The sporicidal activity of yellow-cedar heartwood, essential oil and wood constituents towards *Phytophthora ramorum* in culture

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Summary

In this paper, we demonstrate that 140 mg/kg of essential oil from the wood of yellow-cedar, incense cedar, Port-Orford-cedar or western juniper strongly inhibits zoospore germination and hyphal growth of *Phytophthora ramorum* in culture. Four individual compounds in yellow-cedar heartwood were also tested. Zoospore germination was reduced to 0% with 10, 100 and 1000 mg/kg of nootkatone, carvacrol and valencene, respectively. Nootkatone was the least active compound, with 3.5% zoospore germination at 1000 mg/kg. Sporangia germination was 0% with 500 mg/kg of nootkatone or carvacrol. The disruption of the zoospore outer membrane and the loss of sporangial contents were often observed and indicative of sporicidal activity. Hyphal growth was inhibited by 99.9% with 50 mg/kg of nootkatone or 500 mg/kg of carvacrol, but growth resumed upon removing the inhibitors. The zoosporicidal activity of yellow-cedar heartwood shavings stored dry for approximately 10 years was consistent with the quantity of extractable compounds they contained. Thus, spreading fresh shavings or chips of yellow-cedar heartwood with appreciable higher concentrations of the active compounds, over areas in infection zones where spores might be difficult to control such as trails and parking lots used by hikers and bicyclists, might be useful as part of an integrated program to minimize *P. ramorum* spore distribution.

1 Introduction

*Phytophthora ramorum* is the recently identified fungal pathogen responsible for sudden oak death that has caused extensive mortality of tanoak (*Lithocarpus densiflora*) and various species of oak (Rizzo et al. 2002a) in native and urban forests of central and northern California since 1995. Currently, there are 36 species of known hosts, plus all species, hybrids and cultivars of *Camellia* and *Rhododendron*. In addition, there are 46 associated species or potential hosts (for an updated list, see http://www.aphis.usda.gov/ppq/ispm/pramorum). Hosts are affected by *P. ramorum* in one of the two ways: death of branches or stem, or non-lethal infections of the leaves and twigs (Rizzo et al. 2002b; Rizzo and Garbelotto 2003). Sporangia and germinated chlamydospores of *P. ramorum* sporulate on host foliage during winter or early spring rains, releasing zoospores that infect the wet leaves, or are transported in rainwater and possibly wind to nearby plants, litter, soil and streams (Davidson et al. 2002a,b; Tjosvold et al. 2002a; Garbelotto et al. 2003; Murphy et al. 2005). Various animals and humans can also vector spores (Tjosvold et al. 2002b; Cushman and Meentemeyer 2005). The more resilient chlamydospores may be transported by similar means. Zoospores and chlamydospores are susceptible to dry conditions (Davidson et al. 2002a,b), so those residing on leaf litter at the surface of the forest floor are short lived after spring rains stop (Fichtner et al. 2005). However, spores residing within tissues, and those penetrating into the litter–soil interface or below the soil

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surface where environments are cool and moist, can remain viable for 6 months or more (Aveskamp et al. 2005; Fichtner et al. 2005). Spores in the soil are capable of infecting plants without contact between the soil and foliage (Parke et al. 2005). As spores are the key elements of dispersal, preventing their movement into new areas is a high priority for the current management of this disease (Rizzo and Garbelotto 2003). Various commercial fungicides are effective at inhibiting spore germination, sporangia production or mycelial growth in culture (Garbelotto et al. 2002; Heungens et al. 2005; Turner et al. 2005). In vivo, many of these products are effective also at protecting against infection, or suppressing existing infections, and least effective at eradicating the pathogen from within tissues (Garbelotto et al. 2002; Chastagner et al. 2005; Harnik and Garbelotto 2005; Heungens et al. 2005; Kanaskie et al. 2005; Linderman and Davis 2005; Tjosvold and Chambers 2005; Turner et al. 2005). Government agencies and the nursery industry are monitoring and regulating the movements of commercial plants and potting soils that originate from within infection zones (http://nature.berkeley.edu/comtf/) to minimize the rate of spread. But, controlling spore dispersal from native or urban forests may be a much more daunting task, and will require an integrated approach (Hansen and Sutton 2005; Kanaskie et al. 2005; Slawson et al. 2005; Steeghs and de Gruyter 2005).

