Saccharin-induced systemic acquired resistance against rust (*Phakopsora pachyrhizi*) infection in soybean: Effects on growth and development

Pratibha Srivastava a,*, Sheeja George a, James J. Marois a, David L. Wright a, David R. Walker b

a University of Florida, North Florida Research and Education Center, Quincy, FL 32351, USA
b USDA-ARS, Soybean/Maize Germplasm, Pathology and Genetics Research Unit, Urbana, IL 61801, USA

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**A B S T R A C T**

We examined the effect of saccharin on the systemic acquired resistance (SAR) response of soybean to the fungus *Phakopsora pachyrhizi*, the causal agent of soybean rust. Plants were grown hydroponically in half-strength Hoagland’s solution and were challenged with the pathogen 1, 5, 10 and 15 d after treatment with 3 mM saccharin applied either as a foliar spray or a root drench at the 2nd trifoliate (V3) and early reproductive (R1) stages. Plants were destructively harvested and assessed for visible rust symptoms 2 wk after inoculation. Mode of saccharin application was a significant factor influencing the severity of rust infection. Saccharin applied as a root drench was more effective than the foliar spray treatment at inducing SAR, with increased resistance observed 1 d after application. Systemic protection against rust infection was still apparent 15 d after application of saccharin as a root drench. In contrast, foliar treatment with saccharin did not increase systemic protection until 15 d after treatment. When systemic protection was induced by the application of saccharin in either manner, there was no significant reduction of plant growth, except when plants were inoculated 15 d after the saccharin application as a root drench at the R1 stage of development.

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1. Introduction

Systemic acquired resistance (SAR) is a broad-spectrum defense system that is activated in plants upon challenge by certain pathogens and in response to other environmental stimulants. SAR is effective predominantly against biotrophic pathogens, and is controlled by a signaling pathway that depends on accumulation of salicylic acid (SA) (Walters et al., 2009). Many instances have been reported in which pathogen infection of the lower leaves of a plant induced a resistance response in the upper leaves (Kuc, 1982). Following induction of SAR, the plant is generally resistant to a wide range of pathogens for a period of weeks or months (Ward et al., 1991). The induction of SA signaling and SAR is associated with accumulation of pathogenesis related (PR) proteins such as beta-1,3-glucanases, thaumatin, chitinases and PR1, which are thought to contribute to resistance (Van Loon, 1997). Many of the PR proteins have antimicrobial activity in vitro, but their roles in the establishment of SAR are unclear. However, they serve as molecular indicators for the onset of the defense response (Van Loon, 1997; Durrant and Dong, 2004). Following the activation of SAR, plants resist pathogen attack or slow down pathogen growth by mobilizing a variety of biochemical and molecular defenses (Bowles, 1990).

Establishment of SAR requires an endogenous increase in SA levels (Ryals et al., 1996; Sticher et al., 1997; Dempsey et al., 1999) and its onset is associated with the expression of SAR genes (Ryals et al., 1996), some of which encode PR proteins (Ryals et al., 1996; Sticher et al., 1997; Dempsey et al., 1999). Some PR proteins display antimicrobial activity in vivo (Van Loon and Van Strien, 1999) but their actual role in SAR remains uncertain. Activation of SAR by pathogens has been effective in several plant–pathogen interactions, i.e., common bean infected by *Colletotrichum lindemuthianum* (Dann and Deverall, 1995), Arabidopsis infected by avirulent pathotypes of *Pseudomonas syringae* (Alvarez et al., 1998) and pea infected with an avirulent strain of *Pseudomonas syringae*.

Plant defense responses are a result of a complex network of signaling events that involves the interplay of kinases, hormones, and reactive oxygen species (ROS), leading to reprogramming of the plant transcriptome and the production of defensive compounds to affect resistance. Modifications of signaling components can expedite defense activation upon pathogen attack, thus improving the chances of the plant to successfully respond to current and future encounters with pathogens. In addition to protection conditioned by genes, plant resistance can also be improved by the use of nontoxic chemical substances that elicit the activation of...
natural defense mechanisms (Conrath et al., 2002; Kohler et al., 2002). Knowledge about plant–pathogen interactions could lead to solutions for achieving broad-spectrum protection, long-lasting effects and reduction in pesticide use.

