

Colonization of cut branches of five coniferous hosts of the pitch canker fungus by *Pityophthorus* spp. (Coleoptera: Scolytidae) in central, coastal California

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Abstract—Pitch canker of pines (*Pinus* spp.) and Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) (Pinaceae) is caused by the fungus *Fusarium circinatum* Nirenberg *et* O'Donnell. In California, infections by *F. circinatum* occur largely through wounds caused by insects. Field experiments were initiated to determine whether the colonization activities of twig beetles, *Pityophthorus* spp. (Coleoptera: Scolytidae), could explain the incidence of pitch canker on Monterey pine (*P. radiata* D. Don), Bishop pine (*P. muricata* D. Don), ponderosa pine (*P. ponderosa* var. *ponderosa* Dougl.), knobcone pine (*P. attenuata* Lemm.), and Douglas-fir. Asymptomatic branches were cut from each of four pairs of tree species (Monterey–Bishop, Monterey–ponderosa, Monterey–knobcone, Monterey–Douglas-fir) at four sites and attached to the lower canopy of both heterospecific and conspecific host trees (total of four combinations per pair). After 10 weeks, branches were collected and placed in rearing tubes in the laboratory. Emerging insects were identified and placed on a *Fusarium*-selective medium. Monterey, Bishop, and ponderosa pines were more heavily infested by *Pityophthorus* spp. than Douglas-fir and knobcone pine. Furthermore, more *Pityophthorus* beetles emerged from Monterey pine branches placed in Monterey pine canopies than from Monterey pine branches placed in Bishop or ponderosa pine canopies, indicating that reduced emergence (colonization) was caused by the heterospecific host. Relatively fewer insects emerged from sites containing either Monterey and knobcone pines or Monterey pine and Douglas-fir. *Fusarium circinatum* was not isolated from emerging *Pityophthorus* spp. Susceptibility of the five host species, based on mean lesion lengths resulting from mechanical inoculations, varied significantly. The longest lesions were on Monterey pine and the shortest were on ponderosa pine and Douglas-fir. The low incidence of pitch canker on Douglas-fir and ponderosa pine in nature compared with that on Monterey, Bishop, and knobcone pines may be explained by the low colonization by twig beetles and the greater resistance of Douglas-fir and ponderosa pine to this disease, compared with the other three hosts.

Résumé—Le chancre résineux des pins (*Pinus* spp.) et du sapin de Douglas (*Pseudotsuga menziesii* (Mirbel) Franco) (Pinaceae) est causé par le champignon *Fusarium circinatum* Nirenberg *et* O'Donnell. En Californie, les infections de *F. circinatum* pénètrent surtout par des plaies faites par les insectes. Nous avons mis au point des expériences de terrain afin de

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déterminer si les activités de colonisation des scolytes *Pityophthorus* spp. (Coleoptera : Scolytidae) peuvent expliquer l'incidence du chancre résineux chez le pin de Monterey (*P. radiata* D. Don), le pin muriqué (*P. muricata* D. Don), le pin ponderosa (*P. ponderosa* var. *ponderosa* Dougl.), le pin à cônes pointus (*P. attenuata* Lemm.) et le sapin de Douglas. Nous avons coupé des branches asymptotiques de chacune de quatre paires d'espèces d'arbres (Monterey–muriqué, Monterey–ponderosa, Monterey–cônes pointus, Monterey–Douglas) à quatre sites et les avons attachées à la ramure inférieure d'arbres hôtes de même espèce et d'espèces différentes (un total de quatre combinaisons par paire). Les branches ont été récoltées au bout de 10 semaines et placées dans des tubes d'élevage en laboratoire. Les insectes qui ont émergé ont été identifiés et placés sur un milieu de culture spécifique à *Fusarium*. Les pins Monterey, muriqué, et ponderosa étaient plus fortement infestés par *Pityophthorus* spp. que le sapin de Douglas et le pin à cônes pointus. De plus, un plus grand nombre de *Pityophthorus* ont émergé de branches de pins de Monterey placées dans des ramures de pins de Monterey que de branches de pins de Monterey placées dans des ramures de pins muriqués ou ponderosa, ce qui laisse croire que l'émergence (colonisation) réduite est due à l'hôte d'espèce différente. Relativement moins d'insectes ont émergé des sites contenant ou bien les pins de Monterey et à cônes pointus ou alors le pin de Monterey et le sapin de Douglas. Nous n'avons pas isolé de *Fusarium circinatum* chez les *Pityophthorus* spp. en émergence. La susceptibilité des cinq espèces d'hôtes, déterminée par la longueur moyenne des lésions causées par les inoculations mécaniques, varie de façon significative. Les lésions les plus longues se retrouvent sur les pins de Monterey et les plus courtes sur les pins ponderosa et les sapins de Douglas. La faible incidence du chancre résineux sur le sapin de Douglas et le pin ponderosa en nature par rapport à celle sur les pins de Monterey, muriqués et à cônes pointus peut s'expliquer par la faible colonisation des scolytes sur le sapin Douglas et le pin ponderosa et par la plus grande résistance de ces arbres à la maladie par comparaison aux trois autres hôtes.

