-soybean or soybean-corn). In each main plot, the cash crop rotated each year such that one main plot treatment started with corn in 2015 and the other with soybean. Main plots had one or more border plots on each side to minimize the border effects. At the beginning of the experiment, subplots within the main plots were randomly assigned with the five cover crop rotation treatments (Camelina-Camelina, Rye-Rye, Camelina-Rye, Rye-Camelina, No Cover Crop-No Cover Crop). Because cover crop treatments were first established in the fall of 2015, the 2016 subplots before either corn or soybean included two rye subplots, two camelina subplots, and one no cover crop plot to accommodate the cover crop rotation in future years (Table 1). In 2017 individual treatment subplots within each main plot consisted of one of the five cover crop rotation treatments shown above. However, because corn and soybean were rotated between main plots, main plots planted with corn in 2017 had been planted to soybean in 2016 and therefore the cover crops growing in spring 2017 preceded a different cash crop than in 2016. For example, for the Rye-Camelina cover crop rotation treatment planted in the corn main plots in 2017, the sequence of cover crops and cash crops would have been Rye-Soybean-Camelina-Corn planted in Fall 2015-Spring 2016-Fall 2016-Spring 2017, respectively (Table 1). Lastly, 2018 was also unique in that cover crops had been present in the plots in the spring of all three years on the experiment, i.e., 2016, 2017, and 2018. Again, for the Rye-Camelina cover crop rotation treatment planted in the corn main plots in 2018, the sequence of cover crops and cash crops would have been Camelina-Corn-Rye-Soybean-Camelina-Corn planted in Fall 2015-Spring 2016-Fall 2016-Spring 2017- Fall 2017-Spring 2018, respectively (Table 1). Subplots assigned the No Cover Crop treatment had no cover crop preceding the cash crop in any year. Table 1 shows the sequence of cover crops treatments and cash crops for each year. Data from each year and cash crop will be presented separately because of the differing number of years the cover crop rotation was in place.

Cover crop and cash crop planting. Cover crops were planted each fall using a grain drill with 15.25 cm row spacing after soybean harvest (16 Sept 2015, 15 Sept 2016 and 30 Sept 2017) and corn harvest (2 Oct 2015 and 10 Oct 2016 and 2017), at a rate of 67.25 kg/ha for rye (cv. Elbon) and 2.75 kg/ha camelina (cv. Joelle). The camelina seed used in 2015 was mistakenly a mixture of the winter camelina cultivar Joelle and an unknown spring camelina cultivar, which reduced winter survival and population in spring 2016 (personal observation). After the establishment, fall cover crop stand count data were collected in all plots during the second week of November in all three years. The following spring cover crops were terminated 3 days before the cash crop was planted by spraying with glyphosate at 1.12 kg a.i./ha. The no cover crop control plots were also sprayed with glyphosate for consistency of exposure to glyphosate and to manage weeds, even though very few winter annual weeds were present.

Cover crop shoot biomass samples were collected one day prior to or one day after spraying from two arbitrary locations in each plot designated using a rectangular frame (0.76 m wide by 0.50 m long). Plants were clipped close to the soil surface, placed in a paper bag, dried at 60 °C in a forced-air oven, and weighed to determine cover crop shoot dry biomass. Combined subsamples were finely ground and analyzed for carbon and nitrogen concentration using the dry combustion-gas chromatograph method (Schepers et al. 1989) with an EA1112 Flash NC Elemental analyzer (Thermo Electron Corp., Waltham, MA). Carbon and nitrogen contents were calculated by multiplying cover crop shoot biomass on an area basis by tissue N concentration.

A commercial corn hybrid (PO448AMI; DuPont-Pioneer Hybrid International, Johnston, IA) and a soybean variety (Viking 0878R2n; Albert Lea Seed Co., Albert Lea, MN) were planted 3 days after rye termination. Corn was planted on 3 May 2016, 25 April 2017 and 30 April 2018 at a seeding rate of 86,487 seeds/ha in 0.75-m rows using a five-row no-till planter. Soybean was planted at 444,789 seeds/ha on 5 May 2016, 8 May 2017 and 8 May 2018 using the same planter that was used to plant corn. Average monthly air temperatures and precipitation were obtained from the weather station located approximately 0.5 km from the experimental site (Iowa Environmental Mesonet 2015). Soil temperature at the 5-cm depth was monitored in one subplot for each cash crop and cover crop rotation treatment combination using thermocouples (copper-constantan) attached to a data logger (21X Micrologger; Campbell Scientific, Logan, UT).

Corn plots were fertilized with urea ammonium nitrate injected at planting 5 cm from corn row at 33.6 kg N/ha and injected at the V4 to V5 plant stage 19 cm from the plant row at 201.8 kg N/ha. In the fall of 2015, 2016, and 2017 a dry mixture of monoammonium phosphate and potassium chloride was surface broadcast at a rate of 19 kg N/ha, 40 kg P/ha, and 199 kg K/ha as indicated by soil tests and nutrient removal rates.

Sample collection and processing. In 2016 and 2018, corn seedlings were sampled at the V4 to V5 developmental stage (Abendroth et al. 2011; Pedersen 2007), whereas in 2017 corn seedlings were sampled at the V2 to V3 developmental stage. Soybean seedlings were sampled at the developmental stage V2 in both 2016 and 2017 while in 2018 soybean seedlings were sampled at the V4 to V5 developmental stage. Although, we planned to sample corn and soybean at the same developmental stage we were prevented from going to the field to sample by wet field conditions. Six seedlings, 3 from row 2 and 3 from row 4, of each 5-row plot were dug out using a spade. The soil was carefully removed and roots cleaned with water, bagged samples were transported to the lab on ice, and then seedling shoot height, shoot dry weight, and disease assessments were measured in the lab. Corn shoot height was measured from the base of the shoot to the tip of the longest extended leaf. Soybean shoot height was measured from soil level, as indicated by color change on the hypocotyl, to the tip of the apical meristem. Root disease was assessed as described in Acharya et al. (2017, 2018). Briefly, root rot incidence was estimated based on the presence or absence of lesions observed on the root tissue (i.e., radicle, seminal, nodal and mesocotyl). Disease severity was assessed as the percentage of root tissue rotted, and then converted to a 0-to-5 scales, where 1 =1 to 10% of roots covered with lesions; 2, 3, 4, and 5 =11 to 25%, 26 to 50%, 51 to 75% and 76 to 100% of roots with lesions, respectively (Acharya et al. 2017). Healthy plants with no visible lesions were assigned a value of 0. Disease incidence (DI) and disease severity (DS) were combined into a single disease index (DX), using the formula $DX = DI \times DS/5$ (Li et al. 2013; Kandel et al. 2015). A similar scale was used to assess soybean root rot incidence and severity for taproot and the hypocotyl. After disease assessments shoot dry weight of the seedlings was determined by weighing after drying in a forced air oven at 60ºC.

In 2017 and 2018, samples of corn radicles and mesocotyls, and soybean taproots and hypocotyls were collected from seedlings collected for the visual disease assessment to determine the density of *Pythium* spp. belonging to Clade B and Clade F present in those tissues. Samples were not collected in 2016 because we were not ready at that time to implement the procedure at that scale. In preparation for DNA extraction, sampled corn and soybean roots were washed with tap water and rinsed with sterile distilled water. Root tissue samples of approximately 2 cm length were taken from either the root tip or zone of elongation from radicles of corn and taproot of soybean regardless of disease symptoms observed. However, most of the mesocotyl and hypocotyl tissues were included for DNA processing. Prior to drying, two subsamples of approximately 100 mg fresh weight from the above collected tissue types were collected and prepared for DNA extraction using a Qiagen DNA extraction kit (Catalogue no. 69106).