A number of compounds have been identified to induce SAR, including synthetic chemicals such as β-aminobutyric acid, iso-nicotinic acid (INA), benzo[1,2,3] thiadiazol-7-carbothioic acid-S-methyl ester (BTH) and acibenzolar-S-methyl (ASM, a derivative of BTH). Saccharic acid and phosphates have also been shown to be activators of the SAR response in a variety of host–pathogen systems (Cohen, 2001; Oostendorp et al., 2001; Bokshi et al., 2003; Edreva, 2004; Vallad and Goodman, 2004). The synthetic compound probenazole induces SAR, and has been used to control rice blast (Magnaporthe grisea) and bacterial blight (Xanthomonas oryzae pv. oryzae) (Watanabe et al., 1979). Probenazole and its active metabolite 1,2-benzisothiazole-1,1-dioxide induce SAR in Arabidopsis by stimulating a site upstream of the point of accumulation of SA in the SAR-signaling pathway (Yoshioka et al., 2001). Probenazole enhances some of the resistance mechanisms associated with an oxidative burst that occurs after infection by the rice blast agent (Gozzo, 2003). It also induces the accumulation of unsaturated fatty acids that act as antioxidant factors (Kessmann et al., 1994). Probenazole has been reported to function upstream of SA in Arabidopsis (Iwai et al., 2007) and tobacco (Iyon, 2007). Saccharin (C₇H₅NO₃S) is a metabolite of probenazole (Uchiyama et al., 1973) that is able to induce SAR in rice to improve control of Magnaporthe grisea and Xanthomonas oryzae, possibly via the induction of host defenses, since saccharin has been shown to induce SAR (Oostendorp et al., 2001; Siegrist et al., 1997).

Previous observations have highlighted the potential of saccharin to activate SAR against tobacco mosaic virus (TMV) in tobacco, Colletotrichum lagenarium in cucumber, Uromyces appendiculatus in bean (Siegrist et al., 1998), U. fabae in Vicia faba (Boyle and Walters, 2005) and to the powdery mildew Blumeria graminis f. sp. hordei in barley (Boyle and Walters, 2006) by triggering signaling at a point upstream of SA accumulation. A large number of mechanisms are involved in biocontrol and can involve direct antagonism via production of antibiotics, siderophores, HCN, hydrolytic enzymes (chitinases, proteases, lipases, etc.), or indirect mechanisms in which the biocontrol organisms act in a probiotic fashion by competing with the pathogen for infection and nutrient sites. Biocontrol can also be mediated by activation of SAR by modification of hormonal levels (Bowen and Rovira, 1999; Van Loon, 2007) in the plant tissues.

Soybean rust (SBR), caused by Phakopsora pachyrhizi Syd. & P. Syd., is a serious disease of legumes that can cause devastating yield losses in soybean (Glycine max (L.) Merr). It was first reported in the Eastern Hemisphere more than a century ago (Ogle et al., 1979). In recent decades, the disease has spread to Hawaii (Killgore and Heu, 1994), Africa (Kawuki et al., 2003), South America (Yorinori et al., 2002) and North America (Schneider et al., 2005). P. pachyrhizi differs from most other rust fungi in having a large number of legume hosts (Slaminko et al., 2008).

The objective of this study was to examine the effectiveness of saccharin as an inducer of SAR against P. pachyrhizi in soybean plants. The study also examined the effects of saccharin and saccharin-induced SAR on plant growth.

2. Materials and methods

2.1. Plant materials

The soybean (Glycine max) cultivars Williams 82 and Benning were used. Williams 82 is a maturity group (MG) III cultivar from the Midwest (Bernard and Creemens, 1988), and Benning is an MG VII cultivar developed at the University of Georgia (Boerma et al., 1997). Both of these cultivars are susceptible to soybean rust, including isolates from Quincy, FL (unpublished data). Seeds from the two cultivars were germinated in a medium containing peat and perlite and maintained in a greenhouse at 75 ± 2 °C and 80% humidity. Plants used in the experiments were grown in a hydroponic system (Srivastava et al., 2009). The substrate used to stabilize the plants was rock wool placed in a plastic net pot that was suspended directly in the nutrient solution. An air pump supplied air to an air stone that aerated the nutrient solution and supplied oxygen to the roots of the plants. At the seedling stage, plants were transferred to a continuously aerated 1 L hydroponic container (1 L Nalgene® large polypropylene amber wide-mouth bottles). Each container contained a single plant that was supplied with half-strength Hoagland’s nutrient solution (Hoagland and Arnon, 1950). A 2009 P. pachyrhizi isolate from Quincy, Gadsden County, Florida was maintained on soybean plants in the greenhouse as a source of inoculum, anduredinisporae were collected fresh from leaves of those plants during the days preceding inoculation and were stored at 4 °C until used.