[Traduit par la Rédaction]

Introduction

Biological invasions of pathogens have had major impacts on the ecology of North American forests (Manion 1981; Manion and Lachance 1992; Liebhold *et al.* 1995). Invasion of new habitats by exotic organisms is often accomplished through their association with native organisms in the local environment. Insects are the main consumers of plants and, with their diverse size, form, and behavior, are frequently involved in the spread of plant pathogens, both introduced and native. These have included a number of important pathogens of native North American trees, such as *Ophiostoma novo-ulmi* Brasier, the cause of Dutch elm disease (Brasier 1986), *Ceratocystis fagacearum* (Bretz) Hunt, the cause of oak wilt (Griswold and Neiswander 1953), *Cryphonectria parasitica* (Murr.) Barr, the cause of chestnut blight (Russin *et al.* 1984), and pathogens in the genus *Leptographium* (Harrington 1993).

Pitch canker was discovered in the southeastern United States in 1946 (Hepting and Roth 1946) and is now a problem of plantation and nursery pines in many parts of the world (Gordon *et al.* 2001). The first case of severe damage attributable to pitch canker occurred in slash pine (*Pinus elliotii* Engelm.) (Pinaceae)

plantations in Florida in the mid-1970s (Schmidt 1978; Dwinell *et al.* 1985). More recently, Viljoen and Wingfield (1994) reported a local epidemic of pitch canker affecting 6 million pine seedlings in South Africa. In Japan, pitch canker has infected Ryukyu pine (*Pinus luchuensis* Mayr), a native species occurring on six of the southern, subtropical islands. Some consider the disease to be endemic to these areas (Muramoto and Dwinell 1990; Dwinell 1999), but limited genetic diversity in the pathogen population suggests a recent introduction (Wikler and Gordon 2000). In Mexico, the disease has been identified on 19 pine species in 14 states (Guerra-Santos 1999), where it has caused considerable losses in plantations. In California, the causal pathogen, *Fusarium circinatum* Nirenberg *et al.* O'Donnell (= *F. subglutinans* (Wollenweb *et al.* Reinking) Nelson *et al.* f. sp. *pini*), was discovered on planted Monterey pines (*Pinus radiata* D. Don) in 1986 (McCain *et al.* 1987) in landscape settings. The pathogen is considered a recent introduction into California because of its limited genetic diversity compared with populations in Florida and Mexico (Correll *et al.* 1992; Gordon *et al.* 1996; Hodge and Dvorak 2000; Wikler and Gordon 2000).

