Effect of foliar application of salicylic acid, hydrogen peroxide and a xyloglucan oligosaccharide on capsiate content and gene expression associated with capsinoids synthesis in *Capsicum annuum* L.

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Capsinoids are non-pungent analogues of capsaicinoids in pepper (*Capsicum* spp). The absence of pungency, in addition to their biological activities similar to that of capsaicinoids such as anti-inflammatory, antimicrobial, and antioxidant properties, makes capsinoids an excellent option for increasing use in human and animal nutrition, as well as health and pharmaceutical industries. There are only few sources of pepper producing capsinoids, and one of them (accession 509–45-1), *Capsicum annuum* L., is a potential source for increasing capsinoids content using strategies as controlled elicitation during plant production in the greenhouse. In this research we evaluated the effect of weekly and one-day-before-harvest foliar applications of hydrogen peroxide, salicylic acid and a xyloglucan oligosaccharide on the concentration of capsiate in fruits of this pepper accession, as well as the gene expression of phenylalanine ammonia-lyase (*pal)*, putative aminotransferase (*pamt)*, capsaicin synthase (*at3)* and β-keto acyl synthase (*kas)*. Results showed that the two tested concentrations of H_2O_2 significantly increased capsiate content and gene expression associated with capsaicinoids (*pamt*, *at3* and *kas*) and the phenylpropanoids (*pal)* pathways. Plant yield was not affected using this induction strategy. Our results indicated that the pre-harvest and weekly application of hydrogen peroxide and xyloglucan oligosaccharide improved production of capsiate in *C. annuum* L.

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1. Introduction

The type of diet, lack of exercise, oxidative stress provoked by the environment, among other factors, cause damage to the health of humans (Kampa and Castanas 2008; Cross *et al.* 2010; Booth *et al.* 2012; Kok *et al.* 2013). Phytochemicals are compounds found in plant foods which have bioactive properties that improve health; for this reason, the demand for plants with higher contents of phytochemicals is increasing (Amin *et al.* 2009; Dinkova-Kostova and Kostov 2012; Valin *et al.* 2013; Bigliardi and Galati 2013). The fruits of Capsicum spp have compounds like carotenoids, ascorbic acid, phenolic compounds, vitamins A and E, as well as capsaicinoids, with activities as antioxidant, anticancer and

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anti-inflammatory (Wong and Gavva 2009; Rubi *et al.* 2013). Capsaicinoids are the principal compounds causing pungency in chili peppers and are employed as food additives for human and animal nutrition as well as in pharmaceutical applications (Chapa-Oliver and Mejia-Teniente 2016). In fact, the pungency of capsaicinoids has low levels in many cases for use in certain foods and pharmaceuticals (Jarret *et al.* 2014).

On the other hand, capsinoids are non-pungent analogues of capsaicinoids that were first reported in a sweet pepper cultivar named CH-19 (Kobata *et al.* 1998). Interestingly, capsinoids display biological activities as antioxidants and anti-inflammatory, promoting energy metabolism and suppressing body fat accumulation, similar as those reported for capsaicinoids but with no pungency (Ohnuki *et al.* 2001; Rosa *et al.* 2002; Masuda *et al.* 2003; Tani *et al.* 2004; Sasahara *et al.* 2010). Based on the aforementioned bioactivities, capsinoids are considered important compounds for uses in several industries as additives, and thus it will be necessary to obtain capsinoids-rich sources. A *Capsicum annuum* germplasm containing high contents in capsinoids (ca. 1 mg/g fresh weight) was recently obtained (Jarret *et al.* 2014). Meanwhile, a patent of a genetically modified pepper that produces high levels of capsinoids was published in 2011 (Kisaka *et al.* 2011). This genetically modified pepper was altered in the *pamt* gene of the capsaicinoids pathway, thus abolishing this activity, and then causing a reduction reaction from vanillin to vanillyl alcohol instead of conversion from vanillin to vanillylamine, and a further esterification reaction with branched chain fatty acid, resulting in capsinoids production.