2.2. Saccharin applications to leaves or roots

Saccharin (MP Biomedicals, LLC) was applied as either a root drench or sprayed onto the foliage. For the root drench, each plant received either 30 ml of 3 mM saccharin in deionized water or 30 ml deionized water (as the control) in 1 L half-strength Hoagland’s solution. For the foliar application, at V3 (2nd trifoliate fully expanded leaf) and R1 (first bloom) stage (Fehr et al., 1971) the first fully expanded trifoliate leaf of each plant was treated with 3 mM saccharin or deionized water (for control) using a spray bottle (Fisher brand adjustable-spray wash bottle) until runoff occurred. After addition of saccharin to the nutrient medium, nutrient solution lost via transpiration and uptake was replenished by frequent additions of half-strength Hoagland’s solution to maintain a constant volume.

2.3. Inoculation with P. pachyrhizi

Plants were challenged at 1, 5, 10 and 15 d after treatment (DAT) with saccharin. Auredinisporae suspension (8000 spores/ml deionized water) was applied to the leaves using a hand sprayer (PORTER-CABLE 6-Gallon Air Compressor - Model #: C2002-WK, Porter-Cable Corporation Jackson, TN). Inoculated plants were placed in the vicinity of a humidifier for 24 h to promote uredinisporae germination. Plants were harvested and assessed for visible soybean rust symptoms 2 weeks after inoculation.

2.4. Assessment of the induced disease resistance

Two weeks after inoculation, plants were assessed for disease severity (DS) using a 1–9 scale based on the series of photos in the “Asian Soybean Rust Disease Severity Evaluation Scale” developed by Bayer CropScience (Bayer CropScience, Research Triangle Park, NC). A rating of 1 was assigned to plants showing no visible symptoms and a rating of 9 indicated 67.5–100% disease severity. Sporulation was also rated using a 9-point scale in which a rating of 1 was assigned to plants showing no sporulation and a rating of 9 indicated that 90–100% uredinia were sporulating.

2.5. Biomass analysis

For growth measurements, plant heights were measured and numbers of fully matured leaves were counted. Fresh weights of shoots and roots were determined immediately after harvest, and
thereafter shoots and roots were dried in an oven at 60 °C for 48 h before dry weights were determined.

2.6. Statistical analyses

The experiment was set up as a completely randomized factorial design comprised of 3 treatments × 2 genotypes × 2 plant developmental stages × 4 DAT treatments and each treatment was replicated three times. The GLIMMIX SAS 9.2 statistical program (SAS Institute Inc., Cary, NC) was used for data analysis. The control data from root drench and foliar spray was pooled as there was no significant difference between the controls.

3. Results

3.1. Disease reactions

The application of saccharin before inoculation with *P. pachyrhizi* reduced disease severity compared to the control treatment (Table 1). Leaf position and mode of saccharin application were both significant factors in the severity of rust infection. Saccharin administered as a root drench at the V3 (4.6 DS) and R1 (6.3 DS) developmental stages was apparently more effective at inducing SAR than the foliar spray at V3 (4.5 DS) and R1 (7.5 DS) (Fig. 1). Increased resistance was observed 1 d after application of saccharin as a root drench at V3 (4.5 DS) and R1 (6.5 DS) (Fig. 2). However, systemic protection against rust infection was still apparent 15 d after application at the V3 (6.0 DS) and R1 (6.0 DS) stages, particularly in plants that received the root drench application (Fig. 2). In contrast to the root drench treatment, foliar application of saccharin solution at the R1 stage did not significantly induce SAR protection until 15 d after treatment (6.1 DS).

The root drench was more effective at inducing SAR than the foliar spray, when the plants were at the R1 stage, with the exception of plants that were inoculated 5 d after either treatment (Fig. 2). However, at the V3 stage, application of saccharin as either a root drench or a foliar spray was effective in reducing SBR severity (6.7 DS for V3 and 7.8 DS for R1) (Fig. 1, Table 1).

Application of saccharin at the V3 stage instead of at the R1 stage was more effective in reducing disease severity on all inoculation dates (Fig. 3). For both genotypes, the saccharin root drench was more effective than the leaf treatment at most of the time points when rust severity was assessed (Fig. 2).

![Fig. 1. Effect of treatment in inducing SAR against the soybean rust pathogen in soybean plants at V3 or R1 stage treated with saccharin and challenged later with *Phakopsora pachyrhizi.* Error bars indicate standard errors.](image)

Saccharin administered as a root drench at the V3 (5.0 DS) and R1 (4.2 DS) stages was also slightly more effective than the foliar spray at V3 (5.3 DS) and R1 (5.2 DS) in reducing sporulation (Fig. 4). Decreased sporulation was observed 15 d after the application of saccharin as a root drench at V3 (4.6 DS) and R1 (4.1 DS) (Fig. 5). In contrast to the root drench, foliar treatment with saccharin at V3 and R1 plants did not significantly reduce sporulation.