The density of *Pythium* spp. belonging to Clade B and Clade F present in corn and soybean root tissues were measured using quantitative polymerase chain reaction (qPCR) (BIO-RAD IQ5, IDT, Coralville, IA) following the method described by Acharya et al. (2017). Clade B and Clade F *Pythium* spp. were targeted, as prior work indicated members of these clades constituted the majority of *Pythium* spp. associated with corn and soybean seedling disease in Iowa (Matthiesen et al. 2016; Acharya et al. 2017; Bakker et al. 2017). Due to an error in the sampling process of the 2018 corn mesocotyl tissue, only data for 2017 corn mesocotyl tissue was reported in the current study.

To remove possible errors associated with DNA extraction efficiencies among samples, pathogen DNA present in corn and soybean tissues was expressed relative to corn and soybean DNA content; that is, copies of *Pythium* ITS gene per million copies of α-tubulin, *tua4* gene for corn using the assay of Mideros et al. (2009), and copies of *Pythium* ITS gene per million copies of cyclophilin, *CYP2* gene for soybean using the assay of Jian et al. (2008) with a slight modification for the soybean assay. Briefly, each reaction was performed in 20 ul, which consisted of 5 ul of DNA template equal to 50 ng, 10 ul of SYBR Green Master Mix (Qiagen, Cat. No. 204143 or 204163), 0.6 ul each, *CYP2*F and C*YP2*R primer (Jian et al. 2008) at 300 nM final concentration. The *tua4* gene sequence was obtained from GenBank reference sequence (x73980.1) and *CYP2* gene sequence was obtained from NCBI reference sequence (NM_001357079.1). The standard curve of synthesized *Tua4* and *CYP2* gene (IDT, https://www.idtdna.com/pages) for corn and soybean spanning six orders of magnitude in copy number was prepared. Quantification was done only within the range of standard curve amplification. Amplification with cycle threshold above 37 were assigned as nondetects. The following thermocycler program was used: 10 min at 95°C, followed by 40 cycles of denaturing for 10 s at 95°C, annealing and extension for 30 s at 60 °C. Across qPCR runs, the standard curves always produced an $R^2 > 0.99$, and calculated PCR efficiencies were in the range of 90 to 105%. Measured pathogen densities in corn and soybean tissue were expressed as pathogen ITS gene copies per million copies of the corn *tua4* gene and soybean *CYP2* gene then $\log_{10}$ transformed.

Agronomic assessments. At the end of the season, the number of corn plants, ears, and barren plants were recorded from the center row 18.3 m long section of each plot. Corn yield data were collected from the middle three rows of the entire five row plots on 4 October 2016, 12 October 2017 and 27 September 2018. Similarly, the numbers of soybean plants were recorded from a 5.2 m section of each plots and the yield was obtained from the entire five row plots on 29 September 2016, 20 September 2017 and 17 September 2018. A modified combine (Colvin

1990) was used to harvest and measure corn and soybean grain yield and grain moisture. Yields were adjusted to 0.15 g g^{-1} and 0.13 g g^{-1} grain moisture contents for corn and soybean, respectively.

Statistical analyses. Analysis of variance (ANOVA) was performed for all variables using PROC GLIMMIX in SAS version 9.3 (SAS Institute Inc. Cary, NC). Fixed effect factors were cover crop rotation treatments and replications were a random effect factor. Data were analyzed separately for corn and soybean measurements for each year to examine cover crop rotation treatments within each year. This analysis was planned during experimental design because the history or rotation sequence of cover crops changed with each succeeding year and because of expected variation of cover crop growth and weather among years. Cover crop rotation treatment means were compared using Fisher's protected LSD at $P = 0.05$ when the ANOVA indicated significant treatment differences at the 0.05 level of significance.

Results

Average monthly air temperature and precipitation. Average monthly air temperature and precipitation profiles differed each year. The fall (October through November) of 2015 and 2016 when cover crops were planted and established, was warmer and drier than the fall 2017 (Table 2). Similarly, spring (March through April) air temperatures, which are important for early growth of cover crops, were 6 to 7.5 degrees warmer in 2016 and 2.5 to 7 degrees warmer in 2017 compared to than the same period in 2018 (Table 3). In fact, April 2018 was 6.6 °C below the 30-year average temperature while 2016 and 2017 April average temperatures were above the 30-year average. Conversely, air temperatures during May of 2018 after the cash crops were planted were warmer compared to May 2017 and warmer than the 30-year average for

May. Precipitation varied during each growing season (May through August; Table 3). In general, there were more precipitation in 2018 compared to 2017, except for May.

Average soil temperature at the 5-cm depth in corn plots preceding camelina, fallow, and rye from planting cash crop to sampling cash crop ranged from 20.1 to 20.6 ºC in 2016, 15.4 to 15.9 in 2017 and 20.3 to 20.8 in 2018 respectively (results not shown). Similarly, in soybean plots average soil temperature at the 5-cm depth preceding camelina, fallow, and rye ranged from 21.1 to 22.2 in 2016, 16.8 to 17.1 in 2017, and 21.2 to 21.7 in 2018 respectively (results not shown).

Cover crop and its rotation effect on fall stand count. Cover crop stands were denser when planted after soybean harvest as compared with planting after corn harvest in all three years (Table 4). Moreover, cover crop stand densities were much lower in the first year of the trial establishment compared to the second and the third year. In general, stand densities of rye were greater than those of camelina after both corn and soybean harvest during the study period.

Cover crop spring biomass. Cover crop shoot biomass was considerably lower in spring 2018 compared with spring 2016 and 2017 preceding both corn and soybean (Table 5). Effect of previous year cash crop on spring cover crop biomass accumulation was observed in 2017 only ($P < 0.03$). Spring cover crop biomass of rye was greater than that of camelina in all three years (Table 5). However, less spring biomass of camelina in 2016 was due to planting the mixture of winter and spring camelina cultivars this one year. Total nitrogen content in cover crop shoots was considerably greater in rye than camelina. Average rye shoot nitrogen in treatments with rye before corn or soybean in all three year or camelina in previous year before soybean or corn averaged across year was 40 to 42 kg/ha preceding corn and 44 to 45 kg/ha preceding soybean (results not shown). On the other hand, camelina shoot nitrogen ranged from 18 to 19 kg/ha preceding corn and 17 to 18 kg N/ha preceding soybean (results not shown).

Cover crop effects on corn seedling growth and disease. The effects of cover crop rotation treatments were significant in at least one year for most measured parameters of corn seedlings such as corn shoot height, leaf stage, shoot dry weight, radicle root rot incidence, and the radicle disease index (Table 6).

