Diversity of bacterial endophytes in *Panax ginseng* and their protective effects against pathogens

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Abstract

Although endophytic bacteria are known to colonize *Panax ginseng*, little is known about their diversity and roles. We addressed in the present study by comparing endophytic bacterial populations in *P. ginseng* plants of different ages (2–6 years) and in various tissue types (root, stem, leaf, and flower stalk). A total of 116 strains assigned to 42 species were identified by 16S rDNA sequencing. The predominant phylum was *Firmicutes*. Two-year-old ginseng plants and root tissues showed the greatest diversity of endophytic bacteria, with *Bacillales* being the predominant order. The antifungal activity of isolates against two pathogens, *Cylindrocarpon destructans* and/or *Botrytis cinerea*, was evaluated in dual-culture assays. In total, 28 strains showed antifungal activity with PgBE14 (*Bacillus amyloliquefaciens*), PgBE40 (*B. megaterium*), PgBE39, PgBE45 (*Pseudomonas frederiksbergensis*), and PgBE42 (*Staphylococcus saprophyticus*) inhibiting both pathogens. These results improve our understanding of the structure and diversity of endophytic bacterial communities of *P. ginseng* and identify strains with antifungal activity that have potential applications as biocontrol agents.

Keywords Bacterial endophyte · *Panax ginseng* · *Cylindrocarpon destructans* · *Botrytis cinerea*

Introduction

Endophytic bacteria colonize and interact with plants without causing disease symptoms (Hardoim et al. 2015). They are ubiquitous across plant species and inhabit various plant tissues, and can have beneficial effects such as enhancement of plant growth, phytopathogen inhibition, phytoremediation, and antibiotic production (Ryan et al. 2008). Due to the stable habitat provided by the host plant, endophytic bacteria experience low competition for nutrients and are protected from various sources of external stress (Hardoim et al. 2015; Hong et al. 2015; Park et al. 2007). These bacteria can thus exert more consistent effects than phyllospheric or rhizospheric bacteria that exist outside the plant body. Recent studies have examined endophytic bacterial populations in plants; however, a detailed understanding of their distribution, diversity, and roles in most plants is lacking.

Panax ginseng is cultivated in the shade on a single patch of soil for a minimum of 4–6 years, which makes them highly vulnerable to pathogens and to the external environment (Cho et al. 2008). Therefore, producing ginseng with commercial value requires the continuous use of chemical pesticides that effectively prevent plant diseases but may contaminate soil or water supplies and have toxic effects on mammals. Moreover, their long-term use is associated with reduced soil fertility and diversity of rhizospheric bacteria. Ecofriendly agents have been proposed as an alternative to agricultural chemicals and has resulted in active research aimed at the development and application of biocontrol agents based on rhizospheric and endophytic bacteria such as *Bacillus* and *Pseudomonas* species (Verhagen et al. 2010).

Most studies of ginseng endophytes have focused on the classification and functional characterization of fungi with little known about endophytic bacteria (Eo et al. 2014; Park et al. 2012a, b, 2017); and only a few have examined endophytic bacterial populations in specific tissues and at different ages or in plants from different regions (Cho et al. 2007; Chowdhury et al. 2017; Vandan et al. 2010). One study of 51 bacterial strains isolated from the stems of 1- and 4-year-old ginseng plants found that *Bacillus* and *Staphylococcus* were the predominant genera (Vandan et al. 2010). Additionally,

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Bacillus megaterium, *Micrococcus luteus*, *Bacillus cereus*, and *Lysinibacillus fusiformis* were found to promote plant growth based on expression of the *nitrogen fixation* gene, phosphate solubilization, and indole-3-acetic acid (IAA) production (Vendan et al. 2010). In another study, *Pseudomonas* and *Bacillus* were the common endophyte genera among 63 strains isolated from 5-year-old ginseng roots collected from three regions (Ganghwa, Geumsan, and Jinan) in Korea (Cho et al. 2007). Endophytic bacteria from four phyla (*Proteobacteria*, *Firmicutes*, *Bacteroidetes*, and *Actinobacteria*) were recently isolated from three tissues (root, stem, and leaf) of 4-year-old mountain-cultivated ginseng collected from various areas; analyses of a wide range of properties including β -galactosidase activity, siderophore production, phosphate solubilization, and IAA and hydrogen cyanide production suggested that these bacteria are beneficial to ginseng growth and pathogen defense (Chowdhury et al. 2017).

