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PII: S1049-9644(17)30218-9
DOI: https://doi.org/10.1016/j.biocontrol.2017.10.012
Reference: YBCON 3672

To appear in: *Biological Control*

Received Date: 8 August 2017
Revised Date: 19 October 2017
Accepted Date: 22 October 2017

Please cite this article as: Robles, C.A., Ceriani-Nakamurakare, E., Slodowicz, M., González-Audino, P., Carmarán, C.C., *Granulobasidium vellereum* (Ellis &Cragin) Jülich, a promising biological control agent, *Biological Control* (2017), doi: https://doi.org/10.1016/j.biocontrol.2017.10.012

Granulobasidium vellereum (Ellis &Cragin) Jülich, a promising biological control agent

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Abstract

Studies involving biological control of wood decay fungi and pests in forest areas are scarce. The basidiomycete *Granulobasidium vellereum* (Ellis & Cragin) Jülich has been isolated as wood endophyte from London Plane trees (*Platanus acerifolia* (Ait.) Willd). This basidiomycete produces a variety of sesquiterpenes with antifungal activity. In this study we evaluated the potential activity of *G. vellereum* against wood decay fungi and fungi associated with the ambrosia beetle *Megaplatypus mutatus* Chapuis, an important forest pest in *Populus* sp. A combination of *in vitro* assays was made, in cultures and on wood blocks. *Granulobasidium vellereum*'s Volatile Organic Compounds (FVOCs) were characterized and their potential role in biocontrol was assessed. *Granulobasidium vellereum* did not cause a significant loss of weight on *P. acerifolia* and *Populus* wood and inhibited the growth of the target fungi, mainly when inoculated first. Up to nineteen volatile compounds were determined in *G. vellereum* strains. The growth of all target fungi was inhibited by FVOCs and in some cases the morphology of the fungi was altered. These results indicate that *G. vellereum* can be used as a Biological Control Agent (BCA) of xylophagous fungi and fungi related to forest pests. Further investigations should focus on developing application strategies for *M. mutatus* management.

Keywords

Forestry; Fungal VOCs; *Megaplatypus mutatus*; Wood decay fungi.

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1. Introduction

Biological control of plant pathogens is considered as a method of inhibiting phytopathogens by different microorganisms through mechanisms that mainly involve antibiosis, competition, mycoparasitism, cell wall degrading enzymes or induced resistance (Lo, 1998). Most of the studies involving fungi as Biological Control Agents (BCAs) have focused on the control of soil-borne and foliar plant pathogens (Larran et al., 2016; Schöneberg et al., 2015; Wu et al., 2017). However, studies involving biological control of wood decay fungi and pests in forest areas are scarce (Castrillo et al., 2016; Naidu et al., 2015; Schwarze et al., 2012).

The use of basidiomycetes species as BCAs has been less frequent than the use of ascomycetes. One of the most studied examples is the control of *Heterobasidion annosum* (Fr.) Bref. hyphae by *Phlebiopsis gigantea* (Fr.) Jülich (Annesi et al., 2005; Vainio et al., 2001), mediated through a non-enzymatic diffusible metabolite(s), released only when hyphae are in close proximity. Other examples are *Lentinus squarrosulus* Mont. against *Rigidoporus microporus* (Sw.) Overeem (Sudirman et al., 1992) and *Lenzites betulina* (L.) Fr. against *Coriolus* spp. (Rayner et al., 1987), amongst others.

In a previous study on *Platanus acerifolia* (Ait.) Willd. fungi, symptomatic and asymptomatic trees were sampled (Robles et al., 2015). Several strains of *Granulobasidium vellereum* (Ellis & Cragin) Jülich (syn. *Hypochnicium vellereum* (Ellis & Cragin) Parmasto) were isolated as wood endophytes (from asymptomatic London plane trees) but none were registered from symptomatic trees. This species is a saprotrophic wood-decay basidiomycete fungus found in deciduous forests throughout Europe and East Asia, as well as in North America. It has been reported to produce a variety of secondary metabolites (sesquiterpenes) with potent antifungal, acaricidal or cytotoxic activity (Kokubun et al., 2016; Nord et al., 2013; 2015). Taking into account these characteristics, more thorough research into the compounds with antifungal activity that this species can produce would be relevant.

Volatile organic compounds (VOCs) are low molecular weight compounds, generally lipophilic, which can freely pass through biological membranes and move over great distances, affecting the physiology of competitor organisms. Over 300 Fungal VOCs (FVOCs) have been identified to date, derived from both primary and secondary metabolism pathways (Hung et al., 2015). This number is continuously increasing. These metabolites could be used in biotechnological applications in agriculture, industry and medicine. In agriculture they have potential as biocontrol agents against fungal pathogens, as a sound management strategy by reducing fungicide use on crop plants (Morath et al., 2012). Several fungi have been evaluated for their capacity to produce VOCs with biocide potential. The most studied species belong to the genera *Trichoderma* and *Muscodor,* especially *Muscodor albus* Worapong, Strobel & W.M. Hess (Schalchli et al., 2014). Other fungi have been proved to produce volatile antifungal metabolites as 5-pentyl-2-furaldehyde obtained from *Oxyporus latemarginatus* (Durieu & Mont.) Donk, which inhibited the mycelial growth of pathogens as *Alternaria alternata* (Fr.) Keissl., *Colletotrichum gloeosporioides* (Penz.) Penz. & Sacc. and *Thanatephorus cucumeris* (A. B. Frank) Donk (Lee et al., 2009).

Among the fungal organisms that could be controlled by BCAs are wood decay fungi and fungi associated with ambrosia beetles, both important forest pests in many countries. In Argentina, *Megaplatypus mutatus* Chapuis is a beetle of special importance and it causes extensive damage to poplar plantations (Ceriani-Nakamurakare et al., 2016). The ambrosial mycelia of fungi such as *Raffaelea* spp.., which grow on gallery walls borne by M. mutatus, produce a dark staining that reduces wood quality and its market value (Alfaro et al., 2007).

The aims of this study were: 1) to evaluate the *in vitro* potential activity of the basidiomicete *G. vellereum* as a BCA against xylophagous fungi associated with decayed wood and against fungi associated to *M. mutatus* in *Populus* (ambrosia beetle- forest pest); 2) to evaluate the potential use of *G. vellereum* as a BCA, estimating the degradation capacity of this species on wood of a common forest tree (*Populus* sp.) and a common urban tree (*P. acerifolia*) through dry weight losses, and through oxidase reactions using gallic and tannic acid agar media, tyrosine, paracresol and guaiacol agar media; 3) to characterize the VOCs profile of this basidiomycete and analyze the potential role of FVOCs in biocontrol strategies.

2. Materials and methods

2.1. Strains and culture conditions

The strains used in this study are described in Table 1. All strains were maintained on MEA 2% (Difco Lab.). Mycelial plugs of 5 mm^2 were cut from actively growing colonies for use as inoculum in all assays.