No effect of cover crop treatments on corn seedling height was detected in 2016 and 2018 (*P*= 0.06, *P*= 0.12; Table 6). In 2017, corn seedling height was shortest in the no cover crop treatment compared with three of the cover crop rotation treatments (Cam-S/Rye-C, Cam-S/Cam-C, Rye-S/Cam-C). Additionally, the Cam-S/Rye-C treatment had significantly taller corn plants than the Rye-S/Rye-C treatment indicating a possible effect of the previous cover crop before soybean. In all three years, corn leaf stage of seedlings was lowest with rye before corn (Rye-S/Rye-C or Cam-S/Rye-C) compared with no cover crop or camelina before corn regardless of the cover crop species in the previous spring before soybean. No difference in corn leaf stage was observed between seedlings after camelina and no cover crop. Additionally, shoot dry weight was greater for seedlings following camelina and no cover crop than those following a rye cover crop in all three years. In 2018, corn shoot dry weights following no cover crop also were greater than those of corn following a camelina cover crop (Cam-S/Cam-R, Rye-S/Cam-C). Except for shoot height in 2017, the cover crop grown in the previous spring before soybean did not affect corn shoot growth in either 2017 or 2018.

In general, radicle root rot incidence assessed at corn growth stages V2 to V4 was usually lowest for corn seedlings following the no cover crop treatment (Table 6). In 2017, more corn seedlings following a rye cover crop (Rye-S/Rye-C or Cam-S/Rye-C) had radicle lesions than either seedings following a camelina cover crop (Cam-S/Cam-R, Rye-S/Cam-C) or the no cover crop treatment. In 2018, radicle root rot incidence did not differ among seedlings following either camelina or rye cover crops, but all four of those treatments were significantly greater than the no cover crop treatment. No difference in radicle root rot incidence was detected in corn when it followed a rye cover crop regardless of if rye or camelina were used as a cover crops species in rotation before soybean in previous year (*P*= 0.54 in 2017, and *P*= 0.85 in 2018, data analysis not shown). Effect of cover crop treatment on radicle root rot index was only detected in 2017 and it was greater preceding rye compared to other treatments, however the effect was not as consistent as the radicle root rot incidence.

Cover crop rotation treatments had no detectable effect on seminal root rot incidence in 2016 and 2018 (Table 6). In 2017, the seminal root rot incidence was greater for corn seedlings only following the Cam-S/Rye-C treatment than the no cover crop treatment. However, Rye-S/Rye-C treatment was close to being significantly different from the no cover crop treatment. Seminal root rot incidence for corn planted after a cover crop of camelina (Cam-S/Cam-R, Rye-S/Cam-C) was significantly reduced compared with that of corn planted after rye, and was not different from that of corn planted following no cover crop. No difference in seminal root rot incidence was detected in corn when it followed a rye cover crop regardless of whether rye (Rye-S/Rye-C) or camelina (Cam-S/Rye-C) were used as a cover crops species before soybean in the previous year (*P*= 0.69 in 2017). Similarly, planting camelina before corn in 2017 (i.e. in treatments Cam-S/Cam-C, Rye-S/Cam-C) reduced the radicle root rot index regardless of the cover crop planted in fall of 2015 before soybean. No significant effect of cover crop treatment was detected on the seminal root rot index in any year.

Although some lesions were observed on both the nodal roots and mesocotyls of corn seedlings sampled from all treatments with and without cover crops before corn, root rot incidence was generally minimal (less than 5%) and no significant differences were detected. Therefore, only data for the radicles and the seminal roots are presented.

Cover crop effects on soybean seedling growth and disease. No effect of cover crop treatments was detected on soybean seedling shoot height in 2016 and 2018, on leaf stage in 2016 and 2017 and on shoot dry weight in 2017 (Table 7). In the first year of our trial, 2016, one of the two treatments with rye preceding soybean had smaller shoot dry weights than the other treatments, including the other rye treatment. In 2017, a cereal rye cover crop preceding the soybean crop (Rye-C/Rye-S, Cam-C/Rye-S) increased soybean shoot height relative to the no cover crop control or when camelina preceded soybean (Cam-C/Cam-S, Rye-C/Cam-S). In contrast, in 2018 soybean plants following a cereal rye cover crop had lower leaf stages and smaller shoot dry weights than the other treatments. In all cases, the cover crop in the preceding year before corn did not affect the soybean response.

No root lesions or very low root rot incidence (less than 5%) was observed among soybean seedlings sampled from all cover crop treatments as well as the no cover crop control, and consequently soybean root rot data are not presented.

Quantifying oomycetes populations in corn and soybean root tissue

Oomycetes populations in corn. Cover crop treatment effects were detected for *Pythium* Clade B densities in 2017 and for Clade F population densities in both 2017 and 2018 on radicle root tissue (Table 8). In general, greater populations of Clade B were detected in corn seedlings planted after a cover crop of winter rye compared to either seedlings planted after a cover crop of camelina and seedlings planted after no cover crop treatment. Surprisingly, the cover crop treatment that included rye in previous spring before soybean and camelina before corn (Rye-S/Cam-C) also showed greater Clade B densities than the no cover crop control. Densities of

Pythium Clade F populations in corn following cover crop treatments were much lower than those of Clade B and interestingly, in both 2017 and 2018 corn planted after a rye cover crop had densities of Clade F *Pythium* species that were not different from the no cover crop control, whereas in both years at least one of the treatments with corn following camelina had higher densities than the control.

For corn mesocotyl tissue in 2017, cover crop treatment effects only were observed for *Pythium* Clade F members (P <0.01). As observed in corn radicle tissues, Clade F densities were greater in corn seedlings planted after camelina than those planted after rye. No significant effect of cover crop treatments was observed on Clade B populations of *Pythium.* Although, the differences were not significant the relative ranking of means was similar to that observed for the corn radicles with corn seedlings following rye having the greatest values and those following no cover crop or camelina lower values.

Oomycetes population from soybean. No effect of cover crop treatments were detected for *Pythium* Clade B densities in soybean taproots or hypocotyls in both 2017 and 2018 (Table 9). Greater populations of Clade F only were detected in hypocotyl tissues of soybeans in 2017 when camelina was planted as a cover crop before soybean in 2017 and in the previous year before corn (Cam-C/Cam-S) than in soybeans from the other treatments.

Cover crop effects on corn and soybean in field

Corn yield and agronomic assessments. Final corn stands count and the number of barren plants were not different between treatments in all three study years (Table 10). The number of ears, however, was significantly different among treatments in both 2017 and 2018 (P= 0.02). In 2017, both treatments where corn followed rye had significantly fewer ears than the no cover crop control and the treatment where camelina was planted every year (Cam-S/Cam-C). In 2018, the control and the two rye treatments had significantly fewer ears than one of the camelina treatments (Rye-S/Cam-C).

In general, for all three years, corn yields for at least one of the two treatments with a rye cover crop before corn were reduced compared to corn following a camelina cover crop or the no cover crop control ($P < 0.01$; Table 10). Additionally, in general if there was a yield reduction of corn following camelina the magnitude was smaller than that caused by rye. Specifically, in 2016 one of the two rye before corn treatments had significantly lower yields than the control and the camelina treatments with no other differences among the other treatments. In 2017, the two rye treatments had significantly lower yields than other treatments and the two camelina treatments had lower yields than the control treatment but greater than the rye treatments. Lastly, in 2018 the rye treatments had the lowest yields whereas one of the two camelina treatments had lower yields than the control. Thus, using a camelina cover crop before corn improved corn yield compared to a rye cover crop before corn, but still reduced yield relative to the control in some years. Planting a camelina cover crop every year had no consistent corn yield advantage over planting a rye cover crop before soybean and a camelina cover crop before corn.

