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Effect of Brassicaceae seed meals with different glucosinolate profiles on Rhizoctonia root rot in wheat

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ABSTRACT

The soil-borne pathogen *Rhizoctonia solani* AG 8 causes major yield losses in wheat (*Triticum aestivum*. L) production worldwide. Plant tissues of Brassicaceae species contain glucosinolates that are hydrolyzed in the presence of the enzyme myrosinase into products with pesticidal properties. Growth chamber studies were conducted to determine the effect of the Brassicaceae seed meals (SMs) from *Brassica juncea*, *Brassica napus* and *Sinapis alba* on the suppression of the *R. solani* AG 8 infection of winter wheat. Pasteurized sandy soils were amended with intact and denatured SMs of rape seed and mustard at a rate of 0.5% by soil weight. Regardless of the glucosinolate type and content, all intact and denatured Brassicaceae significantly reduced the infection of winter wheat seedlings by *R. solani* AG 8 compared to the un-amended control. However, soils amended with *S. alba* SMs had the lowest severity of Rhizoctonia root rot relative to other amended soils. Phytotoxicity arising from the use of Brassicaceae SMs was observed particularly in soils amended with high glucosinolate-containing SMs. These studies demonstrate that Brassicaceae SMs can be used to manage disease caused by *R. solani* AG-8. However, future studies will need to focus on strategies for diminishing the crop growth-reducing effects associated with Brassicaceae SM amendment to fully maximize these fungicidal benefits.

1. Introduction

Rhizoctonia solani Kuhn anastomosis group (AG) 8 is the causal agent of *Rhizoctonia* baer patch, an important root rotting disease affecting cereals, pastures and grain legumes in southern Australia and the Pacific Northwest of the United States (Murray and Brown, 1987; Weller et al., 1986). In wheat (*Triticum aestivum* L.), *R. solani* AG 8 attacks the seminal and crown roots, pruning away the root tips and rotting the root cortex, resulting in patches of dead or stunted plants up to several yards in diameter (Schillinger and Paulitz, 2006). This disease is favored by reduced tillage (Rovira, 1986). In South Australia, *R. solani* AG 8 is primarily associated with onion stunting (Twigden, 2005). As in cereals, the stunting in onions develops as circular to irregular patches varying in size from 1 m to 25 m or more in diameter and often occurs elongated in the direction of the seed rows (Wicks and Walker, 2010). The available management options in wheat include fungicide seed treatments, which provide limited protection for germinating seeds but do not protect the roots or increase yield in patchy fields and the reduction of the green bridge carryover of inoculum from volunteer crops and grassy weeds. However, the existing control practices are only partially effective (Okubara et al., 2008).

Isothiocyanates are the hydrolysis products of glucosinolate-containing plants or plant products applied to soil (Angus et al., 1994; Brown and Morra, 1997; Kirkegaard and Matthiessen, 2004; Matthiessen and Kirkegaard, 2006), which play a role in the suppression of soil-borne diseases. Soil-borne pathogen suppression can be achieved by incorporating fresh plant material (green manure), seed meals (SMs) (a byproduct of crushing seed for oil) or dried plant material treated to preserve its isothiocyanate activity (Kirkegaard and Matthiessen, 2004; Matthiessen and Kirkegaard, 2006). The predominant volatile compounds released upon the hydrolysis of glucosinolates in the tested ground seed samples were allyl isothiocyanate, allyl cyanide and 3-butenyl isothiocyanate (Chung et al., 2002).

Several studies have shown that amending soil with the plant tissue of *Brassica* spp. can reduce the disease incidence or inoculum

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level of *Pythium ultimum* and *R. solani* (Charron and Sams, 1999; Cohen and Mazzola, 2006; Lodha and Sharma, 2002). Chung et al. (2002) reported that 10 hydrated ground SMs from tested *Brassica* spp. and the ground SMs of *Brassica juncea*, released volatile compounds that are toxic to *R. solani*.