2.2. Biocontrol effect of G. vellereum in dual cultures

In order to establish the potential of *G. vellereum* as a BCA in dual cultures, pairing combinations were used. Five Petri dishes containing MEA 2% medium were inoculated first with a mycelial plug (5 mm^2) of *G. vellereum* (BAFCcult 4363) and then, 3-4 days later, when the *G. vellereum* mycelia nearly covered half the dish, a mycelial plug of the target fungi (listed on Table 1) was placed on the opposite edge of the dish. Other five dishes were inoculated first with each target fungi, and when the mycelia nearly covered half the dish, a mycelial plug of *G. vellereum* was placed on the opposite edge. Petri dishes containing only the target fungi were used as controls. Cultures were maintained at 24ºC in the dark, and examined every 2-4 days for a month. Colonies radii of the treatments were measured and compared with the radii of the control colonies. Inhibition of radial growth (PIRG) of each target fungi after a month was calculated according to Li et al. (2015): PIRG (%) = ((radius of control colony (cm) – 0.5) – (radius of colony in dual culture (cm) -0.5)) / (radius of control colony (cm) – 0.5) x 100. Interaction values were assessed as follows: (++): overgrowth of the target fungi. (+): no overgrowth but inhibition of the growth of the target fungi. (-): no inhibition of the target fungi. (+/-): inhibition of the target fungi only in some replicates.

Mycelium in the interaction zones was observed under optical microscope.

2.3. Biocontrol effect of G. vellereum on wood blocks

In order to evaluate the effectiveness of *G. vellereum* (BAFCcult 4363) as a biocontrol agent against 4 different decay fungi (*Bjerkandera adusta* (Willd.) P. Karst., *Inonotus rickii* (Pat.) D.A. Reid., *Ganoderma resinaceum* Boud. and *Trametes trogii* Berk.) on London plane tree (*P. acerifolia*) wood blocks, loss in dry weight was calculated. Wood blocks of 1 × 2 × 0.5 cm, including sapwood and heartwood, were cut from either sound *P. acerifolia* or *Populus* branches, accordingly to Robles et al. (2011). Blocks dried at 70ºC for 48 h were conditioned at 30ºC and weighed to determine the initial dry weight. Each block was then saturated by immersion in distilled water for 48 h and sterilized in an autoclave for 20 min at 105 kPa.

Dual culture treatments were performed as follows: MEA 1.25% slopes in 19 cm × 2 cm test tubes were inoculated with a mycelial plug (0.6 diam) of one fungus and then incubated at 25ºC. Once the mycelium covered the surface of the agar, one sterilized wood block was introduced into each test tube. Six days after introducing the wood block, the second fungus was inoculated by placing a mycelial plug on the wood block already colonized by the first fungus. One set of test tubes was inoculated first with *G. vellereum*, followed by one of the white-rot fungi (biocontrol agent + decay fungi). Another set of test tubes was inoculated first with each decay fungus followed by *G. vellereum* (decay fungi + biocontrol agent). Wood blocks without inoculum were used as control. Seventeen replicates were arranged for each treatment. After 3 months of incubation in the dark at 25ºC, wood blocks were removed from the test tubes and the surface mycelium was gently cleaned off. Blocks were dried at 70ºC for 48 h, then at 30ºC and weighed to determine the final dry weight. Initial and final dry weights were used to calculate the dry weight loss (DWL) caused by decay according to Mielnichuk and Lopez (2007): DWL (%) = [(initial dry weight) final dry weight)/initial dry weight] x100. The dry weight loss results were compared with those caused by single cultures of decay fungi on *P. acerifolia* wood blocks (Robles et al., 2011).

2.4. Degradation ability of G. vellereum

Oxidase reactions were performed using gallic and tannic acid agar media (Anedra S.A., Argentina) (Naidu et al., 2015) and tyrosine, paracresol and guaiacol agar media (0.2%) according to Boidin (1954). The relative intensity of the reaction was recorded one week after dark incubation at 25°C.

In order to evaluate the *G. vellereum´*s ability to alter *P. acerifolia* and *Populus* sp. wood blocks, loss in dry weight caused by *G. vellereum* (BAFCcult 4363) was estimated. MEA 1.25% slopes in 19 cm × 2 cm test tubes were inoculated with a mycelial plug (0.6 diam) of the strain of *G. vellereum* and when the mycelium covered the surface of the agar, a wood block (1 × 2 × 0.5 cm), previously dried, weighed and sterilized (as in section 2.3.), was introduced in each test tube. After 3 months of incubation dry weight loss was calculated as explained in section 2.3. Wood blocks without inoculum were used as controls and 20 replicates were arranged for each treatment.

2.5. Analysis of VOCs produced by G. vellereum

Fungal strains (BAFCcult 4362, 4363, 4365, 4366 and 4367) were grown in 50-ml glass vials with 10 ml of MEA 2% with chloramphenicol (100 mg l^{-1}) and kept in the dark at 20ºC for 15 days. During solidification, the vials were placed at a 45 degree angle with respect to the horizontal direction to increase the surface occupied by the culture, and consequently, the concentration of their VOC emissions in equilibrium vapor (Savelieva et al. 2014). After fungal strains growing period, vials were sealed with Teflon caps with a crimp gripper and VOCs were accumulated for 2 days before analysis, under the same conditions as in the growing period.

The volatile compounds produced by the microorganisms were collected by SPME method analysis using a Carboxen/Divinylbenzene/PDMS 50 µm microfibre. For volatile collection and adsorption, the microfibre was conditioned at 240ºC in a gas chromatography injector (Shimadzu GC 2014-FID, Japan) for 30 min and then it was inserted in the sealed inoculated vials with the samples at 30ºC for 25 min. After the volatile collection, the microfibre was inserted in a GC-MS spectrometer injector. Analyses were replicated twice.

Volatile compounds were analyzed on a gas chromatograph coupled to a quadrupole mass spectrometer (Shimadzu QP-2010, Japan) working in EI at 70 eV and a TIC registration mode in a mass range m/z 40/350. Samples were resolved on a DB-5MS J&W Scientific column (30 m × 0.25 mm × 0.25 µm). Compounds were desorbed at 240ºC in a splitless injection port; the column program temperature was 35ºC for 4 min, heating rate of 6ºC min^{-1} until reaching 240ºC for 3 min; interface at 280ºC; column pressure at 43.6 kPa and column flow of 0.95 ml min^{-1}. To determine the chromatographic retention indices under the applied chromatographic conditions, we analyzed mixtures of normal alkanes C7-C20. Retention times of hydrocarbons and samples of volatile compounds were registered for calculation of Kóvats index. The RI values were compared with bibliographic values in non-polar DB-5columns.

Identification of VOCs was performed by spectra comparison with NIST-Wiley 8.0 library with over 90% similarity with compounds of data base [GCMS Solution], Kóvats retention index and by co-elution with standards, when available.

MEA culture medium without any fungal strain was analyzed as system blank and its VOCs were discharged from fungal samples.

2.6. Effect of G. vellereum VOCs in dual cultures

In order to investigate the effect of *G. vellereum* volatiles on the growth of target fungi, two different assays were performed.

In assay A, dual cultures in 90-mm diam bipartite Petri dishes (MEA 2%) were used. Five target fungi were selected: *G. resinaceum*, *I. rickii*, *Fusarium solani* (Mart.) Sacc., *Raffaelea* sp. and *G. basitruncatum*. These fungi were selected based on their susceptibility to *G. vellereum* in the dual culture assays previously performed. A mycelial plug (5 mm^2) of *G. vellereum* (BAFCcult 4363) was inoculated on one side of the dish and a plug of each of the target fungi was inoculated at the opposite side of the dish, either at the same time or after 4 days. Petri dishes with only the target fungi on one side were used as controls. Cultures were maintained at 24ºC in the dark, and examined every 2-3 days until the target fungi covered their side of the dish. In the case of *I. rickii*, *G. basitruncatum* and *Raffaelea* sp. treatments, radial growths were measured until *G. vellereum* began to grow over the division of the plate.