The present study investigated endophytic bacterial communities isolated from various tissues of ginseng plants of different ages, and characterized the inhibitory effect of these bacteria against *Cylindrocarpon destructans* and *Botrytis cinerea*—the major fungal pathogens in ginseng—to evaluate their potential as biocontrol agents.

Materials and methods

Isolation of bacterial endophytes

To isolate endophytic bacteria from ginseng, 2- to 6-year-old plants were collected from the National Institute of Horticultural and Herbal Science of the Rural Development Administration in Chungbuk Province, Republic of Korea (127°45'13.14"E, 36°56'36.63"N). A total of 10 samples of each age were harvested and separated into root, stem, leaf, and flower stalk portions. Soil on the tissue surface was removed by washing with tap water. Samples were disinfected with 70% ethanol for 1 min followed by 12% NaOCl for 3 min and then rinsed three times with sterilized water. Samples of the same age and tissue were combined into a single tube, and 200 mg of each sample were homogenized in 1 ml sterilized water using a tissue lyser. A 100- μ l volume of each suspension diluted to 10^0 , 10^{-1} , 10^{-2} , and 10^{-3} was spread onto a Luria–Bertani agar plate and cultured at room temperature until colonies had formed. Single colonies were isolated and cultured at 28 °C and 200 rpm for 12 h and then stored at –80 °C until use.

16S rRNA analysis

For bacterial identification, 16S rDNA was amplified and the sequence was determined using the universal bacterial

16S rRNA primers 518F (5'-CCAGCAGCCGCGGTAATACG-3') and 800R (5'-TACCAGGGTATCTAATCC-3'). The 16S rDNA sequences were compared with corresponding reference sequences retrieved from GenBank databases by BLAST search. The nucleotide sequences of all 116 ginseng bacterial endophytes have been deposited in GenBank under accession numbers MH144224–MH144340.

In vitro antagonistic assay

C. destructans mycelia were cultured at 20 °C for 1 week and *B. cinerea* mycelia were cultured at 28 °C for 3 days before use. A piece of each fungal mycelium was inoculated on the center of a potato dextrose agar plate. After 1 or 2 days, 10 μ l of the bacterial suspension with OD₆₀₀ = 1.0 or 0.1 was added as a drop and growth inhibition was monitored. Images were obtained after 3 days of co-cultivation of the fungus and endophytic bacteria.

Statistical analysis

Tukey's honest significant difference test was used to compare mean Shannon indices. All statistical analyses were performed using SPSS v.18 software (IBM, Armonk, NY, USA).

Results and discussion

Distribution of endophytic bacteria of *P. ginseng*

A total of 116 strains from 42 different species were isolated from *P. ginseng* plants. The 16S rDNA sequence of each strain showed 97–100% identity to known species (Table 1). The 42 species represented 20 genera, including *Bacillus* ($n=11$ species), *Acinetobacter* ($n=5$), *Microbacterium* ($n=4$), *Pseudomonas* ($n=3$), *Staphylococcus* ($n=3$), *Stenotrophomonas* ($n=2$), *Agrobacterium* ($n=1$), *Brevundimonas* ($n=1$), *Curtobacterium* ($n=1$), *Exiguobacterium* ($n=1$), *Lysinibacillus* ($n=1$), *Massilia* ($n=1$), *Micrococcus* ($n=1$), *Ochrobactrum* ($n=1$), *Paenibacillus* ($n=1$), *Phyllobacterium* ($n=1$), *Ralstonia* ($n=1$), *Rhizobium* ($n=1$), *Sphingopyxis* ($n=1$), and *Variovorax* ($n=1$) in the phyla *Firmicutes* (52%), *Proteobacteria* (39%), and *Actinobacteria* (9%). Notably, 34 strains (i.e., 30% of all strains) belonged to *Bacillus*, which was the predominant genus. *B. aryabhattai* ($n=9$) and *B. amyloliquefaciens* ($n=8$) were the most abundant *Bacillus* strains. The latter is an endophytic bacterium associated with ginseng (Vendan et al. 2010). *Firmicutes*, *Proteobacteria*, *Actinobacteria*, and *Bacteroidetes* have been previously isolated from *P. ginseng* and *Panax notoginseng* (Ma et al. 2013; Vendan et al. 2010). Although there have been no reports on the endophytic bacteria of