On the other hand, elicitors are chemicals or biological factors that can induce physiological and morphological responses in plants and other living organisms (Zhao *et al.* 2005; Mejía-Teniente *et al.* 2013; Chapa-Oliver and Mejia-Teniente 2016). Some elicitors used in plants for inducing secondary metabolites production and crop protection are salicylic acid, oligosaccharides, jasmonic acid and hydrogen peroxide (Zhao *et al.* 2005; Tierranegra-Garcia *et al.* 2011; Mejía-Teniente *et al.* 2013). It is known that the elicitor's recognition, signal transduction, gene expression and secondary metabolites produced by plants can induce different gene expression and biochemical pathways in different parts and times within the plant (Zhao *et al.* 2005). Thus, the induction of specific secondary metabolites must be studied evaluating different elicitors. Several aspects related to elicitors in relation to their concentration and form of application should be studied to be employed in future agricultural production systems. The present work aimed the evaluation of the effect of three elicitors (hydrogen peroxide, salicylic acid and a xyloglucan) on the production of capsinoids (capsiate) in a *C. annuum* L. germplasm. The obtained results suggested significantly increased production of capsiate and gene expression associated with the capsaicinoids and phenyl propanoids biosynthesis pathway. Implications for the development of pepper biosystems for overproducing capsiate for industrial purposes are discussed.

2. Materials and methods

2.1 *Plant material*

Dr Robert L Jarret kindly provided *Capsicum annuum L.* accession 509–45-1 from USDA/ARS/PGRU, USA. The accession 509–45-1 is characterized by producing capsiate and not capsaicinoids.

2.2 *Statistical analysis*

A completely randomized experimental design was used to evaluate the effect of the foliar application of elicitors on capsiate content and gene expression studies. The arrangement of the experiment was 6 treatments with an experimental unit of 12 plants, with triplicates for each treatment (36 plants in total for each treatment). Data were subjected to analysis of variance (ANOVA) and the differences between means were compared using Tukey's test (P=0.05) using the program JMP 8.0.

2.3 *Plant growth*

The seeds of *C. annuum* were immersed for 24 h in a solution of Marci TS growth solution at a concentration of 2 mL/10 L to stimulate germination. Germinated seeds were placed in seedbeds with peat moss substrate. The seedling was placed in a dark room until germination. One month after germination, the transplant was done; the seedlings were placed in plastic bags with tezontle substrate and maintained in a greenhouse of 1000 m^2 with temperature between 25–30°C, relative humidity between 50–60% and photoperiod according to natural light (14 h light/10 h dark).

2.4 *Application of treatments with elicitors*

Elicitors were applied by spray to drop point weekly and one-day prior to harvest. The elicitors used were: 1 mM and 0.1 mM of Salicylic Acid (SA, brand reagent J.T. Baker), 400 mM and 200 mM of hydrogen peroxide (H2O2, brand Golden bell ™ Reagents) and xyloglucan (Xh, PEL 101 GV, ELICYTIL, OligoTech®) to 6 ppm (dose recommended by the manufacturer). As control, deionized water was sprayed in the same times on the plants.

2.5 *HPLC quantification of capsiate in fruits of C. annuum*

The method described by Singh *et al.* (2009), with some modifications was used for capsiate quantification. Capsiate standard was purchased from Chiralix B.V (The Netherlands). Capsinoids extractions consisted of

placing 200 mg of fresh weight ground sample in a falcon tube 50 mL to which was then added 10 mL of HPLC-grade acetonitrile, and then the sample was sonicated in the falcon tubes during 3 h in water bath at 35°C–45°C with intense stirring every 30 min. The falcon tubes were shaken every 30 min, and then centrifuged at 8000 rpm for 10 min at 4°C, the supernatant was filtered on acrodisc with pores of 0.45µm and the filtrate was placed in amber vials. The vials were stored at −20°C until determinations. Quantification was performed on an Agilent 1200 series HPLC, UV-VIS 6120 Quadrupole using an Eclipse plus C18 5µm particle size column. The mobile phase was acetonitrile: water (70:30).

2.6 *Gene expression of pamt, at3, pal and kas genes*

Total RNA extraction of pepper fruits was carried out using TRIzol® Reagent kit in combination with the Promega SV Total RNA Isolation System. Total RNA was converted into cDNA with Revert Aid First Strand cDNA Synthesis Kit Thermo Scientific. The cDNA was taken (500 ng) for the analysis of gene expression in the team CFX96 Touch™ Real-Time PCR Detection Systems (Bio-Rad Laboratories, Inc). Specific oligonucleotides for the genes involved in the capsinoids pathway (*pamt*, *kas* and *at3*), and pal (phenylpropanoids pathway) were used in the analysis, the amplification conditions were according to Abraham-Juarez *et al*. (2008). The ubiquitin gene was used as housekeeping gene in the gene expression analysis. The sequences of all these oligonucleotides are shown in table 1.