Soybean yield and population. In general, neither soybean population or yield were negatively affected by the cover crop treatments relative to the no cover crop control (Table 11). Soybean populations at physiological maturity in the no cover crop treatments were lower than one or more of the other cover crop treatments in 2016 and 2018. In 2016, the control had fewer plants than the two treatments with a camelina cover crop preceding soybean. In 2018, soybean following rye with camelina preceding corn in the previous year had higher populations than the control. In 2017, the two treatments where rye preceded soybean had significantly greater yields than the control and the treatment where a camelina cover crop was planted before both corn and soybean.

Discussion

This research evaluated the effect of a grass (winter cereal rye) and broadleaf (camelina) cover crop on corn and soybean seedling growth and development, root rot, and yield measurements over a three-year study period. Both cash crops were grown in rotation and were present in each year of the study. In general, planting corn after a cover crop of camelina improved corn growth and development, reduced corn root rot and increased the yield of corn compared to planting corn after a cover crop of winter cereal rye, regardless of the cover crop before soybean in the previous spring. Thus, for these two cover crop species, the cover crop preceding the corn crop is more important than the cover crop species in the previous spring. In general, neither of these cover crop species immediately preceding soybean had a consistent negative effect on soybean growth and development, root rot, and yield.

Cover crop stand counts for both cover crop species were greater following soybean compared to stands following corn probably because of the later planting dates after corn and greater corn residue. Soybean harvest occurred 2 to 3 weeks prior to corn harvest, and thus the cover crops were planted following soybean 3 to 4 weeks before those planted following corn, allowing better establishment and growth in the fall. In addition, surface crop residue levels differed considerably between corn and soybean plots. More shoot residue is left on the ground after corn harvest compared to that after soybean harvest (Buyanovsky and Wagner 1986). Because high amounts of surface crop residue reduce drill performance, planting depth, and cover crop seed contact with the soil, establishment of the cover crop can be reduced (Benedict et al. 2014).

In this study, rye shoot biomass production in spring was much greater in 2016 and 2017 compared to 2018. In fact, rye biomass production in 2018 was unusually low probably because of the record low air temperatures that occurred in March and April, which is when most cover crop growth normally occurs in the upper Midwest. In contrast, camelina production was greatest in 2017 and least in 2018 and 2016. In all three years, a rye cover crop produced greater biomass than a camelina cover crop. A cereal rye cover crop has excellent winter hardiness even when planted late in the fall, grows well at cool temperatures, and begins growing early in the spring (Snapp et al. 2005). There have not been many studies on the use of camelina as a cover crop or on its growth characteristics in the upper Midwest (Appelgate et al. 2017; Berti et al. 2017). It is possible that camelina would produce more shoot biomass relative to rye if it was managed differently than it was in this study (e.g. planted earlier, different seeding method, or a higher seeding rate). In general, many farmers prefer to have high biomass production by cover crops in the spring because they associate this with healthier soils as more aboveground biomass indicates greater below ground (root) biomass that positively affects soil health (Bonder et al. 2010; Schutter and Dick 2002). The amount of biomass produced by cover crops is also strongly correlated to their water and nitrogen uptake (Sinclair and Rufty 2012) and erosion protection (Kaspar et al. 2001) and consequently has positive environmental implications. Nonetheless, even though camelina does not produce as much shoot biomass as a cereal rye cover crop, there may be other advantages that may compensate for the lower biomass production.

In the current study, we generally observed less root rot on corn radicle and seminal tissues in 2017 and 2018 when camelina was used as a cover crop before corn rather than rye. No difference in corn root rot between treatments in 2016, the first year of the study, could be due to high background levels of soil pathogens as indicated by the root rot incidence in NC-C treatment. It could also be because this was the first year that cover crop treatments were established for the trial.

Not surprisingly, cereal rye, a grass species like corn, hosts corn pathogens (Bakker et al. 2016). Cereal rye, therefore, may act as a green bridge (i.e. provides a host over the winter fallow period) when it is used as a cover crop before corn (Acharya et al. 2016). It is not known what corn seedling pathogens survive on camelina, although root rot caused by *P. sylvaticum* and *F. graminearum* has been observed (Grazieli 2019). It is possible that camelina does not host many corn pathogens or that the corn pathogens it hosts are not extremely aggressive. Consequently, a cover crop rotation of camelina before corn and cereal rye before soybean may reduce the population of specific soil borne corn pathogens (Supplementary Table 1). However, decreasing some pathogen populations in the soil may require longer periods without a host species to become apparent.

In our study, *Pythium* Clade B was prevalent in corn radicle tissues particularly following rye with a tendency for reduced numbers following a camelina cover crop. In contrast, while *Pythium* Clade F was detected, albeit at reduced numbers compared with Clade B, density of Clade F tended to be higher when corn followed camelina. These data are similar to data that we have reported before that indicated that *Pythium* Clade B is dominant relative to Clade F in corn roots that follow a rye cover crop (Acharya et al. 2017; Schenck et al. 2017). In preliminary research investigating populations of *Pythium* Clade B and Clade F in rye roots immediately prior to termination in 2017, we detected 100 to 1000-fold more DNA of Clade B in rye compared to Clade F (Supplementary Table 1). Moreover, we detected 10 to 100-fold more DNA of Clade F in the roots of camelina. Thus, these data further support our findings that a rye winter cover crop acts a “green bridge” for *Pythium* that infect corn. Interestingly, in the taproot of soybean, we detected Clade F almost exclusively, and the preceding cover crop seemed to have had little effect. Further investigation is needed, however, to more fully understand the particular

Pythium species involved in this system and their relative pathogenicity, particularly as species from both Clades have been recovered from diseased corn and soybean seedlings and rye in the Midwest (Bakker et al. 2016; Matthiesen et al. 2017).

Similar to earlier reports (Acharya et al. 2018) we also detected of almost equal densities of *Pythium* Clade B members from mesocotyl tissue as from to the radicle, although we observed minimal mesocotyl rot. As we have suggested before, we may be detecting latent or very early stage infection in the mesocotyl, which emerges later than the radicle, due to difference in time since these tissues were exposed to the soil microbial environment (Acharya et al. 2018). Similarly, in soybean hypocotyl tissues, we detected similar densities of *Pythium* from both Clades, but no hypocotyl rot was observed.

We detected reduced corn yield following a rye cover crop compared to no cover crop in all three years. The reduced yields in 2017 for the rye cover crop plots were partly a consequence of fewer ears produced, which was combination of fewer plants and more barren plants. In 2016 and 2018, it was not likely that fewer ears caused the reduction in yield and we would hypothesize that grain weight per ear was most likely less in the rye treatments. We did not, however, collect data on ear size or grain weight per ear so we are unable to confirm that these factors contributed to the yield decrease. Greater seedling root disease and reduced corn seedling growth were evident following a rye cover crop. The relatively larger density of *Pythium* Clade B infecting corn radicles after rye in 2017 and 2018, also correspond with the greater corn yield reduction (intercept = -5.00, slope = 18.5 and R^2 = 0.847 in 2017; intercept = 1.53, slope = 26.3 and R^2 = 0.571 in 2018). Other studies, have shown that seedling disease in corn may reduce stand, delay emergence, or reduce plant vigor (Acharya et al. 2017; Munkvold 1999) and consequently contribute to reduced yields due to decreased stands, more barren plants, or plants with smaller ears (Acharya et al. 2017; Buren et al. 1974; Nafzinger et al. 1991; Smith et al. 1982).

