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Efficiency of resistance elicitors in the management of grapevine downy mildew *Plasmopara viticola*: epidemiological, biochemical and economic aspects

Kedma Maria S. Pinto · Luciana Cordeiro do Nascimento · Erbs Cintra de Souza Gomes · Hilderlande Florêncio da Silva · Janaina dos Reis Miranda

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Abstract This paper aimed to evaluate the efficiency of resistance elicitors in the management of grapevine downy mildew (*Plasmopara viticola*), identify the action of the elicitors on host metabolism, and determine their economic viability. The experiments were performed in a commercial vineyard variety 'Isabel' (*Vitis labrusca*) at Vale do Sirijí [Natuba, Paraiba State in Brazil, in the period of September 2009 to January 2010 (first season) and February to June 2010 (second season)]. The statistical design of randomized blocks consisted of eight treatments (untreated control, fungicide (pyraclostrobin+metiram), potassium phosphite, Agro-Mos®, Fungicide+potassium phosphite, Fungicide +Agro-Mos®, potassium phosphite+AgroMós® and Fungicide+potassium phosphite+Agro-Mos®) with four replications, with the experimental unit consisting of 45 leaves. Applications were made every 7 days, starting 20 days after pruning (DAP) with a total of 12 sprays. The evaluations were carried out biweekly, analyzing the following variables: incubation period, disease incidence and severity, area under the disease progress curve, and efficiency of control. The enzymatic determination was performed using pulp extracts from three fruits harvested at 45, 60, 90 and 120 DAP for each treatment. The resistance elicitors were able to reduce the disease incidence under different climatic conditions, indicating their viability as an alternative for the management of *Plasmopara viticola*.

Keywords *Vitis labrusca* L. · Mildew · Resistance induction

K. M. S. Pinto (✉) · L. C. do Nascimento · J. dos Reis Miranda
Programa de Pós-Graduação em Agronomia, Universidade Federal da Paraíba, CCA/UFPB, Campus II, Rodovia PB 079, Km 12, CEP 58397-000 Areia, PB, Brazil
e-mail: kedma_maria@hotmail.com

L. C. do Nascimento
e-mail: luciana.cordeiro@cca.ufpb.br

J. dos Reis Miranda
e-mail: janaina-jua@hotmail.com

E. C. de Souza Gomes
Instituto Federal do Sertão Pernambucano, Petrolina, PE, Brazil
e-mail: ectecnologo@hotmail.com

H. F. da Silva
Laboratório de Fitopatologia CCA/UFPB, Campus II, Rodovia PB 079, Km 12, CEP 58397-000 Areia, PB, Brazil
e-mail: hildinhasilva@hotmail.com

Introduction

Viticulture is a very important agricultural activity for both the social and the economic context worldwide. Italy and China are the two largest producers and Brazil ranks 15th among worldwide grape producers, with a production of 1,365,491 t in 2009 and exporting

US$ 171 million. In Brazil, the south region is the largest producer, followed by the northeast, with a production of 254,093 t (FAO 2011; IBGE 2011).

Plasmopara viticola (Berk. & Curt). Berl. & De Tony, causal agent of grapevine downy mildew, is present worldwide (Agrios 2005) and one of the major pathogens infecting vineyards at the Vale do Siriji. The disease affects all green parts of the plant, causing premature defoliation, which may reduce yield up to 75 % (Brunelli and Cortesi 1990). The disease can also affect the fruits, reaching the clusters at all developmental stages (Amorim and Kuniyuki 2005).

The process of resistance induction is functionally, spatially and temporally complex and is initiated with the host recognition of exogenous signals from the pathogen, continues with the mechanisms of signal transduction, and results in extensive reprogramming of plant cell metabolism involving changes in gene activity (Somssich and Hahbrock 1998). Thus, the products used as inducers or elicitors have no antimicrobial activity, instead they act on the pathogen signalling molecules, which bind to receptor molecules on the plant or fruit, triggering different responses such as hypersensitivity (Durrant and Dong 2004), callus formation, lignification, salicylic acid (SA) accumulation, and phytoalexin production (Goellner and Conrath 2008).

This paper aimed to evaluate the efficiency of resistance elicitors in the management of grapevine downy mildew (*Plasmopara viticola*) as an ecological alternative in the Natuba region, identify the action of the elicitors on the host metabolism, and determine their economic viability.