Five replicate dishes were prepared for each combination. Colonies radii of the treatments were measured and compared with the radii of the control colonies. PIRG of each target fungus was calculated as described above.

In assay B, a double Petri dish dual-culture was used (Li et al., 2015). The bioassay system was set up with the bottoms of two 90-mm lidless Petri dishes, one of which was laid facing down, covering the other and then sealed together with two layers of Parafilm. One plate containing MEA 2% was on the top of the dual-culture system, and contained a 3 day-old culture of the target fungus. The other plate, placed at the bottom, was a 5-day-old culture of *G. vellereum* that covered the entire surface of the plate. Five replicates were conducted. A dual culture system lacking *G. vellereum* in the bottom plate and another with the target fungus in both top (3 day-cultures) and bottom dishes (14 day-cultures) were used as controls. All cultures were incubated in darkness at 25ºC. The growth of the target organism was measured every 2-3 days post inoculation. Inhibition of mycelial growth (%) of each target fungus was calculated using the diameter of the colony, as calculated for PIRG, using the diameter of the colony in the dual culture system lacking *G. vellereum* as control.

2.7. Statistical analyses

Results of effectiveness of *G. vellereum* as a biocontrol agent on wood blocks were analyzed by a two way ANOVA where the main factors were: decay fungi and treatment and *G. vellereum* status (as first colonizer, second colonizer and not inoculated). The statistical significance of the degradation ability of *G. vellereum* on wood blocks (*P. acerifolia* wood and *Populus* wood) was assessed by a one-way ANOVA ($p < 0.01$). Data were transformed using $y' = y^{1/2}$ to achieve homogeneity and normality prior to statistical analysis. All means were analyzed by Tukey's HSD test. All analyses were performed using the InfoStat software 2014 (Di Rienzo et al., 2014).

Mean values of fungal growth in dual cultures were compared using Student's t test, at significance level $\alpha = 0.05$.

3. Results

3.1. Biocontrol effect of G. vellereum in dual cultures

Radial growths of all target fungi showed less growth in dual cultures than in controls when *G. vellereum* was inoculated in the first place (Fig. 1, 2, Table 2), ranging from 34 to 96 % PIRG after one month.

Radial growths of all target fungi, except for *B. adusta*, *T. trogii* and *A. platypodis*, showed less growth in dual cultures than in controls when *G. vellereum* was inoculated later (Table 2), ranging from 12 to 74 % PIRG after one month. *Inonotus rickii* was the species with the highest PIRG (97 % when *G. vellereum* was

inoculated first) and *T. trogii* was the species with the lowest PIRG (34 %, when *G. vellereum* was inoculated first). PIRG of all fungi associated to *M. mutatus* was over 70 % when *G. vellereum* was inoculated in the first place.

Hyphal swellings were observed in all the dual cultures of *F. solani* – *G. vellereum* in the zone where both mycelia meet. Dark hyphae were observed in the zone of hyphal contact in the *Raffaelea* sp. - *G. vellereum*, dual cultures, when *Raffaelea* was inoculated in the first place.

3.2. Biocontrol effect of G. vellereum on wood blocks

G. vellereum significantly reduced decay in wood blocks exposed to *I. rickii* ($p < 0.01$), but it did not affect degradation caused by the other decay fungi ($p > 0.05$) (Fig. 3).Two-way ANOVA revealed a significant effect of the strain ($F = 472.01$; $p < 0.01$), of the biocontrol agent ($F = 19.61$; $p < 0.01$) and of their interaction ($F = 23.30$; $p < 0.01$).

Dry weight loss caused by each wood decay fungus was significantly reduced by preinoculation with *G. vellereum* ($p < 0.01$; Fig. 3). Two-way ANOVA revealed a significant effect of the wood decay strains ($F = 190.01$; $p < 0.0001$), of the biocontrol agent ($F = 699.31$; $p < 0.0001$) and of their interaction ($F = 65.85$; $p < 0.0001$).

3.3. Degradation ability of G. vellereum

All oxidase reactions performed were negative. *Granulobasidium vellereum* did not produce a change in the media in any evaluation.

Granulobasidium vellereum caused, after 3 months, 0.41 ± 0.56 % DWL in *P. acerifolia* wood blocks. This result was not significantly different from control (0.31 ± 0.47 % DWL) ($F = 0.33$; $p = 0.56$). In *Populus* wood blocks *G. vellereum* produced 0.56 ± 0.98 % DWL. This result was not significantly different from control (0.24 ± 0.41 % DWL) ($F = 1.82$; $p > 0.18$).

3.4. Analysis of VOCs produced by G. vellereum

The volatile profiles analyzed by GC–MS showed that *G. vellereum* strains produced several volatile compounds, with the detection of 8-19 different compounds per strain. The esters compounds 2-methylpropyl acetate, 2-methylbutyl acetate and 3-methylbutyl acetate were present in the five strains analyzed. The compounds (3Z)-3,7-dimethylocta-1,3,6-triene ((Z)-β-ocimene) and (1R,4E,9S)-4,11,11-trimethyl-8-methylidenebicyclo[7.2.0]undec-4-ene (β-caryophyllene) were present in four of the strains studied (BAFCcult 4363, 4365-67). Twenty additional FVOCs were detected in the different strains (Table 3).

3.5. Effect of G. vellereum VOCs in dual cultures

In assay A, radial growths of all target fungi in bipartite dishes were not inhibited by *G. vellereum* VOCs, either when inoculated in the first place or when both *G. vellereum* and target fungus were inoculated at the same time. PIRG values after 4-9 days, when the target fungi covered their side of the dish, ranged from 0 to 3% (data not shown).

In assay B, all target fungi were inhibited, although not killed after exposure to volatiles from *G. vellereum* without direct contact or diffusion through the culture media. Results of inhibition of mycelial growth (%) in the presence of *G. vellereum* were: 14.7 ± 7.9 (*G. resinaceum*); 31.0 ± 13.0 (*I. rickii*); 29.5 ± 10.0 (*F. solani*); 52.5 ± 2.5 (*G. basitruncatum*); 41.4 ± 16.5 (*Raffaelea* sp.). All treatments were significantly different from control ($p < 0.05$). The morphology of the colony of some of the target fungi appeared different from the control. Under visual observation, *I. rickii* and *Raffaelea* sp. showed less pigmentation and *F. solani* showed a proliferation of aerial hyphae (Fig. 4).