Although planting a camelina cover crop before corn reduced seedling disease and increased yield compared to planting a rye cover crop before corn, yields were still significantly lower than yields of corn in the no cover crop control plots in two of the three years. This is in spite of very little evidence of increased seedling disease relative to the control of corn planted following a camelina cover crop. It is possible that camelina, like rye, may have reduced nitrogen availability for the corn seedlings, but this seems like less of a possibility for camelina than rye because of much lower camelina shoot biomass production. As mentioned earlier, the use of camelina as a cover crop is relatively new, so improved management may help to prevent even these small corn yield decreases.

As mentioned above, many possible reasons have been proposed for reduced corn yield following a rye winter cover crop. One possible mechanism is that the reduced yield of corn in our rye cover crop treatments may have been related to nitrogen dynamics or availability. We detected greater nitrogen in rye shoot biomass which possibly could have limited the soil nitrogen and have influenced the growth of the following cash crop. The role of nitrogen fertilizer in corn production is well known (Stewart et al. 2005). Pantoja et al. (2016) reported a cereal rye cover crop in a corn-soybean cropping system reduced soil nitrogen availability for the corn crop due to cover crop uptake of soil nitrogen in the spring prior to corn planting. Kaspar et al. (2007, 2012) showed rye cover crop shoot nitrogen and therefore, uptake generally increased as shoot biomass increased Additionally, decomposition of cover crop shoot and root residues may have immobilized N soon after corn planting (Karlen and Doran 1991; Tollenaar et al. 1993;

Wagger and Mengel 1993). Lastly, N availability can also be limited by slow or restricted root growth (Lynch 2013). Because we showed increased root infection following a rye cover crop it is likely that root extension was also reduced, thus limiting access to soil nitrogen. Greater availability of nitrogen early in the growing season may have resulted in higher yields for rye cover crop treatments because of more vigorous early seedling growth. Further research is required to understand the interaction between rye cover crop nitrogen uptake, rye residue decomposition, and seedling root disease inhibition of root extension.

No negative effect of either rye or camelina cover crops on soybean seedling disease, seedling growth, population and yield were detected in this study. This result supports previous findings where a positive or no effect of cover crops on soybean yield were detected (Ruffo et al. 2004; Pantoja et al. 2015; Wen et al. 2017). It is unclear why no significant root rot or seedling disease was observed in soybean following rye in this current study because rye is known to host species of both *Pythium* and *Fusarium* that are reported as pathogenic to soybeans (Bakker, 2016; Broders et al. 2007a, b; Matthiessen et al. 2016). It may be due to the difference in planting dates of corn and soybean that relates to a difference in soil temperature at planting of each cash crop. Temperature affects the pathogenicity of *Pythium* spp. (Matthiesen et al. 2016). Moreover, *Pythium* spp. belonging to Clade B were more pathogenic on corn and soybean at cooler temperatures (13 °C) than species belonging to Clade F that caused more root rot on both crops at warmer temperatures (23 °C) (Matthiesen et al. 2016). Our previous work reported *Pythium* Clade B were most likely the cause of corn root rot after a rye cover crop (Acharya et al. 2017). In this experiment corn was planted 1 to 2 weeks before soybeans were planted when soil temperatures are usually much cooler. Interestingly, in this current study we detected minimal *Pythium* Clade B in soybean roots. We have no explanation especially since previous work from our lab reported no difference in the susceptibility of both corn and soybean to species from *Pythium* Clade B (Matthiesen et al. 2016).

Based on the results from this study, using a winter hardy brassica, like camelina, as a cover crop after soybean and before corn, could be a potential management option to reduce seedling disease in corn and to contribute the sustainability of the corn-soybean production system in the Midwest by including a cover crop before both corn and soybean. Unfortunately, camelina seed is not widely available at this time and more needs to learned about managing it as a cover crop. Winter cereal rye is likely to remain a staple cover crop in the Midwest because it is relatively inexpensive, seed is usually available, overwinters and, perhaps most importantly, grows well between corn and soybean harvest and planting. Because rye has no deleterious effects on soybean, using it as a cover crop before soybean is easier and requires less management. Thus, rye cover crops before soybean are being encouraged as a beginning practice for farmers to increase cover crops on the Iowa landscape and contribute to goals laid out in the Iowa Nutrient Reduction Strategy (J. Benning, personal communication). Still, a further understanding of the factors that contribute to seedling disease that develops on corn seedlings following a cereal rye should allow us to develop strategies like fungicide treatments, early termination of the cover crop, or precision planting of rye cover crops in the interrow to reduce the negative effect of rye on corn. With continued research and increases in camelina seed availability, we expect using that using a camelina cover crop before corn and cereal rye before soybean will have the potential to be a viable cover crop system for the upper Midwest.

Acknowledgments

We thank Iowa Nutrient Reduction Research Center and USDA Hatch Project #IOWO3908 for partial funding for the project, and K. Kohler for establishing and managing the field trial.

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Table 1. Cover crops and crop rotation sequences with treatment descriptions over the three-year field study in Iowa.

Cover crops in Fall 2015[x]	Cash crop in 2016	Treatment description before corn and soybean in 2016[y]	Cover crops in Fall 2016[x]	Cash crop in 2017	Treatment description before corn and soybean in 2017[y]	Cover crops in Fall 2017[x]	Cash crop in 2018	Treatment description before corn and soybean in 2018[y]
No cover crop	Corn	NC-C	No cover crop	Soybean	NC-C/NC-S	No cover crop	Corn	NC-C/NC-S/NC-C
Rye	Corn	Rye-C	Rye	Soybean	Rye-C/Rye-S	Rye	Corn	Rye-C/Rye-S/Rye-C
Camelina	Corn	Cam-C	Camelina	Soybean	Cam-C/Cam-S	Camelina	Corn	Cam-C/Cam-S/Cam-C
Camelina	Corn	Cam-C	Rye	Soybean	Rye-C/Cam-S	Camelina	Corn	Cam-C/Rye-S/Cam-C
Rye	Corn	Rye-C	Camelina	Soybean	Cam-C/Rye-S	Rye	Corn	Rye-C/Cam-S/Rye-C
No cover crop	Soybean	NC-S	No cover crop	Corn	NC-S/NC-C	No cover crop	Soybean	NC-S/NC-C/NC-S
Rye	Soybean	Rye-S	Rye	Corn	Rye-S/Rye-C	Rye	Soybean	Rye-S/Rye-C/Rye-S
Camelina	Soybean	Cam-S	Camelina	Corn	Cam-S/Cam-C	Camelina	Soybean	Cam-S/Cam-C/Cam-S
Camelina	Soybean	Cam-S	Rye	Corn	Rye-S/Cam-C	Camelina	Soybean	Cam-S/Rye-C/Cam-S
Rye	Soybean	Rye-S	Camelina	Corn	Cam-S/Rye-C	Rye	Soybean	Rye-S/Cam-C/Rye-S

[x] Cover crops were established in a corn-soybean rotation field that included both phase of cash crop each year. Cover crop in this study were terminated 3 days before planting corn or soybean.