Table 1 Identification of endophytic bacteria in *P. ginseng*

Isolate	Most closely related species (accession no.)	Tissue	Age (years)	Identity year (%)
PgBE10	<i>Acinetobacter calcoaceticus</i> (NR_042387)	L	3	100
PgBE47, PgBE57	<i>Acinetobacter guillouiae</i> (NR_117626)	L, S	5, 6	98–99
PgBE37	<i>Acinetobacter johnsonii</i> (NR_117624)	L	5	99
PgBE20	<i>Acinetobacter lwoffii</i> (NR_113346)	L	4	99
PgBE3, PgBE16, PgBE18, PgBE26, PgBE34, PgBE46, PgBE52, PgBE237, PgBE241, PgBE243, PgBE245, PgBE246, PgBE252, PgBE255	<i>Acinetobacter pittii</i> (NR_117621)	L, S, F, R	2, 3, 4, 5	99–100
PgBE235	<i>Agrobacterium tumefaciens</i> (NR_115516)	S	2	99
PgBE1, PgBE8, PgBE14, PgBE24, PgBE30, PgBE51, PgBE59, PgBE240	<i>Bacillus amyloliquefaciens</i> (NR_075005)	L, S, F, R	2, 3, 4, 5, 6	99
PgBE2, PgBE22, PgBE38, PgBE54, PgBE62, PgBE231, PgBE242, PgBE254, PgBE258	<i>Bacillus aryabhatai</i> (NR_115953)	L, S, F, R	2, 4, 3, 5, 6	99–100
PgBE247	<i>Bacillus cereus</i> (NR_074540)	R	4	99
PgBE5	<i>Bacillus endophyticus</i> (NR_025122)	R	2	99
PgBE15	<i>Bacillus marisflavi</i> (NR_025240)	S	3	99
PgBE7, PgBE11, PgBE13, PgBE35, PgBE49, PgBE70	<i>Bacillus megaterium</i> (NR_117473)	L, S, F, R	2, 3, 5, 6	99–100
PgBE49	<i>Bacillus safensis</i> (NR_113945)	S	5	99
PgBE6, PgBE23, PgBE25, PgBE230, PgBE238	<i>Bacillus subtilis</i> (NR_027552)	S, R	2, 3, 4	99–100
PgBE61	<i>Bacillus thuringiensis</i> (NR_114581)	R	6	99
PgBE4	<i>Brevibacterium halotolerans</i> (NR_115063)	R	2	99
PgBE249	<i>Brevibacterium frigoritolerans</i> (NR_115064)	R	4	99
PgBE72	<i>Brevundimonas vesicularis</i> (NR_113586)	F	6	99
PgBE223	<i>Curtobacterium citreum</i> (NR_026156)	L	2	99
PgBE19	<i>Exiguobacterium indicum</i> (NR_042347)	L	4	99
PgBE261	<i>Lysinibacillus fusiformis</i> (NR_112628)	L, R	6	98–99
PgBE21	<i>Massilia suwonensis</i> (NR_116872)	L	4	98
PgBE9	<i>Microbacterium foliorum</i> (NR_025368)	S	2	99
PgBE263	<i>Microbacterium natoriense</i> (NR_042983)	R	6	99
PgBE17, PgBE41, PgBE48, PgBE239	<i>Microbacterium oxydans</i> (NR_044931)	S, R	3, 5	99
PgBE67, PgBE224	<i>Microbacterium phyllosphaerae</i> (NR_025405)	L, S	2, 6	97–99
PgBE262	<i>Micrococcus luteus</i> (NR_075062)	L	6	99
PgBE66	<i>Ochrobactrum rhizosphaerae</i> (NR_042600)	S	6	99
PgBE250	<i>Paenibacillus lautus</i> (NR_117185)	R	4	99
PgBE228	<i>Phyllobacterium ifriqiense</i> (NR_043192)	R	2	99
PgBE29, PgBE71	<i>Pseudomonas azotoformans</i> (NR_113600)	F	4, 6	99
PgBE39, PgBE45, PgBE253, PgBE257	<i>Pseudomonas frederiksbergensis</i> (NR_117177)	L, S, R	5	99
PgBE27, PgBE36, PgBE56, PgBE244, PgBE266, PgBE267	<i>Pseudomonas koreensis</i> (NR_025228)	L, S, F	3, 4, 5, 6	99–100
PgBE226, PgBE227	<i>Ralstonia pickettii</i> (NR_102967)	L	2	99
PgBE43	<i>Rhizobium giardinii</i> (NR_026059)	R	5	98
PgBE233	<i>Sphingopyxis chilensis</i> (NR_024631)	R	2	99
PgBE265	<i>Staphylococcus epidermidis</i> (NR_036904)	R	6	99
PgBE31, PgBE32, PgBE33, PgBE42, PgBE44, PgBE53, PgBE55, PgBE60, PgBE64, PgBE65, PgBE68, PgBE225, PgBE236, PgBE251, PgBE256, PgBE259, PgBE260, PgBE264, PgBE268, PgBE269, PgBE270	<i>Staphylococcus saprophyticus</i> (NR_115607)	L, S, F, R	2, 4, 5, 6	98–100
PgBE234	<i>Staphylococcus warneri</i> (NR_102499)	R	2	99
PgBE28	<i>Stenotrophomonas maltophilia</i> (NR_041577)	S	4	99
PgBE12, PgBE58	<i>Stenotrophomonas rhizophila</i> (NR_121739)	L, R	3, 6	99