4. Discussion

The results of our study indicate that it is possible to consider the use of *G. vellereum* as a biological control agent of xylophagous fungi and fungi related to forest pests. This basidiomycete had already been isolated as a wood endophyte from urban trees (Robles et al., 2015) and did not produce a significant loss of weight in the two types of wood involved in this work. This result suggests that inoculation with *G. vellereum* on affected trees, should not promote any further damage to the wood. To our knowledge this is the first study of *G. vellereum* as a potential biocontrol agent against fungi related to sanitary problems in trees, involving the presence of FVOCs. There are previous reports of antagonistic and cytotoxic effects of some *G. vellereum* metabolites, but not FVOCs. Nord et al. (2013) isolated the sesquiterpene radulone A from *G. vellereum*, which inhibited the spore germination of *Phlebiopsis gigantea*, *Coniophora puteana* (Schumach.) P. Karst. and *Heterobasidion occidentale* Otrosina & Garbel. at different concentrations. Other two illudine sesquiterpenes isolated showed a cytotoxic effect on tumor cell lines (Nord et al., 2014).

In dual cultures, *G. vellereum* inhibited the growth of all target fungi when inoculated first. On the other hand, some target fungi, especially wood decay fungi, except for *I. rickii,* were not inhibited when *G. vellereum* was inoculated later. Results in woody substrates were similar. As first colonizer, *G. vellereum* reduced

decay of *P. acerifolia* wood blocks caused by all decay fungi assessed. As second colonizer, it only reduced decay by *I. rickii*. This result suggests that the presence of *G. vellereum* as wood endophyte could prevent the later colonization by wood decay fungi or fungi associated with forest pests. Similar results were obtained by Castrillo et al. (2016); in *in vitro* assays with symbionts of ambrosia beetles they observed that entomopathogenic fungi blocked the spread of symbionts only in primary competition assays, where both symbionts and entomopathogenic fungi were inoculated at the same time. On the other hand, when symbionts were inoculated a week earlier, they overgrew entomopathogenic fungi due to timing of inoculation (Castrillo et al., 2016). The capacity of *G. vellereum* to prevent the growth of other fungi as first colonizers can be due to its high rate of growth and the production of abundant asexual spores (Stalpers, 1978).

Exposure to VOCs from *G. vellereum* showed significant inhibition of all test fungi *in vitro*, especially high in cultures of *Graphium basitruncatum* (Matsush.) Seifert & G. Okada and *Raffaelea* sp. Changes in the morphology of the mycelium were also observed. When analyzing the fungal volatiles emitted by *G. vellereum*, several of them have already been reported as FVOCs or have been reported to cause inhibition of the pathogens growth. Esters compounds 2-methylpropyl acetate, 2-methylbutyl acetate and 3-methylbutyl acetate were present in all strains analyzed in this study. All these esters have been previously registered as fungal volatiles (Strobel et al., 2001). Moreover, the compound 3-methylbutyl acetate produced by endophytic *Muscodor albus* displayed a slight inhibition on growth of plant-pathogenic fungi when they were individually tested, although an additive mechanism of VOCs was proposed as the cause of the biocontrol activity (Strobel et al., 2001). The sesquiterpene β-caryophyllene, present in most of the strains in this study, has been reported as a volatile compound produced by plants that could serve as a defense against bacterial pathogens (Huang et al., 2012). Furthermore, Minerdi et al. (2009) found that the fungal volatile α-humulene could reduce the growth of the pathogen *Fusarium oxysporum* f. sp. *lactucae* and inhibit the expression of putative virulence genes.

Some alcohols were obtained as volatiles in one of the strains of this study. One of them, hexan-1-ol has already been reported as a volatile compound of *Aspergillus* spp., *Alternaria* spp. and *Penicillium* spp. (Magan et al., 2000). On the other hand, octan-1-ol has been obtained from both *Fomitopsis pinicola* and *Fomes fomentarius* and has been shown to attract insects in combination with 1-3-octanol and 1-octen-3-ol (Fäldt et al, 1999). It has also been obtained from *Pleurotus ostreatus* and it showed ability to inhibit the growth of bacteria (Beltran-Garcia et al., 1997). Previous reports (Bruce et al., 2003; Moore-Landecker and Stotzky, 1973), together with the results of the present study, indicate that VOCs of microorganisms may directly or indirectly act to influence the growth or morphology of fungi.

Our results show that *G. vellereum* promotes growth inhibition of xylophagous fungi associated with decayed wood, *G. resinaceum* and *I. rickii*, and against fungi associated to *M. mutatus* in *Populus*: *F. solani, G. basitruncatum* and *Raffaelea* sp., and, at least partly, the mechanism of control involves FVOCs with biological activity.

The use of VOCs as a biofumigant does not require direct contact with the plant, making it a more compatible option with integrated disease or pest management systems than current biological or chemical fungicides that leave polluting residues (Li et al., 2015). Additional studies that focus on the identification of the *G. vellereum* volatiles responsible for the antagonistic effect and field studies on the efficacy of *G. vellereum* as biological control should be carried out to develop application strategies for the management of *M. mutatus* and other ambrosia beetles common in forestry.

Acknowledgments

This study was supported by the National Council for Scientific and Technological Research (CONICET) PIP 112 20150100956 (2015-2017), PICT 2015-1038 (2017-2018) and UBACYT 20020150100067B. We thank Federico Manetti for his help in the dual culture studies.

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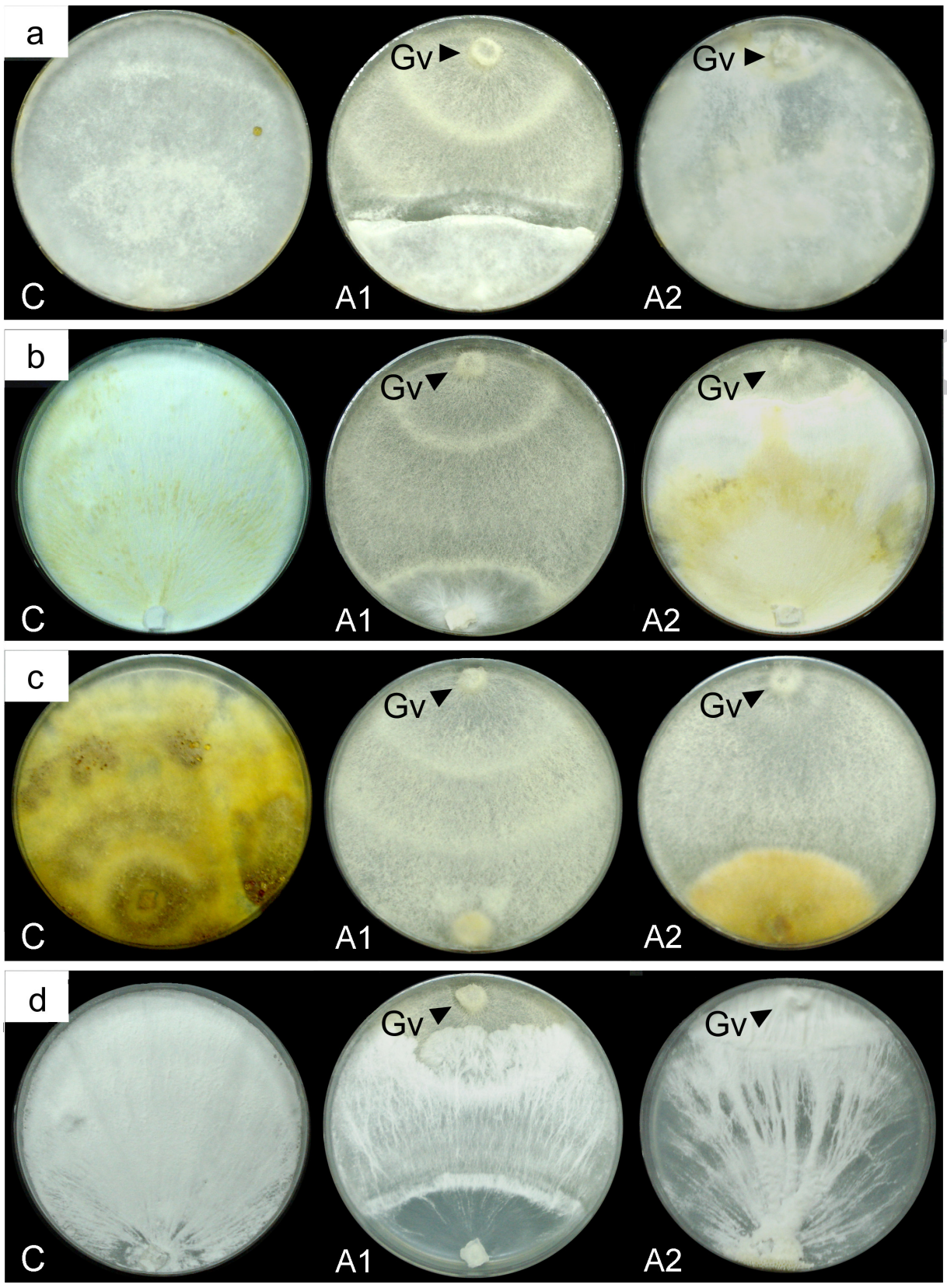
Figure legends