3.2. Time-course response

For the time-course response, when plants were challenged with the pathogen 5 d, 10 d and 15 d after treatment with saccharin at the V3 stage, the root drench application was associated with significant resistance to the disease, whereas the foliar application treatment was significant only at 15 d (Fig. 2). The root drench application was associated with significant resistance to the disease at 1, 10 and 15 d after exposure of soybean, whereas the effect of the foliar application was insignificant. Increased resistance was observed 1 d after root application of saccharin at the R1 stage, and was still apparent 15 d later (Fig. 2). In contrast, the foliar treatment with saccharin at the R1 stage did not increase systemic protection until 15 d after treatment. When plants treated at the V3 stage were challenged with the pathogen at 1, 5, 10 and 15 d after the saccharin treatment, SAR was induced by 5 d and continued for at least 15 d. In plants inoculated at the R1 stage, SAR was induced within one day and seemed to be consistent up to 15 d after treatment. Sporulation was also significantly reduced by the root drench treatment (Fig. 5).

3.3. Biomass

When SAR was induced by application of saccharin, either to the leaf or as a root drench, there were no reductions in plant growth parameters considered (biomass, height and leaves), regardless of how saccharin was applied to plants except for a reduction in height and shoot dry weight when saccharin was applied as a drench in R1 and challenged with the pathogen 15 d after treatment.

For plants that received the root drench application, there was an increase in height, number of leaves, shoot dry weight (SDW) and root dry weight (RDW) in the time-course response for all three treatments except for height and shoot dry weight of plants treated at R1 stage and inoculated 15 d after the root drench application. These data suggest that the saccharin applications had little or no effect on plant growth.

### Table 1

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Levels of significance (***, *P < 0.001; **, *P < 0.01; *, P < 0.05; NS — not significant) were determined using GLIMMIX.
Fig. 2. Time-course responses for protection efficiency of saccharin applications against soybean rust when challenged at 1, 5, 10 and 15 d after treatment (DAT). (Means of three replications, standard errors indicated.)

Fig. 3. Growth stage effect on efficacy of saccharin in inducing SAR in soybean plants subsequently inoculated with Phakopsora pachyrhizi urediniospore suspensions. Error bars indicate standard errors. (DAT = Days after treatment.)

Fig. 4. Effect of saccharin applications on sporulation from uredinia on soybean plants treated at the V3 or R1 stages and subsequently challenged with Phakopsora pachyrhizi. Error bars indicates standard errors.
4. Discussion

The results of the present study demonstrated that Williams 82 and Benning plants, which are susceptible to soybean rust, appear to have developed SAR to *P. pachyrhizi* in response to saccharin application. The method of saccharin application was a significant factor in the severity of rust infection especially when the application occurred at the R1 stage (Fig. 2). Saccharin applied as a root drench was usually more effective than the leaf treatment at inducing protection. A similar response has been observed by others in other plant species (Siegrist et al., 1997; Boyle and Walters, 2005, 2006). The time-course experiments of resistance induction clearly showed that maximum induction was reached within 1 d after treatment when saccharin was applied as a root drench, and that resistance of treated plants was not higher when they were challenged with the pathogen at a later time point (Fig. 2). These results are comparable to those that Boyle and Walters (2005, 2006) reported in broad bean-resistance to the rust fungus *Uromyces viciae fabae*, and in barley resistance against powdery mildew (*B. graminis f. sp. hordei*).

When systemic protection was induced by application of saccharin, either to the leaf or as a drench, there was no significant effect on height or biomass of plants. These data suggest that induction of systemic resistance to rust infection using saccharin had no adverse effect on plant growth. This is consistent with previous work showing that application of various agents to induce resistance in barley was not associated with reductions in plant growth (Dehne et al., 1984; Steiner et al., 1988; Oerke et al., 1989; Kehlenbeck et al., 1994; Mitchell and Walters, 1995; Boyle and Walters, 2005, 2006; Walters et al., 2009).