Brassicaceae tissues can suppress a variety of soil-borne pathogens (Charron and Sams, 1999). *Brassica napus* SMs did not directly control *R. solani* AG 5 in apple (*Malus domestica* Borkh.) roots; instead, the initial disease control was associated with the microbial generation of nitric oxide through the process of nitrification (Cohen et al., 2005). The implication is that the suppression of soil-borne pathogens such as *R. solani* AG 8 through Brassicaceae SM application is not only a function of the amount of glucosinolates in the SM but may be a result of soil microbial changes that are incited by SMs. When a composite of *B. juncea* and *B. napus* SM amendment was applied to the soil, a greater suppression of the apple replant disease pathogen complex (*R. solani*, *Pythium* spp. and the nematode *Pratylenchus* spp.) was achieved than with the use of the SMs from a single *Brassica* species (Mazzola et al., 2007). *B. juncea*, *B. napus* and *Sinapis alba* SMs suppressed the root infection by native *Rhizoctonia* spp. and an introduced isolate of *R. solani* AG 5. However, in certain experiments, *B. juncea* SMs generated a lower level of disease control relative to other SM types (Mazzola et al., 2007).

Various functional mechanisms have been ascribed to the Brassicaceae SM-induced soil-borne pathogen suppression. A rapid increase in microbial populations, which can include plant pathogenic soil fungi and oomycetes, following the incorporation of *Brassica* plant material has been reported (Grunwald et al., 2000; Manici et al., 2004; Cohen et al., 2005). It is not clear, however, if the quantity and type of glucosinolate hydrolysis products influence the microbial population dynamics contributing to soil-borne pathogen suppression.

The objective of this study was to evaluate the efficacy of the intact and autoclaved SMs of *B. napus*, *B. juncea* and *S. alba* as preplant soil amendments for the control of the Rhizoctonia root rot of wheat caused by *R. solani* AG-8.

2. Materials and methods

2.1. Seed meals

SMs produced from locally adapted and grown *S. alba* 'Ida Gold' (Brown et al., 1998), *B. juncea* 'Pacific Gold' (Brown et al., 2004) and *B. napus* 'Dwarf Essex' were used in this study. The glucosinolate analysis was conducted using the procedure described by Daun et al. (1989) and Daun and McGregor (1989). The glucosinolate content and profiles of the SMs are presented in Table 1. The utilized SMs were either intact or possessed an inactivated myrosinase enzyme that was made nonfunctional by autoclaving the SMs for 30 min, which were, therefore, referred to as denatured. The use of denatured SMs was used to test if the glucosinolate hydrolysis products play a role in the soil-borne pathogen suppression mechanism.

2.2. Effect of seed meals on wheat root infection by R. solani AG 8

R. solani AG 8 strain C-1 (Ogoshi et al., 1990) was cultured on 1/5th-strength potato dextrose agar (PDA). An oat grain inoculum of the pathogen was prepared as previously described (Wilkinson et al., 1985). The sandy loam soils used in this study were collected from the Columbia View Experimental Farm located 19.2 km north of East Wenatchee, WA. The soil was pasteurized at 80 °C for 24 h prior to use.

Pasteurized soil was weighed and either intact or denatured SMs were applied at a rate of 0.5% by soil weight and mixed until homogeneously distributed. The soils amended with intact or denatured Brassicaceae SMs were then dispensed into tapered plastic Cone-tainers (4 cm in diameter and 20.5 cm in length; Ray Leach Cone-tainer, Canby, OR, USA).

Each treatment consisted of seven Cone-tainers (Ray Leach Cone-tainer, Canby, OR, USA) and was replicated three times. Two *R. solani* AG-8-colonized oat grains were placed in the soil at a depth of 10 cm. The controls consisted of soil without Brassicaceae SM amendment. The experiment was arranged in a randomized complete block design. The study was conducted three times.

The soil-filled Cone-tainers (Ray Leach Cone-tainer, Canby, OR, USA) were incubated undisturbed for 7 d in a growth chamber set at 16 °C with 95% humidity and a 12 h photoperiod. After 7 d, two seeds of the winter wheat 'Brundage' (Zemetra et al., 1998) were placed on the soil surface, covered with 10 cm^3 of uninoculated pasteurized soil and watered with 10 ml of distilled water. The Cone-tainers (Ray Leach Cone-tainer, Canby, OR, USA) were suspended in their racks and covered with clear polyethylene to prevent the soil from drying. An additional 10 ml of distilled water was added to each Cone-tainer (Ray Leach Cone-tainer, Canby, OR, USA) 10 d after planting. After two weeks, the plants were washed free of soil and debris using a high-pressure stream of tap water before conducting root scans and disease assessments.