Monterey pine is one of the most widely planted pine species in the world (Balocchi 1997) and is particularly abundant in Chile, New Zealand, and Australia, whereas native populations are found in only five locations worldwide. Two of these populations are on islands off the coast of Baja, California, and are morphologically distinct from those on the mainland (Hickman 1993). Mainland populations occur in three disjunct locations along the coast of central California: Monterey (36°36'N, 121°54'W), Año Nuevo (37°06'N, 122°17'W), and Cambria (35°34'N, 121°05'W) (McDonald and Laacke 1990). Pitch canker is now found in 19 coastal counties from Mendocino to San Diego in California, affecting all three native stands (Correll *et al.* 1991; Storer *et al.* 1994; Dallara *et al.* 1995; Gordon *et al.* 1996, 1997, 2001). Recently, pitch canker has been found on Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) (Pinaceae) in El Dorado County, in the central Sierra Nevada (Vogler *et al.* 2004). Losses of Monterey pines to pitch canker disease are important not only to the native forests themselves but also for their effects on a critical resource for genetic improvement of this commercially valuable species.

Pitch canker disease progression on Monterey pines has already been described (McCain *et al.* 1987; Correll *et al.* 1991; Gordon *et al.* 2001; Storer *et al.* 2002; Wikler *et al.* 2003). Initial infection of individual branch tips is usually followed by infection of multiple branches and the tree stem. The infected tree typically responds to infection by producing copious amounts of resin and forming cankers in the sapwood, from which the common name "pitch canker" is derived (Hepting and Roth 1946; Dwinell *et al.* 1985). Multiple branch infections can cause extensive dieback in the crown of the tree and may lead to mortality of the upper crown or the entire tree (Storer *et al.* 2002).

Association of insects with pitch canker disease of Monterey pine in California was first reported in 1987, at which time the role of insects in the incidence and spread of the disease was unknown (McCain *et al.* 1987). Since that time, several insect species, mainly bark beetles (Coleoptera: Scolytidae), have been shown to be capable of transmitting the pathogen (Fox *et al.* 1990a, 1991; Hoover *et al.* 1996; Sakamoto *et al.* 2001; Storer *et al.* 2004). Eleven insect species associated with California pines are known or suspected vectors of pitch canker,

including twig beetles (*Pityophthorus* spp.) (Scolytidae). *Pityophthorus* spp. in North America preferentially colonize branch tips of recently killed, broken, dying, or diseased host trees (Bright 1981). They are also reported to carry inoculum of the pathogens *Gremmeniella abietina* (Lagerb.) Morelet (Smerlis and Finnegan 1981) and *Leptographium procerum* (Kendr.) Wingf. (Nevill and Alexander 1992).

Pityophthorus setosus Blackman is considered to be a vector of the pitch canker fungus because Leach's postulates for transmission of plant pathogens (Leach 1940) have been satisfied (Storer *et al.* 2004). These beetles colonize branch tips (Fox *et al.* 1990b; Dallara 1997; McNee *et al.* 2002) and conelets (Hoover *et al.* 1996) of pitch canker infected Monterey pines. Propagules of *F. circinatum* have been isolated from *P. setosus* emerged from infected and uninfected branch tips of mature Monterey pines (Storer *et al.* 1994; Hoover *et al.* 1995; Dallara 1997; McNee *et al.* 2002). Free-flying beetles transmitted *F. circinatum* to Monterey pine seedlings under laboratory conditions (Fox and Schultz 1991). *Pityophthorus setosus* transmitted the pitch canker pathogen to Monterey pine in field studies when contaminated artificially and caged onto branches and when attracted to trees using the beetle's aggregation pheromone (Storer *et al.* 2004).

Significant range expansion of pitch canker has occurred throughout the central coast of California since the first reported outbreak in 1986 (McCain *et al.* 1987; Storer *et al.* 1994, 1997; Gordon *et al.* 1996, 2001). It is now found in other co-occurring pine species and Douglas-fir in central, coastal California (Gordon *et al.* 1996, 2001). Bishop (*Pinus muricata* D. Don) and knobcone pines (*Pinus attenuata* Lemm.) have been found to be frequently infected, while ponderosa (*Pinus ponderosa* var. *ponderosa* Dougl.) and Torrey pines (*Pinus torreyana* Parry ex Carr.) and Douglas-fir have been found only occasionally infected in the field (Storer *et al.* 1994; Dallara *et al.* 1995; authors' personal observations). Infection of Jeffrey (*Pinus jeffreyi* Grev. & Balf.) and sugar (*Pinus lambertiana* Dougl.) pines has not been observed, but these species are known to be susceptible (Gordon *et al.* 1998a). Currently, little is known about the interaction of insects with other conifer hosts co-occurring with Monterey pines.