Table 1 (continued)

Isolate	Most closely related species (accession no.)	Tissue	Age (years)	Identity year (%)
PgBE229, PgBE248	<i>Variovorax boronicumulans</i> (NR_114214)	R	2, 4	99–100

F flower stalk, L leaf, R root, S stem

Panax quinquefolius, our results suggest that plants of this genus are inhabited by similar bacterial taxa.

Endophytic bacteria of *P. ginseng* according to plant age and tissue type

We examined the distribution and diversity of bacterial taxa with respect to plant age. At the order level, the most abundant strains were *Bacillales* in plants of all ages, except in 3-year-old plants in which *Pseudomonadales* was predominant (Fig. 1a). Similarly, *Firmicutes* was the most abundant phylum in plants of all ages except 3-year-old ginseng, in which *Proteobacteria* was more abundant (Fig. 1b). The 2- and 6-year-old ginseng plants harbored six and seven orders, respectively, with relatively high diversity, although the Shannon diversity indices indicated that the diversity was slightly higher (nine species) in younger plants. On the

other hand, 3-year-old ginseng had a relatively low Shannon diversity index (Fig. 1c). *B. amyloliquefaciens* and *B. aryabhattai* were present in plants of all ages (Fig. 1d). Endophytic bacterial profiles of plants vary according to plant, age, habitat, tissue type, and other environmental factors (Hardoim et al. 2015; Ryan et al. 2008). We found differences in endophytic bacterial abundance among plants of different ages even though they were cultivated in the same region. This could be due to differences in the frequency and concentration of agricultural chemicals used at different stages of ginseng development and the resultant changes in the soil environment.

We analyzed endophytic bacterial abundance according to tissue type (root, stem, leaf, and flower stalk) and found that *Bacillales* was predominant in all tissues except in the stem (Fig. 2a), in which identical numbers of isolates were identified as *Bacillales* and *Pseudomonadales*. At the phylum

Fig. 1 Distribution and diversity of endophytic bacterial taxa in ginseng plants of different ages. Relative abundance at the level of order (a) and phylum (b) in isolates from individual ginseng plants. c Shannon index of bacterial communities in isolates from each ginseng

plant. Bars indicate standard error. ns Non-significant by ANOVA ($n=17$). $*P<0.05$. d Venn diagram representing the number of unique and common strains in ginseng plants of different ages

Fig. 2 Distribution and diversity of endophytic bacterial taxa in different tissues of ginseng. Relative abundance at the level of order (a) and phylum (b) in isolates from individual ginseng plants. c Shannon

level, *Actinobacteria* was not detected in the flower stalk while the root, stem, and leaf tissues harbored *Firmicutes*, *Proteobacteria*, and *Actinobacteria* (Fig. 2b). The proportion of isolates identified as *Firmicutes* was greater in the root and flower stalk than in other parts, and *Proteobacteria* were more abundant in the stem. *Firmicutes* and *Proteobacteria* were equally represented in the leaf. Among strains isolated from mountain-cultivated ginseng, *Firmicutes* was reported to be more abundant in the root and leaf than in the stem (Chowdhury et al. 2017), which is in partial agreement with the results of this study.