At seedling harvest, the shoot length, length of seminal and crown roots, number of seminal roots, seedling weight, root weight, total root length per plant, number of infected seminal roots and root rot disease rating data were collected. The root disease severity rating was based on a disease rating scale of 0–8 with the following criteria: 0 = no lesions, 1 = <50% of the roots with a single lesion, 2 = <50% of the roots with a few lesions each, 3 = >50% of the roots with one or more lesions each, 4 = <50% of the roots with lesions within 1 cm of the seed, 5 = >50% of the roots with lesions within 1 cm of the seed, 6 = >50% of the roots with terminal lesions less than 3 cm from the seed, 7 = >50% of the roots with terminal lesions less than 1 cm from the seed and 8 = 100% of the roots with terminal lesions less than 1 cm from the seed (Kim et al., 1997).

Table 1
Glucosinolate concentrations (μmol g^{-1} of defatted seed meal) in different types of Brassicaceae seed meals.

Glucosinolate type	*B. napus* 'Dwarf Essex'		*B. juncea* 'Pacific Gold'		*S. alba* 'Ida Gold'	
	Intact	Denatured	Intact	Denatured	Intact	Denatured
Allyl	–	–	164.3	134	–	–
3-Butenyl	33.5	28.8	0.8	0.7	–	–
4-Pentnyl	8.2	6.8	–	–	–	–
2-Hydroxy-3-butenyl	7	5.6	–	–	5.8	4.8
2-Hydroxy-4-pentenyl	4.2	3.4	–	–	–	–
2-Phenylethyl	1.4	1.2	0.7	0.6	–	–
4-Hydroxybenzyl	–	–	–	–	195.5	179.6
Total	54.3	45.8	165.8	135.3	201.3	184.4

Of the potential total of fourteen seedlings per treatment and per replication, only twelve seedlings were randomly selected for assessment because, in some cases, not all fourteen of the planted seeds emerged. The root systems of the twelve seedlings were individually digitally scanned using a Hewlett–Packard Scan Jet 5370C scanner (Regent Instruments Inc., Québec, Canada) and were also analyzed using WinRHIZO software (Regent Instruments Inc., Québec, Canada). This software calculated the total root length, diameter and number of root tips (Paulitz et al., 2003). Only the total root length from the WinRHIZO data output was used in the analysis.

2.3. Data analysis

The data collected from the *R. solani* AG 8 studies were subjected to an Analysis of Variance using SAS version 7.1 (SAS Institute Inc., Cary, N.C). The significant differences between the treatment means were examined using Fisher's protected LSD multiple range test (SAS Institute Inc., 1991). Bartlett's test of homogeneity of error variance was performed prior to combining the data from the three studies in the Analysis of Variance.

3. Results

3.1. Seed meal glucosinolate content analysis

The *B. juncea* and *S. alba* SMs used in this study contained more than 40% and 36% higher total glucosinolate content, respectively, than *B. napus* SMs (Table 1). The primary glucosinolate in *B. juncea* SMs was allyl glucosinolate, accounting for more than 99% of the total 176 μmol g^{-1} in the defatted SMs. The primary glucosinolate type in *S. alba* SMs was 4-hydroxybenzyl glucosinolate, accounting for more than 96% of the total. Both mustard species produced low concentrations of 2-hydroxy-3-butenyl glucosinolate. The major glucosinolate types in *B. napus* SMs were 2-hydroxy-3-butenyl and 3-butenyl glucosinolate. Allyl glucosinolate was only present in *B. juncea* SMs, while 4-hydroxybenzyl glucosinolate was found only in *S. alba* SMs. The primary reason for denaturing the SMs was to denature the enzyme myrosinase. The catalytic action of the enzyme myrosinase on SMs in the presence of water results in the release of glucosinolates. On average, all the denatured SMs contained approximately 10% less glucosinolate than their intact SM forms.