3. Results and discussion

The effect of foliar application of the evaluated elicitors in *C. annumm* L. is shown in table 2. Hydrogen peroxide at 200 mM displayed the largest increase in capsiate contents. This concentration induced an augment of 134% compared to control (table 2). The second best treatment increasing (75%) capsiate was 400 mM hydrogen peroxide. The application of xyloglucan to 6 ppm, increased approximately 22% the content of capsiate. SA showed the minor increase in capsiate, but significant in some cases (6% in one-day-before-harvest at 0.1 and 1 mM, and at 1 mM weekly) compared to control. Results of gene expression analysis of capsinoids pathway and *pal* genes are shown in figure 1. As seen in the figure, the application of elicitors, except for SA, significantly increased the expression of genes *pamt*, *kas*, *pal* and *at3*. Hydrogen peroxide was the elicitor with the highest gene expression induction (figure 1). The concentration of hydrogen peroxide at 200 mM, displayed the highest overexpression of the genes involved in capsiate synthesis, especially *pal* and *at3* genes were overexpressed up to 150 and 170 times, respectively, compared to the control. These same genes also displayed a higher expression in the treatment of hydrogen peroxide 400 mM; *pal* expression was up to 40 times, while *pamt* had a 50-times higher expression compared to the control. Treatment with oligosaccharides of xyloglucan (Xh) displayed a similar result as the H_2O_2 400 mM treatment (figure 1). Interestingly, none of the elicitors evaluated in the present study affected height, basal stem diameter and yield of fruits per plant (data not shown). There are some studies using hydrogen peroxide as elicitor showing an increase in the content of phytochemicals in several plants. For instance, Vargas-Hernández *et al.* (2017) evaluated the effect of H_2O_2 on the antimicrobial activity, content of flavonoids, phenolic compounds and capsaicin in methanolic extracts from *C. chinense* fruits. H_2O_2 treatment increased 0.9 to 2 mg of capsaicinoids by gram of dry sample. In other plant species, a similar response was obtained using foliar application of H_2O_2 at 0.05 and 0.5 mM on *Mentha piperita* plants, where this elicitor significantly increased the content of phenolic compounds, flavonoids and other secondary metabolites (Figueroa-Pérez *et al.* 2014). Another study showed that the use of hydrogen peroxide on *Aquilaria sinensis* influenced the sesquiterpene content, a secondary metabolite present in this species (Zhang *et al.* 2014). On the other hand, the use of oligosaccharides increased the content of plant secondary metabolites. Zamboni *et al.* (2006)

Table 1. Sequence of oligonucleotides designed for gene expression analysis of capsiate biosynthesis pathway in *C. annuum* L. 509–45-1

Name	Sequence oligos (5′-3′)	Product size (bp)	Genbank accession No.
*Ca*pAmt-F	GGATCCAAAGCTTGTTTATCCTAA	148	AF085149
*Ca*pAmt-R	GGATCCTGTAAATAATTGTGGATAA		
*Ca*Kas-F	GGATCCTGTCCAAATTTGCTTGT	154	AF085148
*Ca*Kas-R	GGATCCTTAGGTAGAAGGGGT		
*Ca*Ubiqutin-F	CGTGGTGGCTTTTGAGAAT	100	AY496112
*Ca*Ubiqutin-R	AAGCACACAAACACAATGTCA		
*Cfr*AT3-F	AGAAGGGAAACTGCCATTTG	115	AY819026
*Cfr*AT3-R	TCTTTCAGGTCTTCCCCATC		
*Cch*Pal-F	ATTCGCGCTGCAACTAAGAT	94	AF088847
*Cch*Pal-R	CACCGTGTAAGGCCTTGTTT		