Phytophthora lateralis Tucker & Milbrath is closely related to P. ramorum (Werres et al. 2001) and causes root rot of Port-Orford-cedar, Chamaecyparis lawsoniana (A. Murr.) Parl., in forests of northern California and southwestern Oregon (Zobel et al. 1985; Hansen and Lewis 1997). Using grafting studies, McWilliams (2000) found the roots of yellow-cedar, Chamaecyparis nootkatensis (D. Don) Spach (also commonly called Alaska-cedar or Alaska yellow-cedar), to have a low infection rate from P. lateralis compared with Port-Orford-cedar. A mechanism for this difference was not investigated, but could be related, in part, to the antifungal compounds produced by yellow-cedar (Rennerfelt and Nacht 1955; Smith 1970; Smith and Cserjesi 1970). They contribute not only to the trees longevity while alive, but also after death, as demonstrated by the ability of yellow-cedar snags to remain standing for 80 years or more (Hennon et al. 1990a,b), with minimal loss in strength (McDonald et al. 1997; Green et al. 2002). Decreases in the concentrations of snag heartwood constituents (Kelsey et al. 2005) coincide with the loss of decay resistance (deGroot et al. 2000).

Several compounds in yellow-cedar heartwood have antimicrobial properties. Nootkatatin, first isolated by Carlsson et al. (1952), was the most active of the three heartwood constituents tested against various wood decay fungi by Rennerfelt and Nacht (1955). It inhibited mycelial growth at 0.001–0.002% (10–20 mg/kg) in malt extract agar, and was toxic at concentrations ranging from 0.001% to 0.005% (10–50 mg/kg), depending on the fungal species. Removal of nootkatin makes the wood more susceptible to decay (Smith 1970; Smith and Cserjesi 1970). It also inhibits the growth of Candida albicans, a yeast that causes infections in animals, while the steam-distilled essential oil from yellow-cedar heartwood inhibits anaerobic bacteria that infect animals (Johnston et al. 2001).

Carvacrol is another yellow-cedar component identified by Carlsson et al. (1952) that inhibits mycelial growth of wood decay fungi (Voda et al. 2003) and various plant pathogens in the genus Fusarium (Thompson 1996). It is bactericidal towards a variety of human food-borne pathogens (Ultee et al. 1999; Knowles and Roller 2001; Friedman et al. 2002; Burt 2004) and is also nematicidal (Oka et al. 2000). Lastly, carvacrol, the essential oil from yellow-cedar heartwood and other oil components (nootkatone, nootkatol, valencene-13-ol and valencene-13-aldehyde), functions as repellants, insecticides or acaricides towards various arthropod pests (Panella et al. 1997; Ahn et al. 1998; Maistrello et al. 2001; Zhu et al. 2001; Khasawneh 2003; Morales-Ramos et al. 2003).

The antifungal activity of yellow-cedar heartwood constituents towards P. ramorum was initially determined by testing the essential oil from yellow-cedar, Port-Orford-cedar, incense cedar and western juniper at a single concentration in agar dish bioassays using
North American and European isolates of *P. ramorum*. This was followed by further bioassays testing the activity of yellow-cedar heartwood shavings, and four individual essential oil constituents at various concentrations.

## 2 Materials and methods

### 2.1 *Phytophthora ramorum* isolates

Three North American (A2) isolates from infected native plants growing in Curry County, Oregon and three European (A1) isolates from infected ornamental nursery plants in Clackamas, Oregon were obtained from Dr Everett Hansen and maintained on 2% cornmeal agar (CMA) until needed.