The present study was undertaken to evaluate the potential spread of the pitch canker

pathogen from Monterey pines to other co-occurring conifers via insect vectors in central, coastal California. The pathogen could conceivably be introduced into other coniferous forest species in the western United States and other countries through a number of potential pathways via insects (Storer *et al.* 1997; Dick 1998; McNee *et al.* 2002). Introduction of pitch canker poses a significant threat to the forest industry in North America, Chile, New Zealand, and Australia. We are particularly interested in the interaction of *Pityophthorus* spp. with other conifer hosts, because *Pityophthorus* spp. have a broad host range in the western United States, and their hosts are found in major forest types throughout western North America (Wood 1982). Information on alternative tree species that will serve as suitable hosts for *Pityophthorus* spp. would increase our understanding of the risk of spread of this disease in North America. Our objective was to determine whether the colonization preferences of *Pityophthorus* spp. could explain the incidence of pitch canker on Monterey, Bishop, ponderosa, and knobcone pines and Douglas-fir in central, coastal California, where these species co-occur in natural and planted forests.

Methods and materials

Four study sites were located in Monterey (Pebble Beach, Monterey Peninsula), San Mateo (Año Nuevo State Reserve), and Santa Cruz counties (Henry Cowell State Park and University of California Santa Cruz campus) in central, coastal California. The Pebble Beach site contains native Monterey and Bishop pines, and both pine species are heavily infected by *F. circinatum*. Año Nuevo State Reserve contains native Monterey pines and Douglas-fir, and Monterey pines are heavily infected, whereas infections have been observed on only a few Douglas-firs. Henry Cowell State Park in Santa Cruz Co. contains planted Monterey and native ponderosa pines, and Monterey pines are heavily infected, whereas no infection has been found on ponderosa pines in this area. The University of California Santa Cruz campus contains planted Monterey pines, which are heavily infected, and native knobcone pines, which exhibit little infection.

At each site, branch tips (50–60 cm long) were cut from asymptomatic trees (Monterey, Bishop, ponderosa, and knobcone pines and Douglas-fir) and tied to branches in the lower

canopies of the above conifer species. Ten branch tips cut from each pair of tree species at each site were placed on both heterospecific and conspecific host trees, for a total of four treatments per experiment. For example, branch tips taken from Monterey pines at Pebble Beach were placed on both Monterey and Bishop pines, and likewise branch tips of Bishop pines were placed on both Bishop and Monterey pines. At each site, four branches were cut from each of 5 randomly selected trees for each tree species (total of 10 trees). Four branches of a single tree species were placed on each tree (total of 10 trees, 5 per species). After 10 weeks, cut branch tips were brought to the laboratory. This sampling procedure was repeated once every year from 2000 to 2002.

Branch tips taken from the field were placed in tubes (10 cm diameter and 70 cm length) at room temperature and 24 h light for 8 weeks using the methods of Dallara (1997). Each rearing tube contained a single branch tip. A sewn cloth exit cone was fitted with a clear glass collection vial and attached to the opposite end of the tube. The collection vial was oriented toward the light. Before branch tips were collected, rearing tube cloth components were autoclaved, and glass vials and tubes were immersed for 10 min in 1% sodium hypochlorite, followed by a water rinse, to prevent contamination of emerged insects by residue from previous contents. Emerging insects were collected daily and placed in separate sterile vials. All insects were killed by freezing at 0 °C and later identified to species. Branch tips that did not yield any insects were dissected, and any dead beetles found inside were identified. Sterile technique was maintained for collection and identification of emerged insects.