Fig. 1 Effect of *G. vellereum* on wood decay fungi on dual cultures. C: control. A1: dual cultures where *G. vellereum* was inoculated first. A2: dual cultures where *G. vellereum* was inoculated last. a: *Bjerkandera adusta*. b: *Ganoderma resinaceum*. c: *Inonotus rickii*. d: *Trametes trogii.* Gv: *Granulobasidium vellereum.*

Fig. 2 Effect of *G. vellereum* on fungi associated with *M. mutatus* on dual cultures (assay B). C: control. A1: dual cultures where *G. vellereum* was inoculated first. A2: dual cultures where *G. vellereum* was inoculated last. a: *Ambrosiozyma platypodis*. b: *Chaetomium* sp. c: *Fusarium solani*. d: *Geotrichum* sp. e: *Graphium basitruncatum*. f: *Raffaelea* sp.

Fig. 3 Effect of *G. vellereum* on the degradation ability of wood decay fungi. DWL (%) was calculated after 3 months´ incubation . Bars and brackets represent mean and standard deviation (SD) N= 17. Mean values are given above bars. *G. v.* + __: *G. vellereum* inoculated first.___ + *G. v.*: wood decay fungi inoculated first. *B. a.*: *Bjerkandera adusta*; *G. r.*: *Ganoderma resinaceum*; *I. r.*: *Inonotus rickii*; *T. t.*: *Trametes trogii.**significant at 1 % Tukey's test.

Fig. 4 Effect of *G. vellereum* volatile organic compounds in a dual-culture assay. Target fungi were always on the top dish with the culture facing down. T-Gv: *G. vellereum* culture on the bottom dish. C1: control where the bottom dish lacked *G. vellereum.* a: *Ganoderma resinaceum*. b: *Inonotus rickii*. c: *Fusarium solani*. d: *Graphium basitruncatum*. e: *Raffaelea* sp.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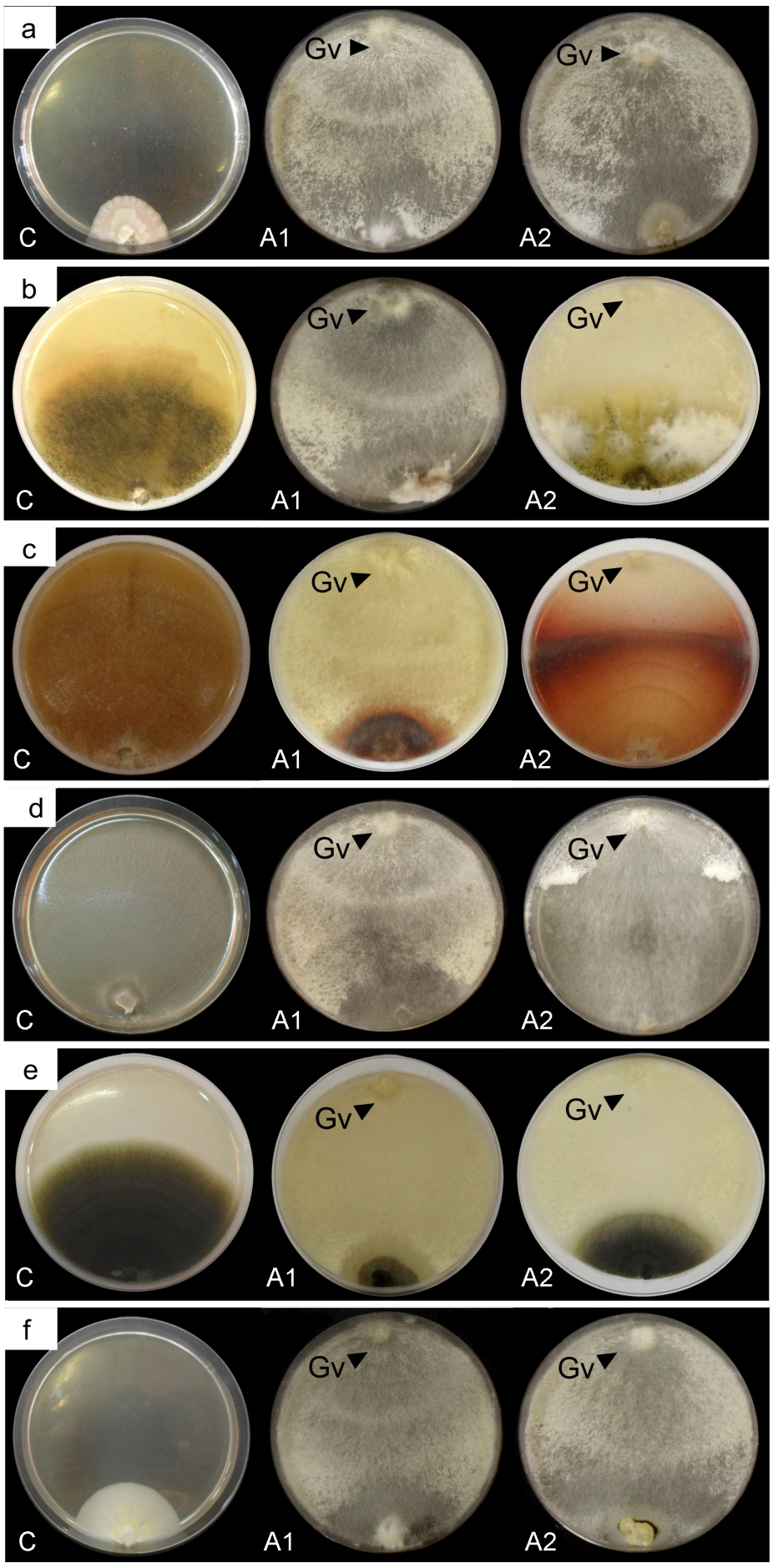
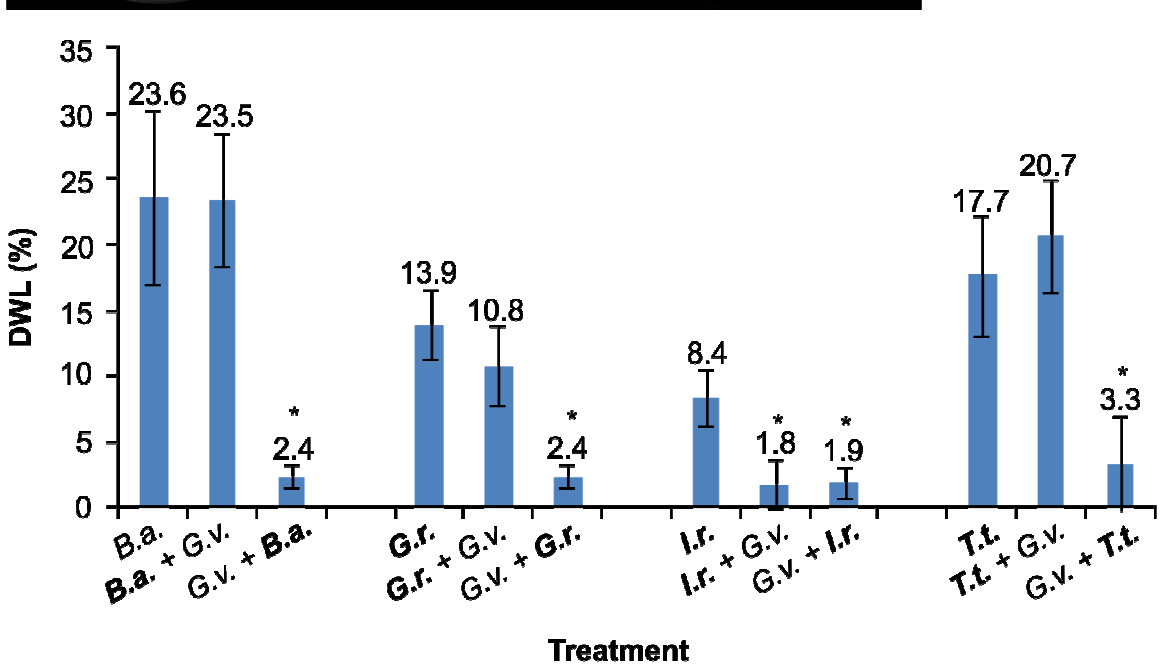