Material and methods

The experiments were performed in a commercial vineyard cultivated with the variety 'Isabel' located in the municipality of Natuba – PB, at Sítio Fervedouro (35 ° 32′W, 07 ° 35′ S). The experimental area consisted of 2.500 m^2, with two harvest times, from September 2009 to January 2010 (first season) and from February to June 2010 (second season).

The efficiency of the resistance elicitors potassium phosphite and Agro-Mos® was compared with chemical treatments alone and in association with the resistance elicitors. The fungicide Metiram+pyraclostrobin was used as the reference for all experiments. The following treatments were evaluated: Fungicide Metiram+pyraclostrobin (2 kg/ha), potassium phosphite (130 g/100 l), Agro-Mos® (3 ml/l), Fungicide Metiram+pyraclostrobin (1 kg/ha)+potassium phosphite (65 g/100 l), Fungicide Metiram+pyraclostrobin (1 kg/ha)+Agro-Mos® (1.5 ml/l), potassium phosphite (65 g/100 l)+Agro-Mos® (1.5 ml/l) and Fungicide metiram+pyraclostrobin (0.67 kg/ha)+potassium phosphite (43 g/100 l)+Agro-Mos® (1 ml/l). The applications of all treatments were carried out every 7 days, beginning 20 days after pruning (DAP), using a manual sprayer, with a total of twelve applications over a period of 4 months. Each treatment consisted of four replications, with the experimental unit represented by 45 leaves for field evaluations of the epidemiological aspects, and three clusters for the enzymatic activity of phenylalanine ammonia lyase (PAL). The untreated control consisted of plants without spraying.

The assessments began at 20 DAP and were carried out biweekly. A total of 45 leaves were evaluated, with nine leaves (three leaves from the branch baseline, three from the middle, and three from the apical portion) collected from each plant within the plot. The following variables were analyzed: incubation period (days) corresponding to the first day of symptom onset; disease incidence (%) related to total percentage of leaves with symptoms in the total number of leaves evaluated; disease severity, assessed by descriptive scale proposed by Regina et al. (2006); area under the disease progress curve (AUDPC) using the indices of severity from eight assessments; and economic viability based on cost comparisons.

The design was a randomized block in factorial arrangement (8×2) with eight treatments and two harvest seasons. The means were compared by Tukey test (P=0.05) performed with the software Assistat 7.5 (Assistat 2010).

The extracts of fruit pulp from different treatments and collected at 45, 60, 90, and 120 DAP were used for the enzymatic activity determination. The extracts were obtained by an adaptation of the technique described by Rhodes and Wooltorton (1971), as follows. From each treatment 2.0 g of pulp were weighed and transferred to a mortar and kept at 0 °C, with subsequent addition of 2.0 ml of extraction buffer (22.2 g Tris, 0.37 g EDTA, 85.5 g sucrose, 10 g of PVP and the volume completed to 1000 ml with distilled water and pH adjusted to 8.0 with KCl and NaOH). The pulp was macerated and subsequently centrifuged at 10,000 rpm for 10 min at 4 °C. The PAL activity was evaluated based on the difference in absorbance resulting from the conversion of phenylalanine to trans-cinnamic acid (Hyodo et al. 1978). For this, 0.5 ml of each enzymatic extract was pipetted to a test tube, then 2.0 ml of extraction buffer were added, and finally 0.5 ml of phenylalanine (49.6 mg/ml) or distilled water for the blank treatment. The mixture was incubated at 40 ° C for 1 h. The reaction was stopped in an ice bath for 5 min and the reading performed using a spectrophotometer at 290 nm. The results were expressed as the UAE g^{-1} fresh matter min^{-1}.

The design was a randomized block in factorial arrangement (8×4) with eight treatments and four evaluation times. The experimental unit consisted of composite samples of three clusters. The means were compared by Tukey test (P=0.05) performed with the statistical software Assistat 7.5 (Assistat 2010).

Results

No significant statistical differences were observed in the incubation period among the treatments. The elicitors performed similarly in the two evaluated seasons (Table 1). The first symptoms were observed at 21.5 DAP in the first season and at 35 DAP in the second season, with no significant difference between the two seasons.

There were no differences in initial disease severity for both seasons. The elicitors were effective in more advanced disease stages, including the final disease severity assessed at 91 DAP when all treatments were statistically superior to the untreated control. The harvest season influenced the initial and final disease severity, showing higher values for these variables in the second season, with two exceptions: plants treated with Agro-Mos® which were not affected by the season concerning the initial disease severity; and the untreated control and the treatments Agro-Mos®, fungicide+potassium phosphite and potassium phosphite+fungicide+Agro-Mos® concerning the final disease severity.