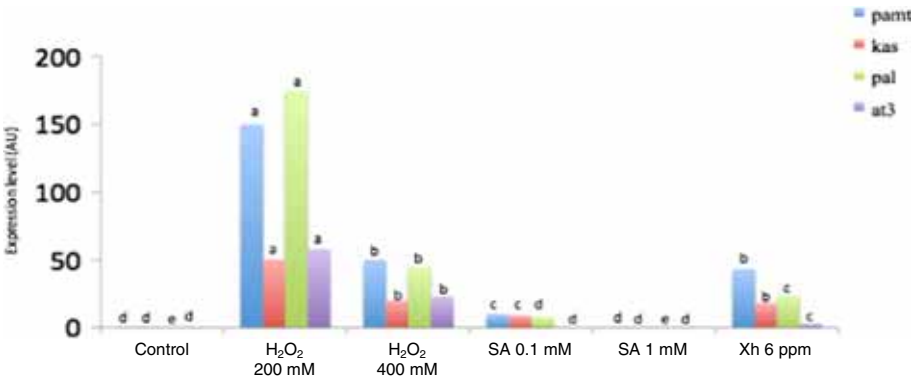

Figure 1. Gene expression one-day-before-harvest of phenylalanine ammonia-lyase (*pal*), putative aminotransferase (*pamt*), b-keto acyl synthase (*kas*) and capsaicin synthase (*at3*) genes in *C. annuum* L. fruits treated with three elicitors. The results obtained for weekly treatments was no significantly different from the ones displayed in this figure (not shown). Different letters in the bars indicate significant difference using Tukey's test (P=0.05).

discovered that the use of oligosaccharides influenced the content of resveratrol in cell culture of different genotypes grape (*Vitis* spp.). The use of oligosaccharides also induces the accumulation of alkaloids in *Papaver somniferum* L, and is known to produce morphine, thebaine, codeine, papaverine and noscapine. Khan *et al.* (2011) showed that a concentration of 120 ppm of alginate oligosaccharides increased the production of morphine 54.3% more than the control, while the content of thebaine, codeine and noscapine did not show significant changes. These data show that use of H_2O_2 and oligosaccharides might increase secondary metabolites contents in several plants including pepper. Hydrogen peroxide within the plant influences gene expression of transcription factors, MAP kinases, miRNAs and other molecules important in plant response to environmental stimuli (Chen *et al.* 2015). The case of *pamt* overexpression is interesting because this is the affected gene that causes the production of capsiate instead of capsaicin in this accession. The aminotransferase encoded by *pamt* catalyses the production of vanillylamine, that is condensed with the 8-methyl-6-nonenoyl-CoA to produce capsiate by *at3*. Our gene expression results strongly indicates that the mutation in *pamt* gene is somehow affecting at post-transcriptional level within the plant, thus explaining the phenotype of capsiate production. Moreover, all the latter results agree with other authors, indicating that plant production of ROS (reactive oxygen species), such as H_2O_2 during the oxidative burst caused by the application of elicitors, is one of the ways in which it can induce overexpression of genes involved in plant defense and secondary metabolism. Chen *et al.* (2015) showed that the use of H_2O_2 at a concentration of 80 µg/mL in cell culture of *Cistanche salsa* influences overexpression of genes related to bioactive components such as phenylethanoid glycosides. Madson *et al.* (2003) showed that structural changes in cell wall hemicellulose induces the activation of defense mechanism of the plant. Regarding the influence of oligosaccharides on the expression of genes involved in the synthesis of secondary metabolites, Ochoa-Villarreal *et al.* (2011) displayed that foliar applications of pectin-derived oligosaccharides on *Vitis vinifera* at a concentration of 1.5 mg/L induces the expression of *pal* gene in fruits of flame seedless grapes. Villegas *et al.* (2016) obtained similar results. These latter authors showed that *pal, myba1, myb5a* genes increased their expression due to the application of pectin-derived oligosaccharides. In the present work the foliar application of a xyloglucan influenced the expression of genes involved in the synthesis of capsinoids. The elicitors evaluated in this work, especially H_2O_2 200 mM, significantly increased both the content of capsiate as well as the gene expression associated with capsiate biosynthesis

Table 2. Capsiate levels in *C. annuum* 509–45-1 fruits in the different elicitation treatments evaluated. Different letters in the column indicates significant difference using Tukey's test (P=0.05)

Treatment	mg capsiate/g fresh sample
One-day-before-harvest	
Control	0.55_e
H_2O_2 200 mM	1.36_a
H_2O_2 400 mM	1.02_b
SA 1 mM	0.62_d
SA 0.1 mM	0.62_d
Xyloglucan (Xh) 6 ppm	0.71_c
Weekly	
Control	0.57_e
H_2O_2 200 mM	1.12_a
H_2O_2 400 mM	1.08_a
SA 1 mM	0.61_d
SA 0.1 mM	0.54_e
Xyloglucan (Xh) 6 ppm	0.68_c

(capsaicinoids and phenyl propanoids pathways). Our results suggested that the use of these elicitors one day before harvest is sufficient to positively influence the production of capsiate in fruits of *C. annuum* L. The strategy of foliar application of elicitors one day before harvesting, especially the use of hydrogen peroxide of 200 mM, may be useful in obtaining a larger amount of capsiate in fruits of *C. annuum* L. Thus, controlled elicitation of the studied capsiate-producing accession using H_2O_2 might be a new strategy to increase the contents of capsiate in these plants.