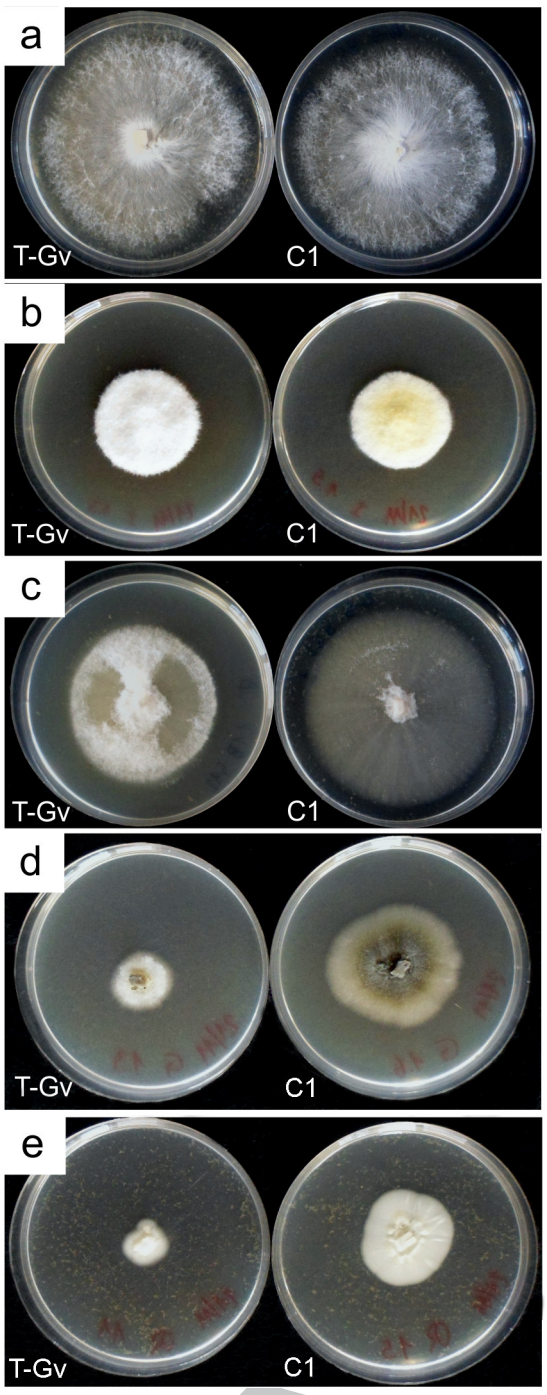


Table 1 Fungal organisms used in this study

Species name	Strain nº	Source	Assays
Granulobasidium vellereum (Ellis & Cragin) Jülich	BAFCcult 4362 GenBank KC881192	Isolated from wood of *Platanus acerifolia* as endophyte	Analysis of VOCs (section 2.5)
Granulobasidium vellereum	BAFCcult 4363 GenBank KC881194	Isolated from wood of *P. acerifolia* as endophyte	Dual cultures (section 2.2), wood blocks (section 2.3), degradation ability (section 2.4), analysis of VOCs (section 2.5), VOCs in dual cultures (section 2.6, assay A and B).
Granulobasidium vellereum	BAFCcult 4365 GenBank KC881191	Isolated from wood of *P. acerifolia* as endophyte	Analysis of VOCs (section 2.5)
Granulobasidium vellereum	BAFCcult 4366 GenBank KC881190	Isolated from wood of *P. acerifolia* as endophyte	Analysis of VOCs (section 2.5)
Granulobasidium vellereum	BAFCcult 4367 GenBank KC881193	Isolated from wood of *P. acerifolia* as endophyte	Analysis of VOCs (section 2.5)
Bjerkandera adusta (Willd.) P. Karst.	BAFCcult 3301 GenBank FJ850965	Isolated from wood of *P. acerifolia* as wood decay pathogen	Dual cultures (section 2.2), wood blocks (section 2.3)
Inonotus rickii (Pat.) D.A. Reid.	BAFCcult 3300	Isolated from wood of *P. acerifolia* as wood decay pathogen	Dual cultures (section 2.2), wood blocks (section 2.3), VOCs in dual cultures (section 2.6, assay A and B).
Trametes trogii Berk.	BAFCcult 3317	Isolated from wood of *P. acerifolia* as wood decay pathogen	Dual cultures (section 2.2), wood blocks (section 2.3)
Ganoderma resinaceum Boud.	BAFCcult 3297 GenBank FJ850966	Isolated from wood of *P. acerifolia* as wood decay pathogen	Dual cultures (section 2.2), wood blocks (section 2.3), VOCs in dual cultures (section 2.6, assay A and B).
Fusarium solani (Mart.) Sacc.	BAFCcult 4500 GenBank KT828717	Isolated from galleries of *M. mutatus* in *Populus deltoides*	Dual cultures (section 2.2), VOCs in dual cultures (section 2.6, assay A and B).
Chaetomium sp.	BAFCcult 4527	Isolated from galleries of *M. mutatus* in *P. deltoides*	Dual cultures (section 2.2)**.**
Raffaelea sp.	BAFCcult 4530	Isolated from galleries of *M. mutatus* in *P. deltoides*	Dual cultures (section 2.2), VOCs in dual cultures (section 2.6, assay A and B).
Graphium basitruncatum (Matsush.) Seifert & G. Okada	BAFCcult 4519 GenBank KT828733	Isolated from galleries of *M. mutatus* in *P. deltoides*	Dual cultures (section 2.2), VOCs in dual cultures (section 2.6, assay A and B).
Ambrosiozyma platypodis (J.M. Baker & Kreger) Van der Walt	BAFCcult 4513 GenBank KT828736	Isolated from galleries of *M. mutatus* in *P. deltoides*	Dual cultures (section 2.2)**.**
Geotrichum sp.	BAFCcult 4509 GenBank KT828726	Isolated from galleries of *M. mutatus* in *P. deltoides*	Dual cultures (section 2.2)**.**