A reduction in disease incidence was observed in all treatments, with efficiency similar to the synthetic fungicide Metiram+pyraclostrobin used as the reference (Table 2). The plants treated with potassium phosphite+Agro-Mos® exhibited lower disease incidence in the first season, being more effective in reducing the disease incidence than the control and fungicide+potassium phosphate treatments. In the second harvest, all treatments differed from the control, but did not differ among them.

Agro-Mos ® and fungicide+potassium phosphite were effective in reducing the incidence of mildew in the two seasons and did not differ from each other. The other treatments were more efficient in the second season, when climatic conditions were less favourable

Table 1 Control of grapevine downy mildew (*Plasmopara viticola*) on grape 'Isabel' (*Vitis labrusca*) with elicitors of resistance during the periods of September 2009 to January 2010 (first season) and February to June 2010 (second season). Natuba-PB

	IP [1]		I.Sev		F.Sev		AUDPC	
Treatments	Season 1	Season 2	Season 1	Season 2	Season 1	Season 2	Season 1	Season 2
Untreatment control	21.5 aA	35.0 aA	1.5 aB	3.4 aA	8.0 aA	8.7 aA	380.8 aB	535.7 aA
Fung.[2]	32.0 aA	38.7 aA	1.1 aB	2.7 aA	4.0 bB	7.0 abA	237.6 bB	351.7 bA
Phos.	35.0 aA	42.5 aA	1.1 aB	2.1 aA	4.5 bB	6.5 abA	235.4 bA	293.1 bcA
Agro-Mós®	25.0 aA	53.7 aA	1.4 aA	1.5 aA	4.0 bA	4.7 bA	221.4 bA	248.5 cA
Fung + Phos.	32.0 aA	35.0 aA	1.4 aB	2.5 aA	5.5 abA	6.2 abA	292.2abA	335.8 bcA
Fung. + Agro-Mós®	35.0 aA	38.7 aA	1.1 aB	2.1 aA	5.0 bB	6.7 abA	231.9 bB	319.4 bcA
Phos. + Agro-Mós®	32.0 aA	38.7 aA	1.1 aB	2.6 aA	4.0 bB	4.1 bA	217.0 bB	312.4 bcA
Fung. + Phos. + Agro-Mós®	32.0 aA	38.7 aA	1.1 aA	2.1 aA	5.7 bA	6.2 abA	242.4 bB	315.9 bcA
CV (%)	33.1		51.4		20.3		15.4	

* Average of 45 leaves. Means followed by same letter do not differ on the line (upper) and column (lower case) by the Tukey test at 5 % probability. (1) IP (incubation period); I.Sev.I (initial disease severity); F.Sev (final disease severity), AUDPC (Area Under Disease Progress Curve). (2) *Fung.* Fungicide, *Phos.*. Potassium phosphite

Table 2 Incidence of grapevine downy mildew (*Plasmopara viticola*) (%) in plants treated with elicitors of resistance in the period of September 2009 to January 2010 (first season) and February to June 2010 (second season). Natuba-PB

Treatments	*P. viticola* Incidence (%)	
	Season 1	Season 2
Untreated control	58.9 aB	70.4 aA
Fung. (1)	11.7 cB	28.7 bA
Phos.	13.3 bcB	22.2 bA
Agro-Mós®	10.6 cA	16.7 bA
Fung. + Phos.	23.9 bA	25.0 bA
Fung. + Agro-Mós®	13.9 bcB	25.93 bA
Phos. + Agro-Mós®	8.9 cB	19.4 bA
Fung. + Phos. + Agro-Mós®	13.3 bcB	25.0 bA
C.V.(%)	22.32	

Averages of 45 leaves. Means followed by same letter do not differ on the line (*upper*) and column (*lower case*) by the Tukey test at 5 % probability. (1) *Fung.* Fungicide, *Phosp.* Potassium phosphite

to the pathogen, demonstrating higher effectiveness of these treatments under less disease pressure, in this work linked to climatic conditions (Fig. 1).