Earlier studies of soybean plant–pathogen interactions showed that soybean resistance to fungal diseases were correlated with the levels of the antibiotic-like phytoalexin glyceollin (Lozovaya et al., 2004a). The pathogen-inducible phenylpropanoid phytoalexins play a crucial role in plant disease resistance and they have been found in many plant species, including legumes (Keen et al., 1972;
Dakora and Phillips, 1996; Dixon, 2001; Lozovaya et al., 2004a,b). The importance of glyceollin in providing resistance against Phytophthora sojae in soybean has been demonstrated in different studies (Ayers et al., 1976; Albersheim and Val lent, 1978; Zahringer et al., 1978; Bhattacharyya and Ward, 1985; Ebel and Grisebach, 1988; Graham and Graham, 1991). Glyceollin is also toxic to many other important soybean fungal pathogens (Lygin et al., 2009). Lignin is also a well-studied plant cell wall aromatic polymer that helps to provide a barrier to fungal entry into plant tissues and to the diffusion of toxins and enzymes which fungal secrete in advance of invasion to prepare or soften the plant cells for colonization (Vance et al., 1980; Bruce and West, 1989; Elfstrand et al., 2002). Synthesis of antimicrobial phytoalexins and reinforcement of cell walls (due to synthesis of various wall-bound phenolic compounds) is part of a plant’s innate or basal resistance that helps to prevent or impede infection by fungi (Lygin et al., 2009). Lygin et al. (2009) reported that phenolic compounds such as glyceollin, for- mononetin, and kaempferol inhibits germination and development of P. pachyrhizi urediniospores and indicated that increased synthesis of glyceollin and lignin could help to improve soybean rust resistance.

The induction of plant defenses following pathogen challenge is known to be energy-dependent (Smedegaard-Petersen and Tolstrup, 1985). It is assumed that resistance induced by use of exogenous agents is therefore also energy-demanding, but an adverse effect on plant growth may only become apparent when the demand on available resources exceeds supplies (Boyle and Walters, 2005). SAR is characterized by the increased expression of a large number of PR genes, in both local and systemic tissues. Although many PR proteins have antimicrobial properties in vitro (Van Loon and Van Strien, 1999) it is generally thought that SAR results from the concerted effects of many PR proteins rather than a specific PR protein (Durrant and Dong, 2004). Malamy et al. (1990) showed that the endogenous SA concentration rises in both local and systemic tissues after infection of tobacco with TMV and this rise correlates with PR gene induction.

Sakamoto et al. (1999) demonstrated that the RPR1 (rice pro- benazole responsive) protein, contained motifs of a nucleotide binding site (NBS) and a leucine-rich repeats (LRR) domain. RPR1 gene expression was up-regulated following treatment with pro- benazole, chemical inducers of SAR such as BTH and SA, and pathogens. The RPR1 protein contained NBS and LRR domains similar to several known R gene products such as Tobacco N (Whitham et al., 1994), RPM1 (Grant et al., 1995) and Mi (Rossi et al., 1998). PR1 has antifungal activities and its synthesis serves as a biomarker of plant responses to pathogens (Rylas et al., 1996; Durner et al., 1998). In addition, enhanced activity of cell membrane GPase, an enzyme involved in intracellular signal transduction pathways, has been observed in rice plants treated with probenazole (Kanoh et al., 1993).

According to Murray and Walters (1992) the elevated rates of photosynthesis that were observed in upper leaves of broad bean expressing systemic protection to rust infection were artificially reduced by shading. The efficacy of the systemic protection was significantly reduced suggesting that the increased rates of photosynthesis in these leaves provide a valuable source of assimilate to fund defense responses. Any factors that influence plant resources could affect the balance and culminate in reduced growth. Therefore, other variables such as the physiological and nutritional status of the plant and environmental factors are likely to influence the ability of a plant to effectively express induced resistance, whether induced biologically or by chemical means (Boyle and Walters, 2005). Results from these experiments suggest that younger plants exhibited a stronger SAR response than more mature ones. Resistance may be established at the time of transition from juvenile to adult during vegetative growth at the flowering transition or with the onset of senescence. The mecha- nism of controlling developmental transitions may also govern the expression of resistance (Deveau-Riviere and Galiana, 2007).

5. Conclusion

In conclusion, this work presents the effect of saccharin on soybean rust control and on plant biomass under two different forms of application and at two different stages of plant develop- ment. A root drench application of saccharin was more effective overall in terms of reducing soybean rust severity. In tissue distant from the inoculation site, SAR was apparently more effective in younger plants. While saccharin did not yield a direct measurable effect on plant growth, its positive role on disease suppression may lead to better plant productivity. Further experiments are being conducted to elucidate the mode of action by which saccharin application reduces disease in soybean plants challenged with soybean rust. Physiological and molecular study of defense responses is required to establish whether the effects observed here represent local and SAR.

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