Fungal isolation

Phoresy rates of the pitch canker pathogen on all insects emerged from rearing tubes and dissected from branch tips were determined by vortexing individual insects with 1 mL of sterilized water for 30 s to dislodge spores carried on the insect and then spreading the water over *Fusarium*-selective medium (Correll *et al.* 1991). *Fusarium circinatum* colonies growing on the medium were counted after 5 days. Isolation plates were incubated (20 ± 4 °C, 12L:12D) for 5 days. Fungal colonies were provisionally identified as *F. circinatum* based on morphology of conidia and microconidiophores (Gordon *et al.* 1996) on the selective medium

Table 1. Total numbers of *Pityophthorus* spp. emerged from asymptomatic branch tips of Monterey, Bishop, ponderosa, and knobcone pines and Douglas-fir in central, coastal California.

Insect species	Total no. of insects	% of total emerged insects	No. of insects by sex	
			Male	Female
<i>P. setosus</i>	1489	66.4	827	622
<i>P. nitidulus</i>	517	23.1	132	385
<i>P. carmeli</i>	149	6.7	45	104
<i>P. californicus</i>	13	0.6	7	16
<i>P. tuberculatus</i>	15	0.7	13	2
Other <i>Pityophthorus</i> spp.	57	2.5		

or, for uncertain identifications, following transfer to carnation leaf agar (Nelson *et al.* 1983).

Inoculations

Branch tips of all five host tree species were inoculated with *F. circinatum* on 1 July 2003 to determine susceptibility to the pitch canker pathogen. In this experiment, the susceptibility of inoculated trees was estimated from the size of the lesion that developed in response to the inoculation. On each tree, three individual branch tips were inoculated as described by Gordon *et al.* (1998a). Each branch tip was inoculated with 500 spores of the known virulent isolate FSP17 (Schmale and Gordon 2003) in 5 μ L of water. Six months after inoculation (24 January 2004), all branch tips were cut and brought to the laboratory to measure lesion lengths. Isolations from all branch tips with lesions <0.3 mm in length, and from a subset of the other branch tips, were conducted to determine whether the pathogen had survived.

Statistical analyses

Mean numbers of insects emerged from rearing tubes were analyzed over time using repeated measures analysis of variance (ANOVA) (Proc Mixed, SAS Institute Inc. 1996), with "branch", "tree", and "*Pityophthorus*" defined as classes, and "numbers of insects" as a continuous variable (treatment effect). Graphical analysis of residuals of raw data (Neter *et al.* 1983) indicated that response variables had normal distributions and error terms. Degrees of freedom were estimated by the Satterthwaite method (SAS Institute Inc. 1996). When significant differences for treatments were found, we used Tukey's test (least square means) to

compare the effects among treatments. Differences in mean lesion lengths among trees were tested using one-way ANOVA, with "species" and "site" defined as classes, "site" as a random statement (blocking factor), and "lesion size" as a continuous variable (treatment effect). The raw data (lesion size) were square root transformed to satisfy assumptions of homogeneity of variance (Neter *et al.* 1983).

Results

A total of 2413 beetles emerged from branch tips placed in rearing tubes. *Pityophthorus* spp. comprised 93% of total emerged insects. The remaining 7% were deathwatch beetles, *Ernobius punctulatus* (LeConte) (Coleoptera: Anobiidae). All *E. punctulatus* emerged from branch tips previously colonized by *Pityophthorus* spp. Among *Pityophthorus* species, *P. setosus*, *P. nitidulus* (Mannerheim), and *P. carmeli* Swaine were the most abundant species that emerged. The female:male ratio was 0.43 for *P. setosus*, 0.74 for *P. nitidulus*, and 0.70 for *P. carmeli*. Other *Pityophthorus* species encountered were *P. californicus* Bright, *P. tuberculatus* Eichoff, and unknown species (Table 1).

Monterey–Bishop pine experiment

The percentages of Bishop and Monterey pine branches colonized by *Pityophthorus* spp. were 90.0% and 76.7%, respectively. Insects dissected from branches were included in these percentages. Forty-five percent ($n = 60$) of the Bishop pine branches that were colonized by *Pityophthorus* spp. were also colonized by *E. punctulatus*, while 38.3% of the Monterey

Table 2. ANOVA of the responses of *Pityophthorus* spp. to four combinations of five conifer species.