[Y] Abbreviations: NC= No cover crop, Cam= Camelina, C= Corn, S= Soybean

Table 2. Average monthly air temperature (°C) and precipitation (millimeters) from September to December 2015, 2016 and 2017 obtained from a weather recording station located 2 km from the experimental site.

	Temperature °C			**Precipitation (mm)**		
Months	**2015**	**2016**	**2017**	**2015**	**2016**	**2017**
September	20.9	20.6	20.0	128.3	200.2	74.1
October	12.4	14.5	11.9	32.3	12.0	160.5
November	6.04	8.2	2.3	69.6	44.2	6.1
December	0.46	-4.1	-3.7	131.8	30.8	11.1

Table 3. Average monthly air temperature (°C) and precipitation (millimeters) from January to December 2016, 2017 and 2018 and the Cumulative 30-year average temperature and precipitation obtained from a weather recording station located 2 km from the experimental site.

	Temperature °C				**Precipitation (mm)**			
Months	**2016**	**2017**	**2018**	**30 year-Average**	**2016**	**2017**	**2018**	**30 year-Average**
January	-6.5	-3.9	-8.6	-5.9	15.3	47.0	43.3	21.3
February	-1.7	2.6	-7.3	-4.1	21.4	55.3	50.6	25.4
March	7.0	3.8	1.3	3.4	38.6	83.3	85.2	61.2
April	11.1	11.5	3.6	10.2	108.8	116.7	66.8	102.6
May	16.3	16.3	20.7	16.7	109.0	189.4	82.1	128.1
June	23.7	22.7	23.5	21.7	24.4	49.3	281.9	129.6
July	23.5	24.4	23.5	23.3	148.6	37.4	106.9	120.6
August	22.7	20.8	16.6	22.2	209.1	92.9	217.7	129.2

Table 4. Fall cover crop stand count before corn and soybean in 2015, 2016 and 2017 in field experiments in Iowa.

Year	Treatments for corn plots[x]	Cover crop previous spring before soybean	Cover crop Fall/spring before corn	Cover crop stand count before corn (Plants/ m2) [X]	Treatments from soybean plots	Cover crop previous spring before corn	Cover crop Fall/spring before soybean	Cover crop stand count before soybean (Plants/ m2) [y]
Fall 2015	Rye-C	None	Rye	188.8	Rye-S	None	Rye	80.0
	Cam-C	None	Camelina	199.6	Cam-S	None	Camelina	99.4
	Cam-C	None	Camelina	119.0	Cam-S	None	Camelina	102.5
	Rye-C	None	Rye	180.8	Rye-S	None	Rye	90.6
	P value			0.08	*P* value			0.43
Fall 2016	Rye-S/Rye-C	Rye	Rye	345.4 a[z]	Rye-C/Rye-S	Rye	Rye	155.0 a
	Cam-S/Cam-C	Camelina	Camelina	323.0 ab	Cam-C/Cam-S	Camelina	Camelina	120.6 ab
	Rye-S/Cam-C	Rye	Camelina	246.2 b	Rye-C/Cam-S	Rye	Camelina	83.4 b
	Cam-S/Rye-C	Camelina	Rye	363.0 a	Cam-C/Rye-S	Camelina	Rye	168.0 a
	P value			0.05	*P* value			0.02
Fall 2017	Rye-C/Rye-S/Rye-C	Rye	Rye	295.0	Rye-S/Rye-C/Rye-S	Rye	Rye	189.4 a
	Cam-C/Cam-S/Cam-C	Camelina	Camelina	288.6	Cam-S/Cam-C/Cam-S	Camelina	Camelina	53.8 b
	Cam-C/Rye-S/Cam-C	Rye	Camelina	292.2	Cam-S/Rye-C/Cam-S	Rye	Camelina	55.3 b
	Rye-C/Cam-S/Rye-C	Camelina	Rye	294.2	Rye-S/Cam-C/Rye-S	Camelina	Rye	144.2 a
	P value			0.99	*P* value			<0.01

[X] Abbreviations: Cam= Camelina, C= Corn, S= Soybean.

[y] After the establishment of cover crops, fall cover crops stand count data were collected in all plots on November second week. Cover crops were counted from 1ft section of a row.

[z] Values followed by the same letter within a column are not significantly different at *P* value 0.05.

Table 5. Cover crop biomass before cash crop planting in spring 2016, 2017 and 2018 in field experiments in Iowa.

Year	**Treatments from corn plots**[x]	**Cover crop previous spring before soybean**	**Cover crop Fall/spring before corn**	**Cover crop biomass before corn (Mg/ha)** [y]	**Treatments from soybean plots**	**Cover crop previous spring before corn**	**Cover crop Fall/spring before soybean**	**Cover crop biomass before soybean (Mg/ha)**[y]
Spring 2016	Rye-C	NA	Rye	4.0 a[z]	Rye-S	NA	Rye	4.8 a
	Cam-C	NA	Camelina	0.3 b	Cam-S	NA	Camelina	0.9 b
	Cam-C	NA	Camelina	0.5 b	Cam-S	NA	Camelina	1.0 b
	Rye-C	NA	Rye	4.6 a	Rye-S	NA	Rye	4.2 a
	P value			<0.01	*P* value			<0.01
Spring 2017	Rye-S/Rye-C	Rye	Rye	3.1 a	Rye-C/Rye-S	Rye	Rye	1.9 b
	Cam-S/Cam-C	Camelina	Camelina	1.4 b	Cam-C/Cam-S	Camelina	Camelina	0.6 c
	Rye-S/Cam-C	Rye	Camelina	1.3 b	Rye-C/Cam-S	Rye	Camelina	0.5 c
	Cam-S/Rye-C	Camelina	Rye	3.2 a	Cam-C/Rye-S	Camelina	Rye	3.0 a
	P value			<0.01	*P* value			<0.01
Spring 2018	Rye-C/Rye-S/Rye-C	Rye	Rye	1.2 a	Rye-S/Rye-C/Rye-S	Rye	Rye	1.6 a
	Cam-C/Cam-S/Cam-C	Camelina	Camelina	0.5 b	Cam-S/Cam-C/Cam-S	Camelina	Camelina	0.3 b
	Cam-C/Rye-S/Cam-C	Rye	Camelina	0.6 b	Cam-S/Rye-C/Cam-S	Rye	Camelina	0.4 b
	Rye-C/Cam-S/Rye-C	Camelina	Rye	1.3 a	Rye-S/Cam-C/Rye-S	Camelina	Rye	1.3 a
	P value			<0.01	*P* value			<0.01

[X] Abbreviations: Cam= Camelina, C= Corn, S= Soybean.

[y] Cover crops, spring biomass were collected at the time of termination using a rectangular frame (0.76 m wide by 0.50 m). Collected shoot biomass were dried at 60 °C and weighed.

[z] Values followed by the same letter within a column are not significantly different at *P* value 0.05.

Table 6. Average effects of cover crop treatments on corn seedling growth and root disease assessed at growth stage V2 to V4 in field experiments in Iowa from 2016, 2017 and 2018.