Table 2 Percentage of inhibition of radial growth (PIRG) of different target species in dual culture assays when paired with *G. vellereum*; mean values and standard deviation. Interaction values are given between brackets. (++): overgrowth of the target fungi. (+): no overgrowth but inhibition of the growth of the target fungi. (-): no inhibition of the target fungi. (+/-): inhibition of the target fungi only in some replicates. * indicates a significant difference between the control and the treatment ($p < 0.05$).

	G. vellereum	
	Inoculated first	**Inoculated last**
Wood decay fungi		
Bjerkandera adusta	65.8 ± 18.3 (+) *	0.0 ± 0.0 (-)
Ganoderma resinaceum	77.2 ± 9.6 (+) *	26.0 ± 4.7 (+) *

Inonotus rickii	96.7 ± 1.9 (++) *	75.2 ± 5.4 (++) *
Trametes trogii	34.0 ± 14.8 (+/-) *	0.0 ± 0.0 (-)
Fungi associated with *M. mutatus*		
Ambrosiozyma platypodis	88.5 ± 4.5 (++) *	11.9 ±7.9 (++)
Chaetomium sp.	74.8 ± 4.9(++) *	21.5 ± 3.6(++) *
Fusarium solani	84.0 ± 1.3 (++) *	42.1 ± 1.3(+) *
Geotrichum sp.	83.8 ± 3.0 (++) *	36.0 ± 1.6 (++) *
Graphium basitruncatum	87.0 ± 6.7 (++) *	47.4 ± 2.4 (+/-) *
Raffaelea sp.	93.3 ± 2.5 (++) *	37.8 ± 7.2(++) *

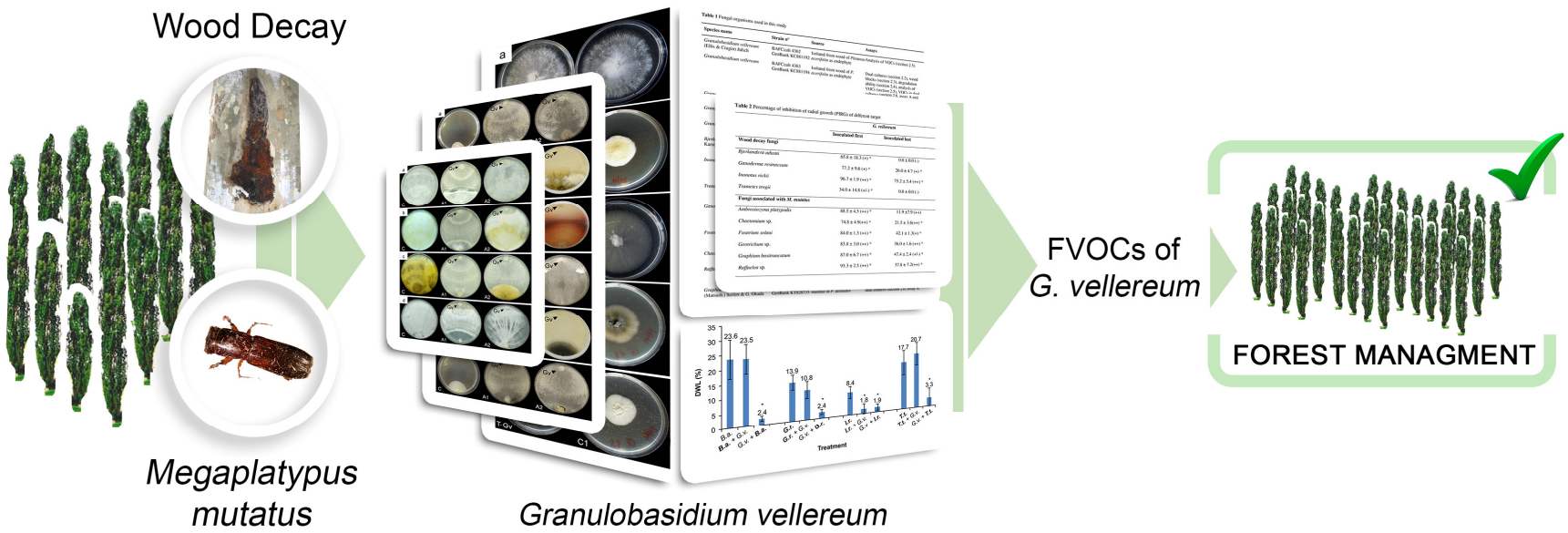
Table 3 GC–MS volatiles profiles of the five *G. vellereum* strains in DB-5 column.