Source of variation	df [†]	Monterey pine × Bishop pine		Monterey pine × ponderosa pine		Monterey pine × Douglas-fir		Monterey pine × knobcone pine	
		F	P	F	P	F	P	F	P
Branch	1,116	0.19	0.661	10.28	0.002	7.45	0.007	6.25	0.014
Tree	1,116	0.78	0.378	9.03	0.003	3.09	0.081	5.96	0.016
<i>Pityophthorus</i> *	4,116	41.79	<0.0001	14.68	<0.0001	11.45	<0.0001	7.11	<0.0001
Branch × Tree	1,116	4.29	0.041	8.29	0.005	0.94	0.334	1.81	0.181
Branch × <i>Pityophthorus</i>	4,116	1.04	0.390	12.67	<0.0001	6.34	0.0001	5.24	0.0006
Tree × <i>Pityophthorus</i>	4,116	0.98	0.421	11.43	<0.0001	7.58	<0.0001	1.86	0.122
Branch × Tree × <i>Pityophthorus</i>	4,116	3.25	0.015	9.65	<0.0001	6.59	<0.0001	0.88	0.479

*Total no. of *Pityophthorus* spp. consisted of mean numbers of *P. setosus*, *P. nitidulus*, *P. carmeli*, *P. californicus*, *P. tuberculatus*, and unknown species of *Pityophthorus*.

[†]Numerator, denominator degrees of freedom (Proc Mixed, SAS Institute Inc. 1996).

pine branches were colonized by both *Pityophthorus* spp. and *E. punctulatus*.

Mean numbers of emerged *Pityophthorus* beetles were similar between branches of different species and between tree species where branches were placed (Table 2), but there were significant branch × tree interaction effects. The mean number of *Pityophthorus* beetles emerged from Monterey pine branches placed on Monterey pines was significantly higher than the mean number emerged from Monterey pine branches placed on Bishop pines or Bishop pine branches placed on Monterey pines (Table 3). There was no difference in mean number of emerged insects between Bishop pine branches placed on Monterey pines and those placed on Bishop pines.

Some species of *Pityophthorus* were more abundant than others (Table 2). Among five *Pityophthorus* species identified, *P. setosus* was the most abundant (71% of total number of *Pityophthorus* beetles), followed by *P. nitidulus* and *P. carmeli*. Interactions between *Pityophthorus* spp. and branch species or between *Pityophthorus* spp. and tree species were not significant; however, there was a significant interaction among all three of these factors (Table 2). Mean numbers of both *P. setosus* ($F_{3,116} = 3.22$, $P = 0.025$) and *P. carmeli* ($F_{3,116} = 3.42$, $P = 0.019$) were significantly higher on Monterey pine branches placed on Monterey pines than on branches in the other three combinations. Mean numbers were similar among the other treatments.

Monterey-ponderosa pine experiment

Ninety-five percent of Monterey pine branches and 61.7% of ponderosa pine branches were colonized by *Pityophthorus* spp. Twenty-five percent of Monterey pine branches ($n = 60$) that were colonized by *Pityophthorus* spp. were also colonized by *E. punctulatus*. *Pityophthorus* spp. and *E. punctulatus* shared 16.7% of the ponderosa pine branches.

Overall, mean emergence of *Pityophthorus* spp. was significantly higher from Monterey pine branches than from ponderosa pine branches (Table 2). Likewise, a significant tree effect indicates that Monterey pines were superior to ponderosa pines for *Pityophthorus* spp. colonization of branches of either species (Table 2). In addition, Monterey or ponderosa pine branches placed on Monterey pines had significantly higher colonization rates than branches

Table 3. Mean numbers of *Pityophthorus* spp. emerged from asymptomatic branch tips of five pine species placed on conspecific and heterospecific pine trees in central, coastal California.