Year	Treatments[s]	Cover crop Fall 2015	Cover crop Fall 2016	Cover crop Fall 2017	Shoot height (cm)[t]	Leaf stage	Shoot dry weight (g)[u]	Radicle RR incidence (%)[v]	Radicle RR index (%)[w]	Seminal RR incidence (%)[x]	Seminal RR index (%)[y]
2016	NC-C	NC	NA	NA	43.0	4.0 a	9.5 a[z]	30.0	1.6	30.0	0.6
	Rye-C	Rye	NA	NA	44.1	3.5 b	5.4 b	46.7	6.3	26.7	3.1
	Cam-C	Camelina	NA	NA	41.0	3.9 a	7.6 a	40.0	2.3	33.3	1.5
	Cam-C	Camelina	NA	NA	40.3	4.0 a	7.7 a	56.7	2.2	46.7	1.3
	Rye-C	Rye	NA	NA	43.7	3.5 b	5.5 b	26.7	4.4	6.7	1.3
	P value				0.06	< 0.01	< 0.01	0.39	0.06	0.18	0.59
2017	NC-S/NC-C	NC	NC	NA	20.6 c	3.0 a	5.5 a	0.0 b	0.0 b	0.0 b	0.0
	Rye-S/Rye-C	Rye	Rye	NA	21.5 bc	2.2 b	3.7 b	26.6 a	3.2 ab	20.2 ab	2.2
	Cam-S/Cam-C	Camelina	Camelina	NA	22.7 ab	2.7 a	5.8 a	0.0 b	0.0 c	0.0 b	0.0
	Rye-S/Cam-C	Rye	Camelina	NA	23.1 ab	2.8 a	5.8 a	6.8 b	0.3 bc	3.4 b	0.14
	Cam-S/Rye-C	Camelina	Rye	NA	23.3 a	2.3 b	4.3 b	33.4 a	4.18 a	26.7 a	5.7
	P value				0.02	< 0.01	< 0.01	0.01	0.03	0.05	0.17
2018	NC-C/NC-S/NC-C	NC	NC	NC	44.6	4.2 a	5.0 a	10.0 c	1.1	0.0	0.0
	Rye-C/Rye-S/Rye-C	Rye	Rye	Rye	40.4	4.0 b	2.7 c	56.7 ab	13.1	40.0	0.2
	Cam-C/Cam-S/Cam-C	Camelina	Camelina	Camelina	41.5	4.4 a	3.8 b	40.0 ab	6.7	30.0	0.2
	Cam-C/Rye-S/Cam-C	Camelina	Rye	Camelina	42.0	4.3 a	4.0 b	30.0 ab	6.7	23.3	0.1
	Rye-C/Cam-S/Rye-C	Rye	Camelina	Rye	40.9	4.0 b	2.8 c	60.0 a	12.2	26.7	0.1
	P value				0.12	< 0.01	< 0.01	0.03	0.13	0.10	0.36

[s] Abbreviations: NC= No cover crop, Cam= Camelina, C= Corn, S= Soybean, RR= root rot

[t] Corn shoot height was measured from ground level to the extended leaf in (6 June 2016, 25 May 2017, and 7 June 2018).

[u] Corn shoot was dried in oven at 60 °C and weighed.

[v] Radicle RR incidence was calculated as the percentage of seedlings with lesions on the radicle (N = 30).

[w] Radicle RR index was calculated using the formula DX = DI × DS/5. Disease severity (DS) was scored on a 1 to 5 scale where 1 =1 to 10% of radicle covered with lesions; 2, 3, 4, and 5 =11 to 25%, 26 to 50%, 51 to 75% and 76 to 100% of radicle roots with lesions. DI = Disease incidence and DX = Disease index.

[x] Seminal RR incidence was calculated as the percentage of seedlings with lesions on the seminal roots (N = 30).

[y] Seminal RR index was calculated using the formula DX = DI × DS/5.

[z] Values followed by the same letter within a column are not significantly different at *P* value 0.05.

Table 7. Average effects of cover crop treatments on soybean seedling growth at growth stage V4 to V5 in field experiments in Iowa.

Year	Treatments[w]	Cover crop Fall 2015	Cover crop Fall 2016	Cover crop Fall 2017	Shoot height (cm)[x]	Leaf stage	Shoot dry weight (g)[y]
2016	NC-S	NC	NA	NA	11.1	2.8	3.3 a[z]
	Rye-S	Rye	NA	NA	11.7	2.5	2.8 a
	Cam-S	Camelina	NA	NA	11.5	2.6	3.1 a
	Cam-S	Camelina	NA	NA	10.8	2.6	3.0 a
	Rye-S	Rye	NA	NA	11.3	2.4	2.0 b
	P value				0.48	0.13	0.02
2017	NC-C/NC-S	NC	NC	NA	15.9 c	2.2	2.2
	Rye-C/Rye-S	Rye	Rye	NA	17.3 ab	2.2	2.3
	Cam-C/Cam-S	Camelina	Camelina	NA	16.3 bc	2.2	2.1
	Rye-C/Cam-S	Rye	Camelina	NA	16.5 bc	2.2	2.4
	Cam-C/Rye-S	Camelina	Rye	NA	17.8 a	2.3	2.3
	P value				0.02	0.98	0.56
2018	NC-S/NC-C/NC-S	NC	NC	NC	34.7	4.8 a	4.9 a
	Rye-S/Rye-C/Rye-S	Rye	Rye	Rye	32.3	4.3 b	4.0 b
	Cam-S/Cam-C/Cam-S	Camelina	Camelina	Camelina	32.4	4.9 a	4.9 a
	Cam-S/Rye-C/Cam-S	Camelina	Rye	Camelina	33.4	5.0 a	4.7 a
	Rye-S/Cam-C/Rye-S	Rye	Camelina	Rye	31.1	4.1 b	3.8 b
	P value				0.15	<0.01	< 0.01

[w] Abbreviations: NC= No cover crop, Cam= Camelina, C= Corn, S= Soybean

[x] Soybean shoot height was measured from ground level to the tip of the apical meristem in (13 June 2016, 12 June 2017, and 18 June 2018).

[y] Soybean shoot was dried in oven at 60 °C and weighed.

[z] Values followed by the same letter within a column are not significantly different at *P* value 0.05.

Note: Disease data from soybean seedlings was not presented in the table due to minimal disease recorded after each cover crop treatments.

Table 8. Density of *Pythium* spp. belonging to Clade B and Clade F in radicles of a corn seedlings sampled in 2017 and 2018 and mesocotyls sampled in 2017 from field experiments in Iowa.

		Radicle root		**Mesocotyl**	
	Treatments[x]	**Clade B copies (Log ITS/*tua4*)**[y]	**Clade F copies (Log ITS/*tua4*)**[y]	**Clade B copies (Log ITS/*tua4*)**[y]	**Clade F copies (Log ITS/*tua4*)**[y]
2017	NC-S/NC-C	0.54 c[z]	0.12 b	0.48	0.18 b
	Rye-S/Rye-C	1.50 a	0.00 b	1.19	0.00 b
	Cam-S/Cam-C	0.70 bc	0.83 a	0.39	0.67 a
	Rye-S/Cam-C	1.17 ab	0.21 b	0.37	0.10 b
	Cam-S/Rye-C	1.76 a	0.19 b	0.61	0.47 ab
	P value	< 0.01	< 0.01	0.22	< 0.01
2018	NC-C/NC-S/NC-C	0.00	0.00 b	-	-
	Rye-C/Rye-S/Rye-C	0.68	0.00 b	-	-
	Cam-C/Cam-S/Cam-C	0.21	0.13 b	-	-
	Cam-C/Rye-S/Cam-C	0.61	0.59 a	-	-
	Rye-C/Cam-S/Rye-C	0.38	0.00 b	-	-
	P value	0.14	< 0.01	-	-

[x] Abbreviations: NC= No cover crop, Cam= Camelina, C= Corn, S= Soybean

[y] Values followed by the same letter within a column are not significantly different at *P* value 0.05.