### 2.2 Materials tested

The materials tested for biological activity include the essential oils from yellow-cedar, *C. nootkatensis*, incense cedar, *Calocedrus decurrens* (Torr.) Florin, Port-Orford-cedar, *C. Lawsoniana* and western juniper, *Juniperus occidentalis* Hook., heartwood shavings of yellow-cedar (stored air dry for approximately 10 years in the laboratory), nootkatin, carvacrol, nootkatone and valencene. Essential oils were obtained by steam distillation of about 1.5-kg batches of variable-sized (0.25–25 mm long, 0.25–5.0 mm wide and 0.25–1.0 mm thick), air-dried heartwood shavings or chips. Heartwood samples were collected from live trees of all species except Port-Orford-cedar, which were obtained from downed logs. The Port-Orford-cedar essential oil was the same as described by Tucker et al. (2000). Nootkatin was isolated as crystals that precipitate from the yellow-cedar essential oil, and nootkatone was isolated by column chromatography fractionation of the yellow-cedar oil on silica gel as described in detail by Xiong (2000). Carvacrol (Aldrich, 98% purity) and valencene (Fluka, 70% purity) were obtained from Sigma-Aldrich (St Louis, MO, USA). The essential oils and individual compounds were dissolved in ethyl acetate (HPLC grade, Fisher Scientific, Pittsburg, PA, USA) to aid in delivery to the agar media. All compounds were added to autoclaved 2% CMA cooled to 55°C and then poured into 90-mm Petri plates, whereas the woodchips were weighed directly into Petri plates prior to the addition of sterile media. The essential oils were tested at 140 mg/kg only. Carvacrol and nootkatin were tested at 1, 5, 10, 50, 100, 500 and 1000 mg/kg, whereas nootkatone and valencene were tested at all but the lowest two concentrations. Wood shavings were tested at 100, 500, 1000, 2000, 5000, 10 000 and 25 000 mg/kg. Control plates were prepared by the addition of ethyl acetate only (same amount as the highest dilution, i.e. maximum amount of ethyl acetate used to prepare test fractions).

### 2.3 Bioassays

All bioassays were conducted using three plates (reps) of each isolate (three European and three North American), and all experiments were conducted twice, except the initial bioassays with essential oils. Zoospore/sporangia solutions (~10⁶ zoospores/ml) were prepared by growing isolates (four 6-mm agar plugs) on clarified V8 agar (6.6%) for 2 weeks. Water (10 ml) was added to the plate surface and spores liberated by incubating the plate at 3°C for 4 h. A 100-μl aliquot of this spore solution was added to each test plate. After 24 h of exposure to the compounds, the number of lysed, ungerminated and germinated spores in each of the five random fields of view (≥100 spores per field of view) was counted under the microscope at 40× magnification (Fig. 1). Zoospore germination (%) was calculated by dividing the number of germinated spores by the total (lysed,
ungerminated and germinated) number of spores present. Similarly, sporangia germination (%), was determined from the same plates at 24 h by recording the number of empty, ungerminated and germinated sporangia in each of the five random fields of view (≥25 sporangia per field of view) under the microscope at 40× magnification (Fig. 2). Hyphae were obtained from isolates grown on 2% CMA, one plug (6 mm) was placed on the centre

Fig. 1. Zoospore observed in the bioassays. KZ, killed zoospore; EZ, encysted zoospore; GZ, germinated zoospore; H, hyphae
of each test plate, and growth from the plug was recorded after 7 days. To determine whether these yellow-cedar compounds were fungitoxic or fungistatic, the hyphal plugs were transferred from the treatment Petri dishes to dishes with fresh agar at the end of the first experiment and allowed to grow for 14 days.

2.4 Chemical analysis of yellow-cedar heartwood

Three subsamples (approximately 0.400 g) of the heartwood shavings used for bioassays were separately weighed into 15-ml vials (20 × 70 mm outside diameter), covered with 4.0 ml of ethyl acetate, sealed and allowed to extract for 48 h at room temperature. One millilitre of the extract was transferred to an autosampler vial, and sealed with a septa after adding 100 μl of an ethyl acetate internal standard solution containing 133 μg of R-(+)-limonene (Aldrich, 97%). Two microlitres of this solution was analysed with a Hewlett Packard (Palo Alto, CA, USA) 5890 Series II gas chromatograph equipped with a flame ionization detector and Phenomenex (Torrance, CA, USA) ZB-5 column (30 m × 0.25 mm inside diameter, 0.25 μm film thickness). The oven programme was held at 100°C for 1.0 min, then increased at 5.0°C/min up to 150°C, followed by 3.0°C/min up to 220°C with no hold at the final temperature. Helium was the carrier gas set at 1.0 ml/min flow through the column oven at 100°C. The injector and detector temperatures were 250°C. A three-level standard curve for carvacrol and nootkatin was prepared using solutions containing 133 μg of limonene as an internal standard.