3.2. Effect of seed meal amendments on seedling root and shoot growth

The number of seminal roots per plant was reduced for seedlings grown in soil amended with intact *S. alba* SMs (Table 2). Wheat seedlings grown in soils amended with any of the intact or denatured SMs exhibited fewer crown and total roots per plant relative to the no-SM control (Table 2). The root weight of the seedlings grown in soils amended with intact *S. alba* SMs was 67% less than that of the seedlings from the un-amended controls. The smallest total root length per plant was observed in the seedlings grown in soils amended with denatured *S. alba*, *B. juncea* SMs or intact *S. alba* SM.

The shoot length of the wheat seedlings grown in soils amended with denatured *B. juncea* or *S. alba* SMs was similar to that of seedlings grown in un-amended soils. Intact *B. napus*, denatured *B. napus* and intact *B. juncea* SM amendment resulted in a significant ($P < 0.001$) increase in seedling shoot length. Seedlings grown in intact *S. alba* SM-amended soils had a significantly shorter shoot length, which was 65% shorter than seedlings from the un-amended soil control (Table 2).

3.3. Effect of seed meal amendments on the suppression of R. solani AG-8

Seedlings grown in soils amended with intact *S. alba* SMs had the lowest number of *R. solani* AG-8-infected seminal roots and the lowest disease rating scores of the treatments (Table 3). The intact *B. napus* and *B. juncea* SMs significantly reduced the disease severity by 71% compared to seedlings grown in the no-SM control. The intact *S. alba* and *B. juncea* SMs had significantly lower disease rating scores than their denatured SM forms.

4. Discussion

The primary reason for denaturing the SMs was to denature their myrosinase enzymes. The catalytic action of the enzyme myrosinase on SM in the presence of water results in the release of glucosinolates.

R. solani AG 8 infection was significantly reduced in the soils amended with denatured SMs, which may suggest that a mechanism other than that involving the glucosinolate hydrolysis products was responsible for the disease suppression. The denatured SMs contain the denatured myrosinase enzyme; therefore, they released little-to-no hydrolysis products compared to the intact SMs. Another possibility is that the myrosinase enzyme existed in the pasteurized soils, causing the hydrolysis of the denatured SMs to release the glucosinolate hydrolysis products, resulting in the fungicidal properties of the SM amendments.

All the SM amendments provided some level of protection to the wheat seedlings with respect to the percentage of infected seminal roots and disease score ratings. These results are in agreement with the findings of Mazzola et al. (2007), who reported that all the SMs suppressed root infection by native *Rhizoctonia* spp. and an introduced isolate of *R. solani* AG 5. *S. alba* SMs significantly reduced the number of infected seminal roots when compared to the *B. napus* and *B. juncea* SM-amended soils. *B. juncea* SMs have been reported to generate a lower level of disease control than other SM types

Table 2
Root and shoot growth in wheat seedlings grown in soils inoculated with *R. solani* AG-8 and amended Brassicaceae seed meals.

Seed meal type	Meal treatment	Number of seminal roots	Number of crown roots	Total number of roots	Shoot length (cm)	Seedling weight (g)	Root weight (g)	Total root length/ plant (cm)
No meal		4.0a[a]	1.3a	5.9a	16.0c	0.308bc	0.253a	101.1ab
B. napus	Intact	4.1a	0.8b	4.9b	19.8a	0.512a	0.223ab	123.3a
	Denatured	3.7a	0.8b	4.5b	18.6ab	0.380b	0.156abc	107.8ab
B. juncea	Intact	3.6a	0.6bc	4.2bc	19.2ab	0.341bc	0.120abc	78.8bc
	Denatured	3.5ab	0.5bc	4.0bc	17.2bc	0.331bc	0.134abc	55.0cd
S. alba	Intact	3.0b	0.3c	3.3c	5.6d	0.130d	0.044c	32.0d
	Denatured	4.1a	0.7b	4.8b	17.3bc	0.252c	0.084bc	29.0d
SE mean		0.2	0.1	0.2	0.6	0.03	0.02	13.7

[a] Means followed with different letters in a column are significantly different ($P < 0.05$).