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References

Abraham-Juarez MD, Rocha-Granados MD, Lopez MG, Rivera-Bustamante RF and Ochoa-Alejo N 2008 Virus-induced silencing of Comt, pAmt and kas genes results in a rediuction of capsaicinoid accumulation in chili pepper fruits. *Planta* **227** 681–895

Amin ARMR, Kucuk O, Khuri FR and Shin DM 2009 Perspectives for cancer prevention with natural compounds. *J. Clin. Oncol*. **27** 2712–2725

Bigliardi B, Galati F 2013 Innovation trends in the food industry: the case of functional foods. *Trends Food Sci. Technol.* **31** 118–129

Booth FW, Roberts CK, Laye MJ 2012 Lack of exercise is a major cause of chronic diseases. *Compr. Physiol*. **2** 1143–1211

Chapa-Oliver AM and Mejia-Teniente L 2016 Capsaicin: from plants to a cancer-suppressing agent. *Molecules* **21** 931–945

Chen J, Yan Y and Guo Z 2015 Identification of hydrogen peroxide responsive ESTs involved in phenylethanoid glycoside biosynthesis in *Cistanche salsa. Cell Culture* **59** 695–700

Cross AJ, Ferrucci LM, Risch A, Graubard BI, Ward MH, Park Y, Hollenbeck AR, Schatzkin A, Sinha R 2010 A large prospective study of meat consumption and colorectal cancer risk: an investigation of potential mechanisms underlying this association. *Cancer Res*. **70** 2406–2414

Dinkova-Kostova AT and Kostov RV 2012 Glucosinolates and isothiocyanates in health and disease. *Trends Mol. Med.* **18** 337–347

Figueroa-Pérez MG, Rocha-Guzmán NE, Mercado-Silva E, Loarca-piña G and Reynoso-Camacho R 2014 Effect of chemical elicitors on peppermint (*Mentha piperita*) plants and their impact on the metabolite profile and antioxidant capacity of resulting infusions. *J. Food Chem.* **156** 273–278

Jarret RL, Bolton J and Perkins B 2014 509-45-1, a *Capsicum annuum* pepper germplasm containing high concentrations of capsinoids. *Hortscience* **49** 107–108

Kampa M and Castanas E 2008 Human health effects of air pollution. *Environ. Pollut.* **151** 362–367

Khan ZH, Khan MMA, Aftab T, Idrees M and Naeem M 2011 Influence of alginate oligosaccharides on alkaloids in opium. *Front. Agric. China* **5** 122–127

Kisaka H, Lang Y, Sugiyama R, Miwa T and Yazawa S 2011 Genetically modified plant capable of biosynthesizing capsinoid. US Patent 2011/0166371A1

Kobata K, Toyoshima M, Kawamura M and Watanabe T 1998 Lipase-catalyzed synthesis of capsaicin analogs using natural oils as an acyl donor. *Biotechnol. Lett.* **20** 781–783

Kok BE, Coffey KA, Cohn MA, Catalino LI, Vacharkulksemsuk T, Algoe SB, Brantley M and Fredrickson BL 2013 How positive emotions build physical health : perceived positive social connections account for the upward spiral between positive emotions and vagal tone. *Psychol. Sci*. **24** 1123–32

Madson M, Dunand C, Li X, Verma R, Vanzin GF, Caplan J, Shoue DA, Carpita NC and Reiter W 2003 The MUR3 gene of arabidopsis encodes a xyloglucan galactosyltransferase that is evolutionarily related to animal exostosins. Plant Cell **15** 1662–1670

Masuda Y, Haramizu S, Oki K, Ohnuki K, Watanabe T, Yazawa S, Kawada T, Hashizume S and Fushiki T 2003 Upregulation of uncoupling proteins by oral administration of capsiate, a nonpungent capsaicin analog. *J. Appl. Physiol*. **95** 2408–2415

Mejía-Teniente L, Durán-Flores FD, Chapa-Oliver AM, Torres-Pacheco I, Cruz-Hernández A, González-Chavira MM, Ocampo-Velázquez RV and Guevara-González RG 2013 Oxidative and molecular responses in *Capsicum annuum* L. after hydrogen peroxide, salicylic acid and chitosan foliar applications. *Int. J. Mol. Sci.* **14** 10178–10196