3 Results

All four essential oils at 140 mg/kg strongly inhibited zoospore germination and hyphal growth of *P. ramorum*, with no differences among the four oils (Table 1). There were no interactions between the isolates and essential oil extracts (p = 0.3314 and 0.3268, respectively), and no differences among isolates for either measurement (p = 0.8442 and 0.5994, respectively), thus allowing a single mean for each oil.

Results from the two replicated experiments testing heartwood shavings and individual compounds were similar, with values from the last replicate presented here. Heartwood

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*Fig. 2. Sporangia observed in the bioassays. KS, killed sporangia; GS, germinated sporangia; ES, empty sporangia; H, hyphae*
Shavings started showing activity at about 1000 mg/kg, and were strongly inhibitory by 10 000 mg/kg in all three bioassays (Fig. 3a,c,e). Nootkatin exhibited the strongest activity of the four individual compounds tested (Fig. 3b,d,f), with some inhibition of zoospore germination and hyphal growth at 1.0 mg/kg, and complete inhibition at 10, 100 and 500 mg/kg for zoospores, hyphae and sporangia, respectively. Carvacrol was the second most active compound with some inhibition of hyphal growth at 10 mg/kg, and strong activity in all assays at 100–500 mg/kg (Fig. 3b,d,f). Nootkatone and valencene were similar in their antifungal properties. Both were weak inhibitors of sporangia germination, even at 1000 mg/kg (Fig. 3d). Their inhibition of hyphal growth started at 50 mg/kg and was approaching 100% at 1000 mg/kg (Fig. 3f), whereas their inhibition of zoospore germination started at 10 mg/kg and reached complete inhibition at 1000 mg/kg of valencene and nearly 100% with 1000 mg/kg of nootkatone (Fig. 3b). Inhibition of the *P. ramorum* hyphal growth for all compounds was the result of fungistatic rather than fungitoxic activity because hyphal growth resumed after being transferred to fresh plates without the inhibitors present.

Six major components were identified and quantified [mg/kg dry weight (DW)] in the heartwood shavings: nootkatone (503), valencene-11,12-diol (469), carvacrol (375), nootkatol (315), *epi*-nootkatol (114), valencene-13-ol (107) and a total (1883). There was no detectable nootkatin.

### 4 Discussion

Shavings of yellow-cedar heartwood, essential oil from the heartwood, and individual compounds occurring in the oil all had antifungal activity towards *P. ramorum*. Nootkatin, a tropolone long known for its fungistatic or fungitoxic activity towards various wood decay fungi (Rennerfelt and Nacht 1955; Smith 1970; Smith and Cserjesi 1970), was the most active of the compounds tested, starting at about 1 mg/kg. The membrane surrounding zoospores appeared to instantaneously decompose in the presence of nootkatin (Fig. 1). Carvacrol was the second most active compound tested, starting at about 10 mg/kg. It is an aromatic monoterpene that also occurs as a major component in the leaves of oregano and thyme (Burt 2004), the herbs used for flavouring food. Its antimicrobial activity towards food-borne pathogens is associated with destroying or disrupting membrane functions (Helander et al. 1998). The phenolic hydroxyl group in carvacrol is required to destabilize the cytoplasmic membrane of *Bacillus cereus* and subsequently deplete the internal ATP pool, leading to cell death (Ultee et al. 1999, 2002). Valencene and nootkatone were similar in their impacts on *P. ramorum* zoospore germination and hyphal growth, but at concentrations about 10 times or greater than