Table 3
Severity of Rhizoctonia root rot of wheat in soils inoculated with *R. solani* AG-8 and amended with Brassicaceae seed meals.

Seed meal type	Meal treatment	Number of infected seminal roots	Percentage number of infected seminal roots	Disease rating (0–8)
No meal		3.9a[a]	98.0a	4.8a
B. napus	Intact	3.3ab	77.6b	2.8c
	Denatured	3.1b	84.0b	3.4bc
B. juncea	Intact	3.0b	82.9b	2.8c
	Denatured	3.0b	84.5b	3.6b
S. alba	Intact	1.7c	55.2c	1.4d
	Denatured	3.3ab	80.4b	3.4bc
SE mean		0.22	4.39	0.20

[a] Means followed with different letters in a column are significantly different ($P < 0.05$).

(Mazzola et al., 2007). However, in our study, this observation was true only when *B. juncea* was compared to the *S. alba* SM amendment. A possible reason for this result could be related to the observation that the disease control was achieved when *B. juncea* SMs and *R. solani* were introduced into a soil system simultaneously, but no disease control was detected if the pathogen infestation was delayed until 24 h post SM amendment (Mazzola et al., 2007). In our study, *B. juncea* SMs and *R. solani* were introduced into the planting pots simultaneously.

The glucosinolate levels of intact *B. juncea* SMs are higher than those of intact *B. napus* SMs and yet, they achieved the same level of root rot disease suppression; thus, the argument that fungicidal properties are only a function of glucosinolate levels does not hold with respect to the findings in this study. This finding is in agreement with the belief that, in soils amended with *B. juncea* SMs, the initial disease control was directly related to the release of glucosinolate hydrolysis products; however, long-term disease control in response to *B. juncea* SM amendment required the activity of the microbial community present in the amended soil (Weerakoon et al., 2012). This belief suggests that an alternative mechanism enables *B. napus* SMs to elicit the same efficacy as the higher glucosinolate content of the *B. juncea* SM amendment. These mechanisms may be directly or indirectly associated with the glucosinolate hydrolysis products. More recently, disease control has been related to functional mechanisms other than allelochemicals, occurring as a consequence of green manures or SM incorporation and attributed to the stimulation of resident streptomycetes or actinomycetes (Mazzola et al., 2007; Wiggins and Kinkel, 2005). The differences observed between SM types may be partially accounted for by the fact that different AGs of *R. solani* have varying degrees of sensitivity to allyl glucosinolate (Smith and Kirkegaard, 2002), implying that the different glucosinolate profiles and contents in the Brassicaceae SMs may have affected the suppression of *R. solani* differently.

The incorporation of SMs into the soil involves an enrichment in the carbon source that may alter or even stimulate the resident or introduced beneficial or pathogenic microflora (Mazzola et al., 2001). This enrichment may explain why the seedlings grown in soils amended with relatively low glucosinolate-containing SMs had the highest seedling weights. On the contrary, the parameters of root and shoot growth of wheat seedlings grown in soils amended with high glucosinolate-containing Brassicaceae SMs were negatively impacted, suggesting that these amendments may inhibit root growth. Interestingly, seedlings grown in soils that were not amended with SMs had the highest number of seminal and crown roots when compared to seedlings grown in SM-amended soils.

Brassicaceae SMs were effective in managing *R. solani* AG 8 in wheat. However, future studies will need to focus on strategies for diminishing the crop growth-inhibiting effects associated with Brassicaceae SMs, especially intact *S. alba* SMs, which were observed to have the most efficacy in reducing Rhizoctonia root rot severity in this study. Overcoming these crop growth-inhibiting effects of high glucosinolate-containing SMs will ensure the full maximization of the fungicidal benefits available from Brassicaceae SM amendments. Such utilization of Brassicaceae SMs could possibly be extended to high-value crops that are affected by *R. solani* AG 8. The management of onion stunt is difficult and to date, no satisfactory control strategies have been developed (Wicks and Walker, 2010). The use of Brassicaceae SMs to manage *R. solani* AG 8 has the potential to be used in the management of onion stunt disease as well as in organic wheat farming systems where *R. solani* AG 8 management options are limited.

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