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Induction of resistance to *Phakopsora pachyrhizi* in soybean using proteins from *Pycnoporus sanguineus*

Indução de resistência em soja contra *Phakopsora pachyrhizi* usando proteínas de *Pycnoporus sanguineus*

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Highlights

Pycnoporus sanguineus gel filtration chromatography revealed five protein peaks.
Protein III reduced by 46.1% the number of uredia per pustule of *P. pachyrhizi.*
The number of lesions per cm^2 was reduced in leaves treated with protein III.
P. sanguineus is promising in controlling *P. pachyrhizi* in soybean.

Abstract

Asian soybean rust (*Phakopsora pachyrhizi*) is an important disease, and the induction of resistance is a promising alternative method for its control. The objective was to evaluate proteins isolated from the *Basidiomycota Pycnoporus* sanguineus to control soybean rust. The treatments consisted of three proteins (III, IV, and V), a non-fractionated extract (crude extract - CE) of *P. sanguineus,* the fungicide tebuconazole, and water. The proteins did not show any inhibition of spore germination. Protein III and the CE reduced the number of lesions only on treated leaves. Thus, *P. sanguineus* contains non-fungitoxic protein capable of locally inducing resistance in soybean against *P. pachyrhizi.*
Key words: Antimicrobial activity. Basidiomycota. Chromatography. *Glycine max.* Soybean rust.

Resumo

A ferrugem asiática da soja (*Phakopsora pachyrhizi*) é uma doença importante da cultura, e a indução de resistência é um método alternativo promissor para seu controle. O objetivo do trabalho foi avaliar proteínas isoladas do fungo *Basidiomycota Pycnoporus* sanguineus para controle da ferrugem asiática.

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Os tratamentos consistiram em três proteínas (III, IV e V), um extrato não fracionado (extrato bruto - CE) de *P. sanguineus,* fungicida tebuconazol e água. As proteínas não mostraram nenhuma inibição na germinação de esporos. A proteína III e o CE reduziram o número de lesões somente em folhas tratadas. Portanto, *P. sanguineus* possui proteína não fungitóxica que é capaz de induzir resistência local na soja contra *P. pachyrhizi.*

Palavras-chave: Atividade antimicrobiana. Basidiomycota. Cromatografia. Ferrugem da soja. *Glycine max.*

Introduction

Soybean (*Glycine max* (L.) Merr.) is one of the most widely produced crops in the world and has great economic and social value. Brazil is among the world's main grain producers, with an increase in cultivated area of 4.9% in the last year and production of approximately 151 million tons, a value 20.6% higher than the previous harvest (Companhia Nacional de Abastecimento [CONAB], 2023). However, soybean is affected by several diseases, such as rust, which reduce productivity and increase production costs due to the intensive use of fungicides (Pelin et al., 2020).

Rust, caused by the fungus *Phakopsora pachyrhizi* H. Sydow & P. Sydow, is considered the most severe disease in soybean, causing significant production losses (Langenbach et al., 2016). Symptoms are initially characterized by small, tan-colored lesions containing uredinia that release numerous urediniospores; under favorable environmental conditions, lesions increase in number and size, leading to intense plant defoliation (Rosa et al., 2015).

Fungicides are the most commonly used control method due to the lack of resistant cultivars that are immune to the pathogen (Godoy et al., 2016). However, the continuous use of pesticides can cause several problems, such as environmental contamination and effects on non-target microorganisms, in addition to the selection of pathogen populations resistant to active ingredients (Klosowski et al., 2016). In this context, the induction of resistance becomes a viable alternative for the control of phytopathogens (Stangarlin et al., 2011).

Resistance induction is the activation of latent defense mechanisms in plants through the application of an inducing agent containing molecules that elicit resistance genes (Pascholati & Dalio, 2018). Plants use physical and/or biochemical constitutive and induced defense responses to protect themselves against pathogen infection, such as phenolic compounds and phytoalexins, cell wall lignification, and pathogenesis-related proteins. Induced defense may occur locally at the treatment site or systemically through signaling pathways mediated by salicylic and jasmonic acids (Mejri et al., 2021).