Compound	BAFCcult 4362			BAFCcult 4363		
	Similarity	Kóvats index	t sample	Similarity	Kóvats index	t sample
Alcohols						
hexan-1-ol	97	870.08	8.909	--	--	--
octan-1-ol	97	1070.94	14.969	--	--	--
Phenylmethanol	95	1034.39	13.939	--	--	--
3-phenylpropan-1-ol	95	1230.43	19.135	--	--	--
Esters						
2-ethylhexyl acetate	97	1147.34	17.023	--	--	--
Ethylbutanoate	94	802.8	6.696	--	--	--
2-methylpropyl acetate	99	772.58	5.820	97	772.82	5.827
2-methylbutyl acetate	97	879.81	9.229	97	879.66	9.224
3-methylbutyl acetate	98	878.05	9.171	98	877.9	9.166
Non-terpenoid hydrocarbons						
Decane	97	999.71	12.961	--	--	--
2,4-diisopropyl-1-methyl-1-vinyl cyclohexane	--	--	--	93	1391.89	22.919
Octane	96	799.97	6.603	--	--	--
3E-octadiene	91	825.87	7.455	92	825.78	7.452
(3E)-octa-1,3-diene	--	--	--	--	--	--
Terpenoids						
β-bisabolene ((4S)-1-methyl-4-(6-methylhepta-1,5-dien-2-yl) cyclohexene)	93	1509.74	25.438	--	--	--
α-caryophyllene ((1E,4E,8E)-2,6,6,9-tetramethylcycloundeca-1,4,8-triene)	--	--	--	--	--	--
β-caryophyllene ((1R,4E,9S)-4,11,11-trimethyl-8-methylidenebicyclo[7.2.0]undec-4-ene)	92	1424.57	23.629	92	1424.71	23.632
β-citronellol (3,7-dimethyloct-6-en-1-ol)	97	1225.94	19.026	--	--	--
2-β-elemene ((1S,2S,4R)-1-ethenyl-1-methyl-2,4-bis(prop-1-en-2-yl)cyclohexane)	96	1391.85	22.918	96	1391.85	22.918
β-elemene ((1S,2S,4R)-1-ethenyl-1-methyl-2,4-bis(prop-1-en-2-yl)cyclohexane)	--	--	--	--	--	--
β-farnesene ((6E)-7,11-dimethyl-3-methylidenedodeca-1,6,10-triene)	94	1452.22	24.220	--	--	--
α-humulene ((1E,4E,8E)-2,6,6,9-tetramethylcycloundeca-1,4,8-triene)	96	1460.46	24.396	94	1460.88	24.405
(E)-β-ocimene ((3E)-3,7-dimethylocta-1,3,6-triene)	--	--	--	96	1046.98	14.294
(Z)-β-ocimene ((3Z)-3,7-dimethylocta-1,3,6-triene)	96	1036.66	14.003	96	1036.48	13.998
α-selinene ((3S,8aS)-5,8a-dimethyl-3-prop-1-en-2-yl-2,3,4,4a,7,8-hexahydro-1H-naphthalene)	--	--	--	--	--	--

Compound	BAFCcult 4365			BAFCcult 4366		
	Similarity	Kóvats index	t sample	Similarity	Kóvats index	t sample
Alcohols						
hexan-1-ol	--	--	--	--	--	--
octan-1-ol	--	--	--	--	--	--
Phenylmethanol	--	--	--	--	--	--
3-phenylpropan-1-ol	--	--	--	--	--	--
Esters						
2-ethylhexyl acetate	--	--	--	97	1147.34	17.023
Ethylbutanoate	--	--	--	--	--	--
2-methylpropyl acetate	96	772.96	5.831	96	773	5.832
2-methylbutyl acetate	97	879.66	9.224	97	879.66	9.224
3-methylbutyl acetate	97	878.05	9.171	97	878.05	9.171
Non-terpenoidhydrocarbons						

Decane	--	--	--	--	--	--
2,4-diisopropyl-1-methyl-1-vinyl cyclohexane	--	--	--	--	--	--
Octane	--	--	--	96	800	6.604
3E-octadiene	92	825.81	7.453	--	--	--
(3E)-octa-1,3-diene	--	--	--	92	825.97	7.458
Terpenoids						
β-bisabolene ((4S)-1-methyl-4-(6-methylhepta-1,5-dien-2-yl) cyclohexene)	--	--	--	93	1509.64	25.436
α-caryophyllene ((1E,4E,8E)-2,6,6,9-tetramethylcycloundeca-1,4,8-triene)	95	1460.97	24.407	95	1460.97	24.407
β-caryophyllene ((1R,4E,9S)-4,11,11-trimethyl-8-methylidenebicyclo[7.2.0]undec-4-ene)	92	1424.75	23.633	--	--	--
β-citronellol (3,7-dimethyloct-6-en-1-ol)	--	--	--	--	--	--
2-β-elemene ((1S,2S,4R)-1-ethenyl-1-methyl-2,4-bis(prop-1-en-2-yl)cyclohexane)	92	1391.98	22.921	--	--	--
β-elemene ((1S,2S,4R)-1-ethenyl-1-methyl-2,4-bis(prop-1-en-2-yl)cyclohexane)	--	--	--	--	--	--
β-farnesene ((6E)-7,11-dimethyl-3-methylidenedodeca-1,6,10-triene)	--	--	--	--	--	--
α-humulene ((1E,4E,8E)-2,6,6,9-tetramethylcycloundeca-1,4,8-triene)	--	--	--	--	--	--
(E)-β-ocimene ((3E)-3,7-dimethylocta-1,3,6-triene)	96	1047.09	14.297	--	--	--
(Z)-β-ocimene ((3Z)-3,7-dimethylocta-1,3,6-triene)	96	1036.52	13.999	--	--	--
α-selinene ((3S,8aS)-5,8a-dimethyl-3-prop-1-en-2-yl-2,3,4,4a,7,8-hexahydro-1H-naphthalene)	--	--	--	--	--	--

BAFCcult 4367			
		Kóvats	
Compound	**Similarity**	**index**	**t sample**
Alcohols			
hexan-1-ol	--	--	--
octan-1-ol	--	--	--
Phenylmethanol	--	--	--
3-phenylpropan-1-ol	--	--	--
Esters			
2-ethylhexyl acetate	--	--	--
Ethylbutanoate	--	--	--
2-methylpropyl acetate	96	773.03	5.833
2-methylbutyl acetate	96	879.87	9.231
3-methylbutyl acetate	99	878.11	9.173
Non-terpenoidhydrocarbons			
Decane	--	--	--
2,4-diisopropyl-1-methyl-1-vinyl cyclohexane	--	--	--
Octane	--	--	--
3E-octadiene	--	--	--
(3E)-octa-1,3-diene	--	--	--
Terpenoids			
β-bisabolene ((4S)-1-methyl-4-(6-methylhepta-1,5-dien-2-yl) cyclohexene)	--	--	--
α-caryophyllene ((1E,4E,8E)-2,6,6,9-tetramethylcycloundeca-1,4,8-triene)	--	--	--
β-caryophyllene ((1R,4E,9S)-4,11,11-trimethyl-8-methylidenebicyclo[7.2.0]undec-4-ene)	93	1427.09	23.683
β-citronellol (3,7-dimethyloct-6-en-1-ol)	--	--	--
2-β-elemene ((1S,2S,4R)-1-ethenyl-1-methyl-2,4-bis(prop-1-en-2-yl)cyclohexane)	--	--	--
β-elemene ((1S,2S,4R)-1-ethenyl-1-methyl-2,4-bis(prop-1-en-2-yl)cyclohexane)	94	1392.11	22.924
β-farnesene ((6E)-7,11-dimethyl-3-methylidenedodeca-1,6,10-triene)	--	--	--
α-humulene ((1E,4E,8E)-2,6,6,9-tetramethylcycloundeca-1,4,8-triene)	96	1461.21	24.412
(E)-β-ocimene ((3E)-3,7-dimethylocta-1,3,6-triene)	95	1047.27	14.302
(Z)-β-ocimene ((3Z)-3,7-dimethylocta-1,3,6-triene)	97	1036.66	14.003
α-selinene ((3S,8aS)-5,8a-dimethyl-3-prop-1-en-2-yl-2,3,4,4a,7,8-hexahydro-1H-naphthalene)	92	1500.99	25.261



Highlights

- *Granulobasidium vellereum* is proposed as an antagonist of fungi related to damage of forest wood.
- *G. vellereum* inhibited the growth of all target fungi when inoculated first *in vitro* cultures.
- FVOCs of *G. vellereum* inhibited the growth of all target fungi.
- These volatiles can be considered for forest management strategies.