Considering the variable AUDPC, all treatments affected negatively disease development when compared to the untreated control, with the exception of potassium phosphite+fungicide, which did not differ from the untreated control in the first season. Over the two seasons, the lowest values were observed in the first, with the exception of the treatments potassium phosphite, Agro-Mos®, and fungicide+potassium phosphite in which the AUDPC did not differ between the two seasons. These higher levels of disease severity and AUDPC observed in the second season were due to the fact that the climatic conditions represented by higher rates of precipitation and temperature (Fig. 1) were more conducive to the development of *P. viticola*.

In this study the resistance elicitors were not able to slow down the symptom development of mildew in the grapevines. Levels of 41.86 and 53.61 % of mildew control on grapevine treated with Agro-Mos® were observed in the two seasons respectively (Fig. 2 and 3).

The resistance elicitors represent viable alternatives to control plant diseases. As well as being environmentally friendly for the management of grapevine downy mildew, they also have reduced costs compared to chemical treatments (Table 3).

The PAL activity in grapevine 'Isabel' was influenced by the treatments and the sampling periods. In the first harvest, plants treated with potassium phosphite exhibited the highest activity as early as 45 days, indicating a faster defence response in relation to other treatments. The maximum activity was observed as early as 60 days (101.8 UAE min^{-1} g^{-1}) which did not differ at 90 (101.1 UAE min^{-1} g^{-1}) and 120 days (96.94 UAE min^{-1} g^{-1}). The elicitor AgroMós enhanced PAL production only at 60 days, and in this period, there was no observed difference between the treatments potassium phosphite, fungicide+potassium phosphite, and potassium phosphite+AgroMós treatments (Table 4).

PAL activity increased gradually for most treatments according to the sampling period. Only the treatments involving application of AgroMós, potassium phosphite mixed with the fungicide, and the mix of the two elicitors (potassium phosphite and AgroMós) produced the peak of enzyme activity in the

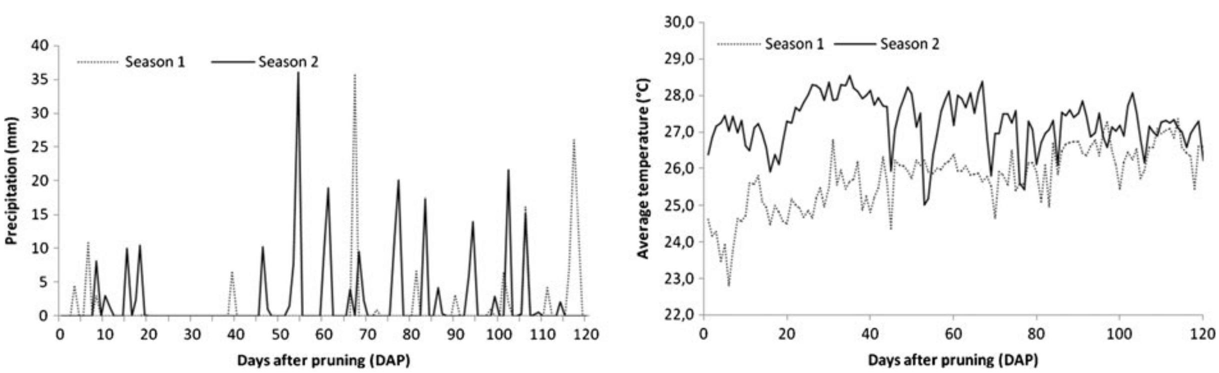

Fig. 1 Daily data of temperature and precipitation in the city of Natuba-PB in the periods from September 2009 to January 2010 (first season) and from February to June 2010 (second season)