This work underestimates the potential activity of fresh heartwood shavings because the material we used had been stored in a sealed plastic bin for 10 years under laboratory conditions and contained only six of the 12–16 major constituents that normally occur in live yellow-cedar (Kelsey et al. 2005). These six constituents combined averaged 1883 µg/g DW, or the equivalent of 9.4 mg/kg in 5000 mg/kg of shavings that inhibited zoospore germination nearly the same as 10 mg/kg nootkatin, indicating these shavings have excellent antifungal activity when based on their chemical composition. Fresh samples from trees contain about three to seven times higher concentrations of each compound than the shaving tested in this experiment, including about 1000–2000 mg/kg DW of carvacrol, nootkatone and carvacrol. Neither compound had much effect on sporangia germination. Nootkatone and the oxygenated derivatives of valencene (valencene-13-ol and valencene-13-aldehyde) are active repellants or toxins for fleas, ticks, fruit flies, mosquitoes or termites (Panella et al. 1997; Ahn et al. 1998; Miyazawa et al. 2000; Maistrello et al. 2001; Zhu et al. 2001; Khasawneh 2003).

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2000 mg/kg DW of nootkatin and 14 000 mg/kg DW of all compounds combined (Kelsey et al. 2005). Thus, we project that 50–500 mg/kg of fresh shavings from heartwood of live yellow-cedar would provide the same level of antifungal activity as the 5000-mg/kg shavings in Fig. 3a. Additional bioassays comparing the antifungal activity of extracts from fresh yellow-cedar heartwood with the extracts from heartwood of several other conifers are in progress.

Shavings or chips of yellow-cedar heartwood have potential for use in an integrated management programme to help minimize P. ramorum spore distribution. A layer of shavings could be spread over areas where spores are likely to occur, but difficult to control by other means, such as paths through the forest and parking lots used by hikers and bicyclists, because spores are known to move along these corridors (Cushman and Meentemeyer 2005). They might be used at collection sites where infected woody residues are gathered and processed for disposal or utilization (Shelly et al. 2005). In urban forests, shavings could be spread around infected high-value trees to minimize the build-up of spores in the litter and soil where they remain viable for longer periods (Aveskamp et al. 2005; Fichtner et al. 2005).

The fungicidal compounds in yellow-cedar heartwood have a low solubility in water, allowing them to be released slowly over an extended period. This low water solubility could extend the compounds’ residence time in the soil, increasing their ability to eliminate future spore deposition and/or spores that have penetrated deep into the litter layer, compared with other more water-soluble fungicides. Although the fungicidal activity of yellow-cedar heartwood shavings against P. ramorum chlamydomspores was not tested, the compounds’ lack of water solubility and presumed persistence in the soil would increase the likelihood that a single application would be active against chlamydomspores when they do break dormancy (i.e. after extended periods of soil rehydration, Fichtner et al. 2005); generating new sporangia and zoospores (Werres et al. 2001), which are susceptible to the yellow-cedar compounds. Furthermore, yellow-cedar heartwood is a natural material and has minimal restrictions for application, unlike fungicides. In Alaska, yellow-cedar sawdust and shavings that accumulate during milling have been used as fill for forest roads (authors’ personal observation). Still, the effects on non-target organisms would need to be studied.

Yellow-cedar is most abundant in the coastal forests of southeast Alaska and British Columbia, but is found also in the Cascade Range of Oregon and Washington (Harris 1990). The wood is highly desired in foreign markets, especially Japan. However, since the 1880s, yellow-cedar in southeast Alaska has been experiencing a decline, believed to be initiated by climatic warming, that continues to this day (Hennon et al. 1990a,b; Hennon and Shaw 1994, 1997). As a consequence, there is an abundance of dead standing yellow-cedar snags widely spread over more than 200 000 ha that is largely unused, except for firewood. The heartwood of snags dead 14 years or less has essentially the same concentrations of bioactive constituents as live trees (Kelsey et al. 2005). Concentrations of these compounds begin to decrease when the snags have been dead about 26 years, but based on the composition and activity of the shavings tested in this experiment, even the heartwood of these older snags would have ample activity towards P. ramorum. Gathering, transporting and processing these snags at an affordable cost would be the greatest challenge for utilizing them in combating the unwanted distribution of P. ramorum spores. Alternatively, lower quality trees with minimal value in foreign markets could be used in place of, or in combination with, snags.