Pycnoporus sanguineus (Fries) Murrill is a basidiomycete fungus, a saprophyte that forms sessile, woody basidiocarps, orange-red in color (Téllez-Téllez et al., 2016). Extracts of *P. sanguineus* have induced resistance in pathosystems involving fungi, bacteria, and nematodes, such as *Colletotrichum lindemuthianum* (Baldo et al., 2011), *Pseudocercospora griseola* (Viecelli et al., 2009, 2010), and *Xanthomonas axonopodis* pv. phaseoli (Toillier et al., 2010) in common bean, and Xanthomonas vesicatoria (Assi et al., 2017), Alternaria solani (Alencar et al., 2020), and *Meloidogyne javanica* (Barbosa et al., 2021) in tomato.

This study aimed to evaluate the potential of proteins from P. sanguineus basidiocarps, obtained by gel filtration chromatography, to induce soybean resistance against rust.

Material and Methods

Aqueous extract of P. sanguineus

Basidiocarps of *P. sanguineus* (Brazilian Protocol SISGEN no. AF83853) were produced on a solid substrate and harvested 50 days after inoculation (Portz et al., 2025). They were then dried in an oven at 40 ºC for 2 h and ground using a knife mill (Baldo et al., 2011). To obtain the aqueous extract, dry powder of P. sanguineus basidiocarps was hydrated for 24 h at 4 °C in sterile water at a ratio of 14 mL per gram of powder (Di Piero et al., 2006). After this period, the mixture was filtered through qualitative filter paper with an 11 µm pore diameter and subsequently through a 0.22 µm membrane. The resulting solution was referred to as crude extract (CE).

Gel filtration chromatography (GFC)

For gel filtration chromatography, a glass column (1 cm × 60 cm) filled with Sephacryl S-100-HR (Sigma) was used, forming a sedimented gel. One milliliter of CE was applied to the column and eluted with 10 mM Tris-HCl buffer (pH 8.0), with 1 mL fractions collected at a flow rate of 1 mL min^{-1}. Proteins in the fractions were monitored using a spectrophotometer at 280 nm, and the presence of carbohydrates was determined according to Lever's method (Lever, 1972).

The relative molecular mass of each detected protein was estimated using the calibration curve $y = 8867.4^{e-3.231x}$ (Gonçalves-Trevisoli et al., 2016), obtained for this column considering the molecular masses (y value of the equation in KDa) of thyroglobulin (670 KDa), globulin (158 KDa), ovalbumin (44 KDa), myoglobin (17 KDa), and vitamin B12 (1.35 KDa), and the ratio between elution volume (Ve) and void volume (Vo) (x value of the equation). The void volume was determined using blue dextran (2000 KDa) (Vo = 26 mL).

Control of rust in soybean

Soybean seeds were sown in 4-L pots containing soil, organic matter, and sand (2:2:1). The third leaf was treated at the V5 phenological stage, and 72 h after treatment, the third (treated) and fourth (untreated) leaves were inoculated with 8×10^4 uredospores mL^{-1} of *P. pachyrhizi.* Treatments included four fractions from GFC: proteins III (3.44 KDa), IV (2.79 KDa), and V (1.82 KDa), and a carbohydrate fraction; crude extract (CE); tebuconazole fungicide (0.5 g active ingredient L^{-1}); and water. These proteins and the carbohydrate fraction were selected due to the available quantity (solution volume) being sufficient for the assays, unlike peaks I and II, which had very small volumes.

Severity was assessed 10 days after inoculation, when plants showed visible symptoms of the disease. Treated and inoculated leaves (third leaf) and only inoculated leaves (fourth leaf) were collected, and the number of lesions per cm^2 was counted, along with the number of uredia per lesion.

Antimicrobial activity

Antimicrobial activity was evaluated microscopically by assessing the germination of *P. pachyrhizi* uredospores. Spores were obtained from inoculum donor soybean plants maintained in a greenhouse. A total of 50 µL of a suspension containing $1x10^4$ uredospores mL^{-1} and 50 µL of the treatments (the same as in the rust control assay) were applied to a Petri dish containing 1% water-agar. The plates were incubated at 23 ºC in the dark, and germination percentage was determined after 18 h by adding lactophenol cotton blue to stop germination, followed by observation under an optical microscope.

Analysis of results

The trials were conducted in a completely randomized design with four replicates. Each experimental unit was represented by a Petri dish with a slide for the antimicrobial activity assays or a pot with two plants for the rust control assays. The data were assessed for normality using the Shapiro-Wilk test and for homogeneity of variances using Levene's test. Data that met the assumptions were subjected to analysis of variance (ANOVA). When the ANOVA indicated a significant effect, treatment means were compared using Tukey's test ($P < 0.05$) with Sisvar software (D. F. Ferreira, 2011).