Table 9. Density of *Pythium* spp. belonging to Clade B and Clade F in taproot and hypocotyl of soybean seedlings in different cover crop treatments sampled from field experiments in 2017 and 2018.

		Taproot		**Hypocotyl**	
	Treatments[x]	**Clade B copies (Log ITS/*CYP2*)**[y]	**Clade F copies Log ITS/*CYP2*)**[y]	**Clade B copies (Log ITS/*CYP2)***[y]	**Clade F copies Log ITS/*CYP2*)**[y]
2017	NC-C/NC-S	0.00	0.59	0.07	0.03 b[z]
	Rye-C/Rye-S	0.07	0.59	0.00	0.24 b
	Cam-C/Cam-S	0.00	1.28	0.05	1.06 a
	Rye-C/Cam-S	0.00	0.85	0.25	0.36 b
	Cam-C/Rye-S	0.00	0.67	0.17	0.00 b
	P value	0.38	0.16	0.47	< 0.01
2018	NC-S/NC-C/NC-S	0.27	0.91	0.00	0.06
	Rye-S/Rye-C/Rye-S	0.20	0.58	0.00	0.00
	Cam-S/Cam-C/Cam-S	0.14	1.22	0.77	0.35
	Cam-S/Rye-C/Cam-S	0.03	0.78	0.77	0.00
	Rye-S/Cam-C/Rye-S	0.00	1.26	0.00	0.28
	P value	0.43	0.36	0.57	0.19

[x] Abbreviations: NC= No cover crop, Cam= Camelina, C= Corn, S= Soybean

[y] Values followed by the same letter within a column are not significantly different at *P* value 0.05.

Table 10. Average final plant stand, number of barren plants, number of ears and yield of corn following cover crop treatments in field experiments in Iowa.

Year	Treatments[x]	Cover crop Fall 2015	Cover crop Fall 2016	Cover crop Fall 2017	Mature plants/ha	Barren/ha	Ears/ha	Yield (Mg/ha)[y]
2016	NC-C	NC	NA	NA	84927	1004	83922	12.6 ab[z]
	Rye-C	Rye	NA	NA	83635	1004	82631	10.6 c
	Cam-C	Camelina	NA	NA	80336	1004	79332	12.8 a
	Cam-C	Camelina	NA	NA	82057	1147	80909	12.3 ab
	Rye-C	Rye	NA	NA	80623	861	79762	11.4 bc
	P value				0.87	0.99	0.89	0.01
2017	NC-S/NC-C	NC	NC	NA	80336	1435	78901 a	11.5 a
	Rye-S/Rye-C	Rye	Rye	NA	76463	3299	73163 c	8.4 c
	Cam-S/Cam-C	Camelina	Camelina	NA	80766	2009	78758 a	10.0 b
	Rye-S/Cam-C	Rye	Camelina	NA	80336	2439	77897 ab	10.0 b
	Cam-S/Rye-C	Camelina	Rye	NA	77754	3730	74024 bc	8.6 c
	P value				0.15	0.11	0.02	< 0.01
2018	NC-C/NC-S/NC-C	NC	NC	NC	77180	861	76319 c	13.3 a
	Rye-C/Rye-S/Rye-C	Rye	Rye	Rye	78901	1435	77467 bc	10.1 c
	Cam-C/Cam-S/Cam-C	Camelina	Camelina	Camelina	81914	1004	80909 ab	12.5 ab
	Cam-C/Rye-S/Cam-C	Camelina	Rye	Camelina	81914	574	81340 a	12.2 b
	Rye-C/Cam-S/Rye-C	Rye	Camelina	Rye	79188	2009	77180 c	10.8 c
	P value				0.08	0.13	0.03	< 0.01

[x] Abbreviations: NC= No cover crop, Cam= Camelina, C= Corn, S= Soybean

[y] Corn yield data were collected from the middle three rows of each plot

[z] Values followed by the same letter within a column are not significantly different at *P* value 0.05.

Table 11. Average number of plants and yield of soybean following cover crop treatments in field experiments in Iowa.

Year	Treatments[x]	Cover crop Fall 2015	Cover crop Fall 2016	Cover crop Fall 2017	Population/ha	Yield (Ma/ha)[y]
2016	NC-S	NC	NA	NA	186402 c[z]	2.7
	Rye-S	Rye	NA	NA	258328 ab	2.4
	Cam-S	Camelina	NA	NA	290239 a	2.5
	Cam-S	Camelina	NA	NA	208689 bc	2.4
	Rye-S	Rye	NA	NA	269472 a	2.5
	P value				< 0.01	0.43
2017	NC-C/NC-S	NC	NC	NA	279602	2.2 b
	Rye-C/Rye-S	Rye	Rye	NA	309994	2.5 a
	Cam-C/Cam-S	Camelina	Camelina	NA	232495	2.2 b
	Rye-C/Cam-S	Rye	Camelina	NA	275550	2.4 ab
	Cam-C/Rye-S	Camelina	Rye	NA	299357	2.5 a
	P value				0.09	0.03
2018	NC-S/NC-C/NC-S	NC	NC	NC	203792 b	3.7
	Rye-S/Rye-C/Rye-S	Rye	Rye	Rye	225033 ab	3.7
	Cam-S/Cam-C/Cam-S	Camelina	Camelina	Camelina	217139 ab	3.7
	Cam-S/Rye-C/Cam-S	Camelina	Rye	Camelina	219435 b	3.8
	Rye-S/Cam-C/Rye-S	Rye	Camelina	Rye	241537 a	3.7
	P value				0.035	0.94

[x] Abbreviations: NC= No cover crop, Cam= Camelina, C= Corn, S= Soybean

[y] Soybean yield data was obtained from the entire five rows plot.

[z] Values followed by the same letter within a column are not significantly different at *P* value 0.05.

Supplementary Table 1. *Pythium* Clade B and Clade F population densities detected in cover crop roots sampled before or at planting of the cash crop from plots planted to corn or soybean the previous year in field experiment in Iowa in 2017.

Treatments from corn plots in 2017	**Population detected in cover crop roots sampled in spring 2017 preceding corn and planted after soybean in 2016**		**Treatments from soybean plots in 2017**	**Population detected in cover crop roots sampled in spring 2017 preceding soybean and planted after corn in 2016**	
	Clade B (Copies/ITS)/reaction	Clade F (Copies/ITS)/ reaction		Clade B (Copies/ITS)/reaction	Clade F (Copies/ITS)/ reaction
Rye-S/Rye-C	19979.0 a[x]	8.6	Rye-C/Rye-S	72975.0 a	0
Cam-S/Cam-C	21.5 b	270.6	Cam-C/Cam-S	0.0 b	2201.4
Rye-S/Cam-C	209.7 b	3588.1	Rye-C/Cam-S	1.81 b	622.5
Cam-S/Rye-C	18584.0 a	7.4	Cam-C/Rye-S	61222.0 a	29
P value	0.02	0.09	*P* value	<0.01	0.18

[x] Values followed by the same letter within a column are not significantly different at *P* value 0.05.