The root tissue had a higher Shannon diversity index than other tissues and harbored the largest number of tissue-specific species and overall species (Fig. 2c). Four species were common to all tissues—namely, *B. amyloliquefaciens*, *B. aryabhatai*, *B. megaterium*, and *Staphylococcus saprophyticus* (Fig. 2d). Root tissue has the largest population of endophytic bacteria, with a lower abundance in the above-ground parts of the plant (McInroy and Kloepper 1995). This was confirmed in the present study, suggesting that the endophytic bacteria of ginseng mainly interact with the root tissue, which is the main part of the plant that is used for commercial purposes. Additionally, many endophytic

indices in different tissues. Bars indicate standard error. ns, Non-significant by ANOVA ($n=21$). * $P<0.05$. d Venn diagram representing the number of strains unique or common to the four tissues

bacteria are known to co-exist with rhizobacteria, which colonize the plant via the root hairs (Hardoim et al. 2015). Given that several soil-borne pathogens are known to affect ginseng root tissue, the presence and interactions of these bacteria can potentially be exploited for biocontrol. Ginseng adventitious root biomass and ginsenoside accumulation have been shown to increase following treatment with the ginseng endophytic bacterium LB 5-3 (Song et al. 2017). Thus, clarifying the functions and interactions of endophytic bacteria can contribute to the stable cultivation and harvesting of ginseng.

Antagonistic activity of endophytic bacteria of *P. ginseng*

In vitro screening of the 116 isolates for antifungal activity against host pathogens was performed (Fig. 3). *C. destructans* and *B. cinerea* cause root rot and gray mold disease in ginseng plants. A total of 26 and seven strains showed antifungal activity against *C. destructans* and *B. cinerea*, respectively. Two species each of *Bacillus* (PgBE14 and PgBE40) and *Pseudomonas* (PgBE39 and PgBE45) and one species of *Staphylococcus* (PgBE42) showed inhibitory

Fig. 3 Antifungal activity of isolates against ginseng pathogens. **a** *Cylindrocarpon destructans* was cultured on a potato dextrose agar (PDA) plate for 7 days at 20 °C. **b** *Botrytis cinerea* was cultured on a PDA plate for 2 days at 28 °C in the dark. After 2 days of pre-culti-

vation of the indicated fungal pathogen, 10 µl of bacterial suspension (OD₆₀₀=0.1 or 0.01) or distilled water (DW; control) were added as a drop to the plate 1.5–2.0 cm away from the fungal disc. Images were obtained after 2–3 days of co-cultivation

activity against both pathogens (Fig. 3). These results are in accordance with a previous report that *Bacillus* suppressed ginseng root rot pathogen proliferation (Jang et al. 2011). Interestingly, for endophytic bacteria with inhibitory effects against both *C. destructans* and *B. cinerea*, the pattern of inhibition differed depending on the target pathogen. Although there was no visible zone of inhibition,

Pseudomonas species directly suppressed the growth of *C. destructans*. In the case of *B. cinerea*, a clear zone of inhibition was formed that was concentration independent (Fig. 3b). In contrast, *Bacillus* and *Staphylococcus* showed more potent inhibition of *C. destructans* and relatively weak inhibition of *B. cinerea*. These results suggest that Gram-negative and -positive bacteria act via distinct inhibitory

mechanisms or release pathogen-specific metabolites. The strains isolated in this study that exhibit strong antifungal activity likely produce diverse physiologically active substances and may, therefore, be useful for the development of effective biocontrol agents.

Concluding remarks

The results of this study showed that the community composition and structure of endophytic bacteria that colonize *P. ginseng* differ according to plant age and tissue type. Given that several isolates showed antifungal activity against the major fungal pathogens of *P. ginseng*, additional studies are warranted to identify the specific metabolites inhibiting pathogen growth.