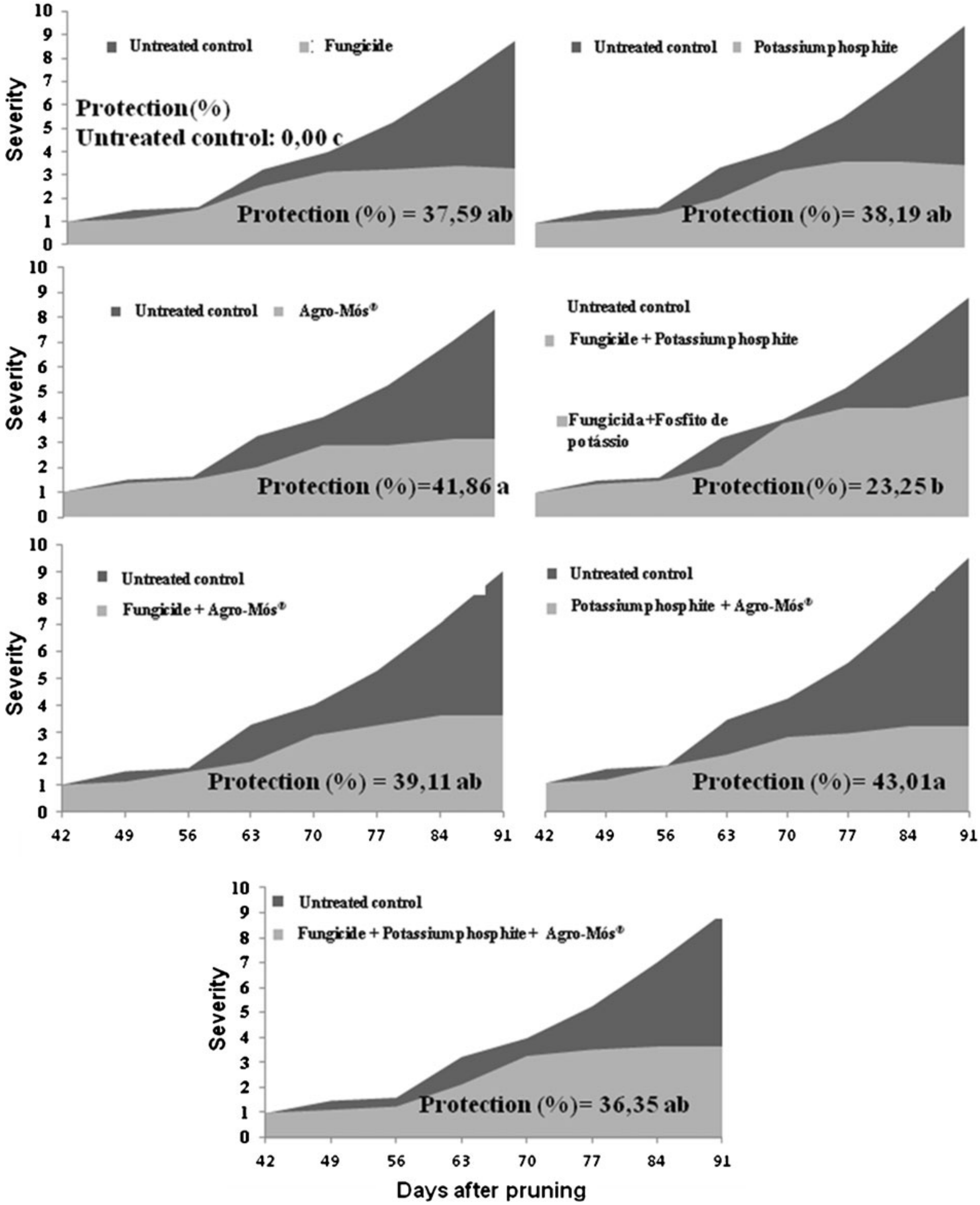

Fig. 2 Protection levels of grapevines 'Isabel' (*Vitis labrusca*) treated with different elicitors of resistance against *Plasmopara viticola* in Natuba-PB in the period from September 2009 to January 2010 (season 1)