Ochoa-Villarreal M, Vargas-Arispuro I, Islas-Osuna MA, González-Aguilar G and Martínez-Téllez MÁ 2011 Pectin-derived oligosaccharides increase color and anthocyanin content in flame seedless grapes. *J. Sci. Food Agric.* **91** 1928–1930

Ohnuki K, Haramizu S, Oki K, Watanabe T, Yazawa and Fushiki T 2001 Administration of capsiate, a non-pungent capsaicin analog, promotes energy metabolism and suppresses body fat accumulation in mice. *Biosci. Biotechnol. Biochem.* **65** 2735–2740

Rosa A, Deiana M, Casu V, Paccagnini S, Appendino G, Ballero M and Dessi MA 2002 Antioxidant activity of capsinoids. *J. Agric. Food Chem.* **50** 7396–7401

Rubi M, Campos S, Gómez KR, Ordoñez YM and Ancona DB 2013 Polyphenols, ascorbic acid and carotenoids contents and antioxidant properties of habanero pepper (*Capsicum chinense*) fruit. *Food Nutr. Sci.* **4** 47–54

Sasahara I, Furuhata Y, Iwasaki Y, Inoue N, Sato H, Watanabe T and Takahashi M 2010 Assessment of the biological similarity of three capsaicin analogs (capsinoids) found in non-pungent chili pepper (CH-19 sweet) fruits. *Biosci. Biotechnol. Biochem.* **74** 274–278

Singh S, Jarret R, Russo V, Majetich G, Shimkus J, Bushway R and Perkins B 2009 Determination of capsinoids by HPLC-DAD in capsicum species. *J. Agric. Food Chem.* **57** 3452–3457

Tani Y, Fujioka T, Sumioka M, Furuichi Y, Hamada H and Watanabe T 2004 Effects of capsinoid on serum and liver lipids in hyperlipidemic rats. *J. Nutr. Sci. Vitaminol.* **50** 351–355

Tierranegra-Garcia N, Salinas-Soto P, Torres-Pacheco I, Ocampo-Velazquez RV, Rico-Garcia E, Mendoza-Diaz SO, Feregrino-Perez AA, Mercado-Luna A, Vargas-Hernandez M, Soto-Zarazua GM and Guevara-Gonzalez RG 2011 Effect of foliar salicylic acid and methyl jasmonate applications on protection

against pill-bugs in lettuce plants (*Lactuca sativa*). *Phytoparasitica* **39** 137–144

Valin H, Sands RD, van der Mensbrugghe D, Nelson GC, Ahammad H, Blanc E, Bodirsky B, Fujimori S, Hasegawa T, Havlik P, Heyhoe E, Kyle P, Mason-D'Croz D, Paltsev S, Rolinski S, Tabeau A, van Meijl H, von Lampe M and Willenbockel D 2013 The future of food demand: understanding differences in global economic models. *Agric. Econ*. **45** 51–67

Vargas-Hernández M, Torres-Pacheco I, Gautier F, Álvarez-Mayorga B, Cruz-Hernández A, García-Mier L, Jiménez-García SN, Ocampo-Velázquez RV, Feregrino-Perez AA and Guevara-Gonzalez RG 2017 Influence of hydrogen peroxide foliar applications on in vitro antimicrobial activity in *Capsicum chinense* Jacq. *Plant Biosyst. -Int. J. Deal. Asp. Plant Biol.* **151** 269–275

Villegas D, Handford M, Alcalde JA and Perez-Donoso A 2016 Exogenous application of pectin-derived oligosaccharides to grape berries modifies anthocyanin accumulation, composition and gene expression. *Plant Physiol. Biochem*. **104** 125–1

Wong GY and Gavva NR 2009 Therapeutic potential of vanilloid receptor TRPV1 agonists and antagonists as analgesics: recent advances and setbacks. *Brain Res. Rev.* **60** 267–277

Zamboni A, Vrhovsek U, Kassemeyer HH, Mattivi F and Velasco R 2006 Elicitor-induced resveratrol production in cell cultures of different grape genotypes (Vitis spp.). *Vitis* **45** 63–68

Zhang Z, Zhang X, Yang Y, Wei, J-he, Meng H, Gao Z-h and Xu Y-h 2014 Hydrogen peroxide induces vessel occlusions and stimulates sesquiterpenes accumulation in stems of *Aquilaria sinensis*. *Plant Growth Regul.* **72** 81–87

Zhao J, Davis LC and Verpoorte R 2005 Elicitor signal transduction leading to production of plant secondary metabolites. *Biotechnol. Adv.* **23** 283–333

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