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Author contributions I-HJ, CEH, JUK, JWL and SWL conceived and designed the experiments; CEH performed the experiments; IHJ and CEH analyzed the data; CEH and I-HJ wrote the manuscript. All authors critically read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

- Cho KM, Hong SY, Lee SM, Kim YH, Kang GG, Lim YP, Kim H, Yun HD (2007) Endophytic bacterial communities in ginseng and their antifungal activity against pathogens. *Microb Ecol* 54:341–351
- Cho HS, Jeon YH, Do GR, Cho DH, Yu YH (2008) Mycological characteristics of *Botrytis cinerea* causing gray mold on ginseng in Korea. *J Ginseng Res* 32:26–32
- Chowdhury EK, Jeon J, Rim SO, Park YH, Lee SK, Bae H (2017) Composition, diversity and bioactivity of culturable bacterial endophytes in mountain-cultivated ginseng in Korea. *Sci Rep* 7:10098
- Eo JK, Choi MS, Eom AH (2014) Diversity of endophytic fungi isolated from Korean ginseng leaves. *Mycobiology* 42:147–151
- Hardoim PR, van Overbeek LS, Berg G, Pirttilä AM, Compant S, Campisano A, Döring M, Sessitsch A (2015) The hidden world within plants: ecological and evolutionary considerations for defining functioning of microbial endophytes. *Microbiol Mol Biol Rev* 79:293–320
- Hong CE, Jo SH, Moon JY, Lee JS, Kwon SY, Park JM (2015) Isolation of novel leaf-inhabiting endophytic bacteria in *Arabidopsis thaliana* and their antagonistic effects on phytopathogens. *Plant Biotechnol Rep* 9:451–458
- Jang YL, Kim SG, Kim YH (2011) Biocontrol efficacies of *Bacillus* species against *Cylindrocarpum destructans* causing ginseng root rot. *Plant Pathol J* 27:333–341
- Ma L, Cao YH, Cheng MH, Huang Y, Mo MH, Wang Y, Yang JZ, Yang FX (2013) Phylogenetic diversity of bacterial endophytes of *Panax notoginseng* with antagonistic characteristics towards pathogens of root-rot disease complex. *Antonie Van Leeuwenhoek* 103:299–312
- McInroy JA, Kloepper JW (1995) Survey of indigenous bacterial endophytes from cotton and sweet corn. *Plant Soil* 173:337–342
- Park SY, Yang SH, Choi SK, Kim JG, Park SH (2007) Isolation and characterization of endophytic bacteria from rice root cultivated in Korea. *Kor J Microbiol Biotechnol* 35:1–10
- Park YH, Kim YC, Park SU, Lim HS, Kim JB, Cho BK, Bae H (2012a) Age-dependent distribution of fungal endophytes in *Panax ginseng* roots cultivated in Korea. *J Ginseng Res* 36:327–333
- Park YH, Lee SG, Ahn DJ, Kwon TR, Park SU, Lim HS, Bae H (2012b) Diversity of fungal endophytes in various tissues of *Panax ginseng* Meyer cultivated in Korea. *J Ginseng Res* 36:211–217
- Park YH, Kim Y, Mishra RC, Bae H (2017) Fungal endophytes inhabiting mountain-cultivated ginseng (*Panax ginseng* Meyer): diversity and biocontrol activity against ginseng pathogens. *Sci Rep* 7:16221
- Ryan RP, Germaine K, Franks A, Ryan DJ, Dowling DN (2008) Bacterial endophytes: recent developments and applications. *FEMS Microbiol Lett* 278:1–9
- Song X, Wu H, Yin Z, Lian M, Yin C (2017) Endophytic bacteria isolated from *Panax ginseng* improves ginsenoside accumulation in adventitious ginseng root culture. *Molecules* 22:pii: E837
- Vendan RT, Yu YJ, Lee SH, Rhee YH (2010) Diversity of endophytic bacteria in ginseng and their potential for plant growth promotion. *J Microbiol* 48:559–565
- Verhagen BW, Trostel-Aziz P, Couderchet M, Hofte M, Aziz A (2010) *Pseudomonas* spp.-induced systemic resistance to *Botrytis cinerea* is associated with induction and priming of defence responses in grapevine. *J Exp Bot* 61:249–260