Results

Gel filtration chromatography (GFC)

Gel filtration chromatography (GFC) of the aqueous extract (AE) of *P. sanguineus* fractionated five protein peaks (I, II, III, IV, and V), with molecular masses of 5.18, 3.87, 3.44, 2.79, and 1.82 KDa, respectively, in addition to one carbohydrate peak (Figure 1). Due to the small quantity (solution volume) obtained for protein peaks I and II, only the remaining fractions were used in the assays.

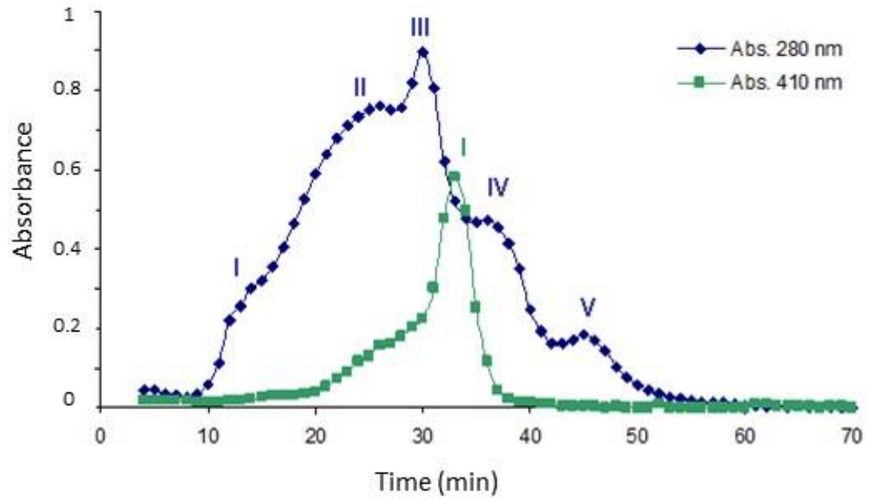

Figure 1. Gel filtration chromatography of the aqueous extract of *Pycnoporus sanguineus.* Protein and carbohydrate peaks identified by absorbance at 280 nm and 410 nm, respectively.

Antimicrobial activity

There was no direct toxicity of GFC fractions to *P. pachyrhizi* spores (Table 1), with an average inhibition of uredospore germination of 1.75%, which was statistically similar to water control and differed only from the fungicide tebuconazole, which completely inhibited spore germination.

Table 1
Germination of *Phakopsora pachyrhizi* uredospores. Proteins III, IV, and V and carbohydrate are fractions obtained by gel filtration chromatography (GFC) from aqueous extract of *Pycnoporus sanguineus* basidiocarps

Treatment	Spore germination (%)
Protein III	98 b[1]
Protein IV	98 b
Protein V	99 b
Carbohydrate	98 b
Crude extract	99 b
Tebuconazole	0 a
Water	96 b
CV (%)	11.68

[1]Means followed by the same letter do not differ from each other using the Tukey test at 5% probability.

Control of rust in soybean

For the treated and inoculated leaf (third leaf) (Figure 2a), a reduction in the number of rust lesions per cm² was observed for treatments with protein III (3.44 KDa) and crude extract, both not differing from tebuconazole (only these three treatments differed from water). For the fourth leaf (untreated), there was no difference among treatments (Figure 2b).