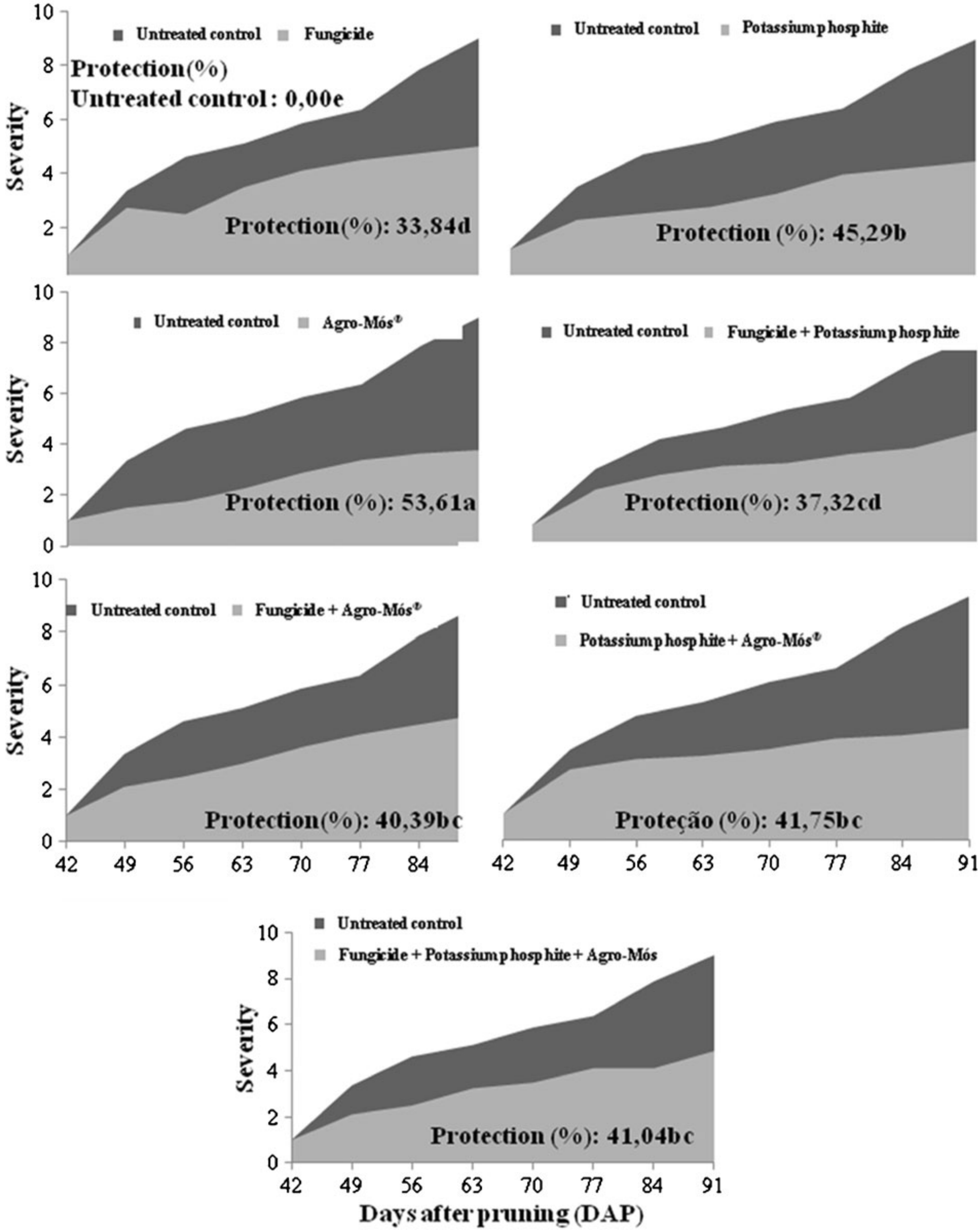

Fig. 3 Protection levels of grapevines 'Isabel' (*Vitis labrusca*) treated with different elicitors of resistance against *Plasmopara viticola* in Natuba-PB in the period from February to June 2010 (season 2)

Table 3 Implementation costs of elicotors of resistance in an area of 1 ha of grapevines 'Isabel', during the crop cycle (4 months)

	Unit cost (R$)	Cost per dosage R$	Total cost
Fung. (1)	45.00	90.0	1,080.0
Phos.	32.00	41.6	499.2
Agro-Mós®	45.00	135.0	1,620.0
Fung. +Phos.	77.00	65.8	789.6
Fung. +Agro-Mós®	90.00	112.5	1,350.0
Phos. +Agro-Mós®	90.00	88.3	1,059.6
Fung. + Phos. + Agro-Mós®	112.00	88.9	1,066.9

(1) *Fung.* Fungicide (*Metiram* pyraclostrobin); *Phos.* Potassium phosphite

intermediate periods with a decrease at the end of the grapevine cycle.

The maximum PAL activity among the control plants was recorded at 120 days, however, at this evaluation time it was higher than any other treatment. Among plants treated with fungicide elevated activity was observed even after 60 days, showing the synthesis of phenolic compounds in these plants.

In the second harvest, the control plants exhibited the maximum enzyme activity at 120 days (92.02 UAE min^{-1} g^{-1}), as observed in the previous season (UAE 176.02 min^{-1} g^{-1}). However, it was lower than the plants treated with potassium phosphite (123.55 UAE min^{-1} g^{-1}) and with the mix of fungicide, potassium phosphite and AgroMós (151.45 UAE min^{-1} g^{-1}), which recorded the highest activity for this period (Table 5).