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Résumé

Activité sporicide du bois de cœur, des huiles essentielles et des constituants du bois du Chamaecyparis jaune (Chamaecyparis nootkatensis) vis-à-vis de Phytophthora ramorum en culture

Dans cet article, nous montrons que 140 mg/kg d’huile essentielle de bois de Chamaecyparis jaune (Chamaecyparis nootkatensis), de cèdre à encens (Calocedrus deccurrens) de Chamaecyparis de Lawson (Chamaecyparis lawsoniana), ou de genévrier occidental (Juniperus occidentalis) inhibent fortement la germination des zoospores et la croissance des hyphes de P. ramorum en culture. Quatre composés du bois de cœur de Chamaecyparis jaune ont été testés. La germination des zoospores a été complètement inhibée à 10, 100 et 1000 mg/kg pour la nootkatine, le carvacrol, et le valencène respectivement. La nootkatone est le composé le moins actif, avec 3,5% de germination des zoospores à 1000 mg/kg. La germination des sporanges est nulle à 500 mg/kg de nootkatine ou de carvacrol. La destruction de la membrane externe des zoospores et la perte de contenu des sporanges ont souvent été observés, indiquant une activité sporicide. La croissance des hyphes a été inhibée à 99,9% à 50 mg/kg de nootkatine ou 500 mg/kg de carvacrol, mais la croissance reprend quand les inhibiteurs sont retirés. L’activité zoosporicide de copeaux de bois de cœur de Chamaecyparis jaune conservés au sec depuis environ dix ans, est conforme à leur contenu en composés extractibles. L'application de copeaux frais de bois de cœur de Chamaecyparis jaune, avec des concentrations de composés actifs nettement supérieures, pourrait être utilisé dans le cadre de programmes de lutte intégrée pour minimiser la distribution des spores de P. ramorum, en particulier dans les zones où la lutte est difficile, comme les chemins et parkings utilisés par les randonneurs et cyclistes.

Zusammenfassung

Sporizide Wirkung von Kernholz, ätherischen Ölen und Holzbestandteilen von Chamaecyparis nootkatensis gegen Phytophthora ramorum in vitro

Es wurde nachgewiesen, dass 140 mg/kg ätherisches Öl aus dem Holz von Chamaecyparis nootkatensis, Chamaecyparis lawsoniana oder Juniperus occidentalis die Zoosporenkeimung und das Hyphenwachstum von Phytophthora ramorum in vitro stark hemmen. Außerdem wurden vier spezifische Komponenten aus dem Kernholz von C. nootkatensis getestet. Die Zoosporenkeimung wurde vollständig gehemmt bei 10 mg/kg Nootkatin, 100 mg/kg Carvacrol und 1000 mg/kg Valencen. Nootkaron war am wenigstens wirksam (3,5% Zoosporenkeimung bei 1000 mg/kg). Die Keimung der Sporangien wurde durch 500 mg/kg Nootkatin oder Carvacrol vollständig gehemmt. Die sporizide Wirkung äusserte sich im häufigen Aufreissen der äusseren Zoosporennembran und im Verlust des Zytoplasmas. Das Hyphenwachstum wurde mit 50 mg/kg Nootkatin oder 500 mg/kg Carvacrol zu 99,9% gehemmt, die Hyphen wuchsen aber weiter, wenn sie auf ein hemmstofffreies Medium gesetzt wurden. Die sporesontötende Wirkung von Spänen von C. nootkatensis, die ca. 10 Jahre lang trocken gelagert worden waren, ging mit der Menge an Extraktstoffen zusammen. Somit könnte das Ausbringen von frischen Spänen oder Fragmenten des frischen Kernholzes von C. nootkatensis mit deutlich höherem Wirkstoffgehalt in den Zonen, wo eine Kontrolle von P. ramorum schwierig ist (z.B. Wanderwege oder Parkplätze) als Komponente eines integrierten Programmes zur Reduktion der Verbreitung dieses Pathogens sinnvoll sein.

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