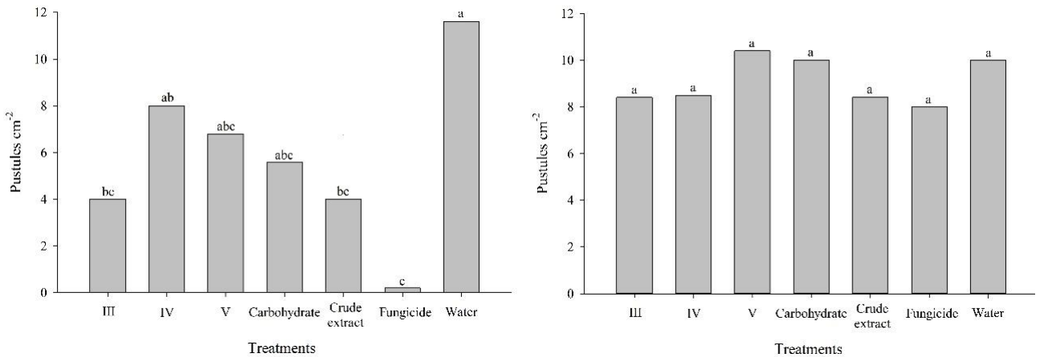

Figure 2. Number of pustules per cm² of rust on the third leaf of soybean plants treated with fractions of *Pycnoporus sanguineus* and inoculated with *Phakopsora pachyrhizi* (a), and on the fourth leaf only inoculated (b). Means followed by the same letters do not differ according to the Tukey test at 5% probability. CV (%) = 41.30. Proteins III, IV, and V and carbohydrate are fractions obtained by gel filtration chromatography (GFC). Fungicide: tebuconazole (0.5 g L^{-1}).

Regarding the number of uredia per pustule, for the third leaf (treated and inoculated) (Figure 3a), a reduction was observed only for protein III and tebuconazole compared to the water treatment. There was an average reduction of 46.1% in the number of uredia per pustule compared with the water treatment. In the fourth leaf (only inoculated) (Figure 3b), no differences were observed among treatments.

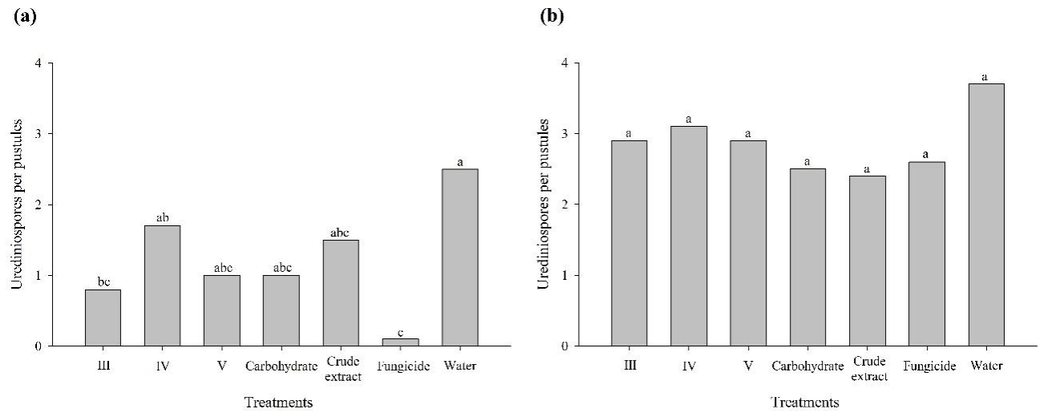

Figure 3. Number of uredia per rust pustule on the third leaf of soybean plants treated with fractions of *Pycnoporus sanguineus* and inoculated with *Phakopsora pachyrhizi* (a), and on the fourth leaf only inoculated (b). Means followed by the same letters do not differ according to the Tukey test at 5% probability. CV (%) = 32.33. Proteins III, IV, and V and carbohydrate are fractions obtained by gel filtration chromatography (GFC). Fungicide: tebuconazole (0.5 g L^{-1}).

Discussion

Gel filtration chromatography (GFC)

Five protein fractions and one carbohydrate fraction were eluted from the GFC of the *P. sanguineus* extract. A similar number of proteins was reported by Di Piero et al. (2006), who identified six protein fractions from the aqueous extract of *Lentinula edodes,* a basidiomycete that also has elicitor potential for disease control in plants. In *L. edodes,* the protein with biological activity had a molecular mass of 29 kDa. In *P. sanguineus,* proteins purified from basidiocarps showed low molecular masses, ranging from 1.82 to 5.18 kDa. Antifungal molecules of a protein nature with low molecular mass have also been identified in other microorganisms, such as a 1.2 kDa peptide and its analogues occidiofungin and burkholdine, isolated from *Burkholderia* sp., capable of inhibiting the growth of *Ganoderma boninense* (Prihatna et al., 2022).

Antimicrobial activity

The low inhibition of *P. pachyrhizi* uredospore germination by treatments with GFC fractions indicates the absence or low antimicrobial activity of *P. sanguineus;* however, this characteristic may depend on the pathogen species. Viecelli et al. (2010) found that aqueous extracts of *P. sanguineus* mycelium inhibited the germination of *Pseudocercospora griseola* conidia. Antimicrobial activity was also observed against *Colletotrichum lindemuthianum,* with 97% inhibition of conidial germination (Baldo et al., 2011). Specifically for rust-causing fungi, Baldo et al. (2008) reported 79% inhibition of

Phakopsora euvitis uredospore germination and 87% for *Uromyces appendiculatus.* Similarly, for bacterial pathogens, the multiplication of *Xanthomonas axonopodis* pv. phaseoli was reduced by up to 91% by *P. sanguineus* basidiocarp extract (Toillier et al., 2010).