All treatments showed increasing enzymatic activity associated with the time of evaluation. The plants treated with the mix of the two elicitors (potassium phosphite and AgroMós) showed the highest PAL activity as soon as at 60 days, with the maximum activity observed at 120 days, and only the plants treated with fungicide and with potassium phosphite had their maximum PAL activity recorded only at 120 days.

Discussion

Amorim and Kuniyuki (2005) pointed out the importance of temperature and humidity on disease severity, reporting that the most serious epidemics of downy mildew occur after a wet winter followed by a spring also humid and a rainy summer. These climatic conditions ensure the survival of oospores, with abundant germination in the spring, and enable rapid development of the disease at the time of vegetative growth of the plant. The sporangia of *P. viticola* can be dispersed by the wind, under high relative humidity and raindrops.

The results observed in these experiments corroborate those obtained by Gomes et al. (2007), who reported the efficiency of these elicitors in control of powdery mildew (*Uncinula necator* (Sxhw.) Burrill) on grapevine 'Italia' and 'Cabernet Sauvignon', at the Vale do São Francisco.

In this study, potassium phosphite was efficient in controlling the disease. When used alone, it provided protection levels of 38.19 % in the first season, and 45.29 % in the second season, performing superior to the fungicide treatments.

Table 4 Phenylalanine ammonia lyase activity (UAE*min^{-1}*g^{-1}) at different developmental periods of grapevine 'Isabel' treated with elicitors of resistance in the period from September 2009 to January 2010 (first season). Natuba-PB

	Days after pruning (DAP)			
Treatments	45	60	90	120
Untrated control	11.0 bC	82.3 cB	90.7 abB	176.0 aA
Fung. (1)	5.7 bC	91.8 bcB	113.8 aA	124.2 bA
Phos.	62.4 aB	101.8 abcA	101.1 abA	96.9 cA
Agro-Mós®	3.2 bC	116.7 aA	101.0 abAB	95.3 cB
Fung. + Phos.	3.6 bC	93.3 abcA	85.9 bA	26.3 dB
Fung. + Agro-Mós®	3.3 bC	25.5 dB	84.1 bA	87.2 cA
Phos. + Agro-Mós®	2.0 bC	115.1 abA	95.6 abAB	89.2 cB
Fung. + Phos. + Agro-Mós®	1.0 bB	81.5 cA	94.4 abA	100.4 bcA
C.V. (%)	13.1			

Means followed by same letter do not differ on the line (*upper*) and column (*lower case*) by the Tukey test at 5 % probability. (1) *Fung.* Fungicide, *Phos.*. Potassium phosphite

Table 5 Phenylalanine ammonia lyase activity (UAE*min^{-1}*g^{-1}) at different developmental periods of grapevine 'Isabel' treated with elicitors of resistance in the period from February to June 2010 (Season 2). Natuba-PB

	Days after pruning (DAP)			
Treatments	45	60	90	120
Untreated control	37.3 abC	73.6 bC	86.8 bcAB	92.0 cA
Fung. [1]	35.2 abC	72.4 bcB	77.0 cB	101.4 cA
Phos.	34.1 abC	95.6 aB	106.5 abAB	123.5 bA
Agro-Mós®	28.2 bC	58.0 cB	95.5 abcA	100.9 cA
Fung. + Phos.	51.5 aB	92.8 abA	110.3 aA	104.7 bcA
Fung. + AgrMós®	52.2 aB	58.9 cB	88.9 bcA	89.2 cA
Phos. + Agro-Mós®	53.9 aB	83.3 abA	93.1 abcA	93.9 cA
Fung. + Phos. + Agro-Mós®	41.0 abC	85.0 abB	98.3 abB	151.4 aA
C.V. (%)	10.3			

Means followed by same letter do not differ on the line (*upper*) and column (*lower case*) by the Tukey test at 5 % probability. (1) *Fung.* Fungicide, *Phos.*. Potassium phosphite

The efficiency of phosphite application in certain pathosystems is due to the fact that the plant has better assimilation in the presence of phosphorus and potassium, making it able to activate defence mechanisms and to produce phytoalexins, natural self-defence substances that confer resistance against pathogens (Jackson et al. 2000; Nojosa et al. 2005). Several studies have shown the effectiveness of potassium phosphite in controlling *P. viticola* (Reuveni and Reuveni 1995; Dalbó and Schuck 2003; Gomes et al. 2007) as well as in other pathosystems where this salt has promoted the reduction in disease severity in corn, cucumber and mango (Reuveni and Reuveni 1995; Reuveni et al. 1996; Panicker and Gangadharan 1999).