The method used to obtain the extract can also interfere with antimicrobial activity. The *in vitro* activity of cold, hot, and ultrasonic hydroalcoholic extracts of *P. sanguineus* was evaluated against *Fusarium* sp., causing an inhibition of conidial germination ranging from 34% to 92%, depending on the extraction method (Figueiredo & Silva, 2014).

The biological activity of these proteins may also vary depending on the genus of the basidiomycete. In *Hypsizygus marmoreus,* two proteases of 30.2 and 33.7 kDa were identified that reduced the viability of *Panagrellus redivivus* by up to 52% (Soares et al., 2019). In Flammulina velutipes (J. M. Ferreira et al., 2019) and *Pleurotus eryngii,* proteases and chitinases have been identified in fungal filtrates with activity against nematodes (Sufiate et al., 2017).

In this study, the unfractionated aqueous extract of *P. sanguineus* also did not show antifungal activity against *P. pachyrhizi,* despite the known presence of compounds with antimicrobial potential, such as phenoxazines (Li et al., 2007) and phenolic compounds (I. C. F. R. Ferreira et al., 2009; Degenkolb & Vilcinskas, 2016).

Control of rust in soybean

The number of lesions per cm^2 was reduced by up to 66% in leaves treated with protein III (3.44 KDa) and by up to 64% with CE; however, no systemic effect of these treatments was observed. The systemic effect of resistance induction depends on the pathosystem. The severity of angular leaf spot in common beans was reduced by 82%, both locally and systemically, following treatment with *P. sanguineus* extracts (Viecelli et al., 2010). Another example of the systemic resistance-inducing effect of *P. sanguineus* is its control of the root-knot nematode *M. javanica,* in which the aqueous extract of basidiocarps was sprayed weekly on tomato leaves, resulting in 90% control. This clearly indicates a systemic effect, as there was no direct contact between the extract and the nematodes or infected roots (Barbosa et al., 2021).

This potential for plant disease control by *P. sanguineus* has also been observed in other pathosystems. In tomato plants infected with *Alternaria solani* and *Xanthomonas vesicatoria*, there was a 58% reduction in the area under the disease progress curve (Assi et al., 2017).

Similarly, other basidiomycetes have demonstrated this eliciting effect, such as *Agaricus blazei* (Silva et al., 2008) and *Lentinula edodes* (Silva et al., 2007) in controlling bacterial wilt caused by *Ralstonia solanacearum* in eggplant and tomato, respectively. For the basidiomycete *Ganoderma* sp., there are also studies on disease control in plants, such as the use of mycelial extracts to control powdery mildew in soybean (Cruz et al., 2019), Fusarium wilt in cotton (Zhang et al., 2019), viral diseases (Sangeetha et al., 2020), and Septoria leaf spot in tomato (Cruz et al., 2022).

Reactive oxygen species may be a plant defense mechanism involved in the

resistance induced by *P. sanguineus* in soybean. Hydrogen peroxide (H_2O_2) was detected in common bean leaf tissue 48 h after inoculation with *Colletotrichum lagenarium* only in treatments with basidiocarp aqueous extract of *P. sanguineus,* while superoxide (O_2^-) was mainly detected in treatments with *P. sanguineus* mycelial extract 48 h after inoculation (Baldo et al., 2011). An increase in antioxidative metabolism, including elevated activities of superoxide dismutase, ascorbate peroxidase, catalase, peroxidase, and glutathione reductase, in hexanoic acid-treated plants helped reduce hydrogen peroxide and superoxide anion accumulation in soybean leaves infected with *P. pachyrhizi* (Rodrigues et al., 2023), indicating the involvement of an oxidative burst in the signaling process during resistance induction in this pathosystem. Additional assays are being conducted by our group to elucidate the interaction between *P. pachyrhizi* and soybean plants treated with *P. sanguineus* proteins.

Conclusion

Pycnoporus sanguineus has non-fungitoxic proteins capable of locally inducing resistance in soybean against *P. pachyrhizi.*

Declaration of competing interest

The authors declare that they have no conflict of interest.

Data availability

Data will be made available on request.

Acknowledgments

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