The mode of action of phosphites on plant diseases control is still unclear, because some research shows antimicrobial effect of these and other salts related to disease control by activation of defence mechanisms in plants against pathogen (Fenn and Coffey 1984; Ribeiro et al. 2006). For example, Araújo et al. (2008) detected the antimicrobial action of potassium phosphite against *Glomerella* leaf spot, where the action of this salt showed a curative effect, reducing up to 90 % disease severity when applied in apple trees 24 h after inoculation, not having been effective when used early.

Araújo et al. (2010) evaluated different potassium phosphite formulations incorporated into the culture medium and observed inhibition of up to 94 % in the mycelial growth and mycelial growth velocity index (MGVI) of *C. gloeosporioides*, isolated from apple trees when the formulation 0-40-20 was used.

As well as abiotic elicitors, it is also possible the activation of defence mechanisms in plants against many pathogens through biotic elicitors. *Saccharomyces cerevisiae* is the most studied often inducing defence responses in plants against pathogens (Silva and Pascholati 1992; Piccinin et al. 2005; Tavares et al. 2009; Zanardo et al. 2009). Similarly, Agro-Mos® is a mannanoligosaccharide phosphorylated derivative from the cell wall of *S. cerevisiae* 1026 (Hansen) (Oliveira et al. 2004).

Induced resistance is characterized by the activation of biochemical mechanisms that may involve biosynthesis and increasing activity of peroxidase, ß-1,3-glucanase, chitinase, phenylalanine ammonia lyase, and polyphenoloxidase (Agrios 2005).

Phenylalanine ammonia-lyase is considered a key enzyme involved in the phenylpropanoids and its derivatives biosynthesis pathway regulation, catalyzing the conversion of the amino acid phenylalanine to trans-cinnamic acid by de-amination, which is the first step in the biosynthesis of plant phenolics (Cheng et al. 2001).

However, according to Kouki and Manetas (2002), the availability of plant resources also promotes regulatory effects on the activity of essential enzymes for biosynthetic pathway of these metabolites. Janas et al. (2000) pointed out that the activity of phenylalanine ammonia-lyase and accumulation of phenolic compounds occur as a result of biotic stresses such as infections by microorganisms, herbivore and abiotic stresses such as temperature, light water availability (Gobbo-Neto and Lopes 2007).

The high PAL activity since the beginning of the tests could have been responsible for of host defence mechanisms activation even before pathogen germination and penetration, which could explain the high levels of protection against mildew. One of the most effective treatments for grapevine downy mildew control, which implies the signalling of pathways of plants defence mechanisms do not include the production of phenylalanine ammonia lyase. This observation is consistent with the delay of the plant response to the elicitor application. Romeiro (2008) showed the occurrence of an incubation period between application of the elicitor and its effect. Hammerschmidt and Kuc (1995) demonstrated that the induction expression is not immediate, with the systemic acquired resistance (SAR) or induced systemic resistance (ISR) expression by the plant taking up to 1 week. The exceptional PAL activity in the two periods in which the experiments were conducted was probably due to climate changes that imposed particular environmental challenges to the plant. Thus, the protein expression in "challenged" plants is not only dependent on the challenge process, but also on the environmental conditions and consequently the plant physiological condition (Janas, et al. 2000).

In cowpea plants inoculated with *Colletotrichum destructivum*, the increase in seedling resistance induced by ASM was associated with the rapid and effective increase in the activity of two key enzymes in the phenylpropanoid pathway (phenylalanine ammonia-lyase - PAL and chalcone isomerase - CHI), which led to a rapid accumulation of substances within the flavonoid group, kievitonas, and faseolidina (Latundê-Dada 2001)

Conclusions

Agro-Mos® and potassium phosphite, when used alone or in combination, can reduce *Plasmopora viticola* incidence on grapevine 'Isabel' and promote high levels of control efficiency. The activity of phenylalanine ammonia lyase in grapevines 'Isabel' is influenced by the application of the elicitors Agro-Mos and potassium phosphite, as well as by the disease occurrence and the stage of fruit development. Potassium phosphite applied alone or in combination with fungicide Metiran +pyraclostrobin is an economically viable option for grapevine downy mildew management.

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