Branch × host combinations		Mean (±SE) no. of <i>Pityophthorus</i> spp. [‡]				
Branch	Host	% of branches infected*	Total no. of <i>Pityophthorus</i> beetles [†]	<i>P. setosus</i>	<i>P. nitidulus</i>	<i>P. carmeli</i>
Pebble Beach (Monterey Peninsula, Monterey)						
Monterey	Monterey	80.00	24.0±9.9a	14.9±5.7a	6.9±3.4	1.6±0.6a
Monterey	Bishop	73.34	10.4±4.2b	8.2±2.9b	1.7±0.8	0.5±0.3b
Bishop	Bishop	93.33	12.6±4.7ab	10.4±3.4b	1.5±0.7	0.5±0.3b
Bishop	Monterey	86.67	8.9±4.0b	6.4±2.6b	2.1±1.1	0.3±0.2b
Henry Cowell State Park						
Monterey	Monterey	80.00	5.9±1.4a	4.7±1.1a	0.9±0.2ab	0.2±0.0b
Monterey	Ponderosa	100.00	1.7±0.6b	0.9±0.4b	0.5±0.1b	0.2±0.0b
Ponderosa	Ponderosa	36.67	0.3±0.1b	0.2±0.1b	0.1±0.0b	0.0±0.0b
Ponderosa	Monterey	86.67	4.5±1.7a	1.5±0.8b	1.9±0.6a	0.9±0.3a
Año Nuevo State Park						
Monterey	Monterey	40.00	1.3±0.4	0.8±0.2ab	0.2±0.0ab	0.23±0.0
Monterey	Douglas-fir	61.72	1.2±0.5	1.1±0.4a	0.03±0.0b	0.1±0.05
Douglas-fir	Douglas-fir	30.00	0.5±0.2	0.1±0.0c	0.4±0.2a	0.1±0.0
Douglas-fir	Monterey	26.67	0.5±0.1	0.2±0.0bc	0.0±0.0b	0.2±0.0
University of California Santa Cruz						
Monterey	Monterey	30.00	0.4±0.1	0.13±0.0	0.1±0.0b	0.1±0.0
Monterey	Knobcone	10.35	0.1±0.0	0.0±0.0	0.1±0.0b	0.0±0.0
Knobcone	Knobcone	20.00	0.3±0.0	0.0±0.0	0.2±0.0b	0.03±0.0
Knobcone	Monterey	33.33	0.7±0.2	0.1±0.0	0.6±0.1a	0.0±0.0

*Includes emergence and dissection data.

[†]Total no. of *Pityophthorus* beetles consisted of mean numbers of *P. setosus*, *P. nitidulus*, *P. carmeli*, *P. californicus*, *P. tuberculatus*, and unknown species of *Pityophthorus*.

[‡]Means followed by the same letter within a column for each site are not significantly different (repeated measures analysis in Proc Mixed, SAS Institute Inc. 1996; Fisher's Protected LSD test ($P < 0.05$) was used for multiple comparisons).

of either species placed on ponderosa pines (Table 3).

Abundance of emerged *Pityophthorus* spp. showed variation among the four combinations (Table 2). *Pityophthorus setosus* was the most abundant species overall (60% of total number of *Pityophthorus* beetles), followed by *P. nitidulus*. In addition, significant *Pityophthorus* spp. × branch, *Pityophthorus* spp. × tree, and *Pityophthorus* spp. × branch × tree interaction effects indicate that major *Pityophthorus* species showed significant differences in emergence from branches of either pine species as well as the host trees on which the branches were placed (Tables 2 and 3). The highest emergence of *P. setosus* occurred from Monterey pine branches placed on Monterey

pines ($F_{3,116} = 3.34$, $P = 0.022$) (Table 3). There were no differences in mean numbers of *P. setosus* among the other three treatments. Emergence of *P. nitidulus* was significantly higher when ponderosa pine branches were placed on Monterey pines than when they were placed on ponderosa pines and when Monterey pine branches were placed on ponderosa pines ($F_{3,116} = 2.99$, $P = 0.033$). Although mean numbers of *P. carmeli* were low, the emergence of this species was higher from ponderosa pine branch tips placed on Monterey pines than from branches in the other treatments ($F_{3,116} = 2.89$, $P = 0.038$).

Monterey pine – Douglas-fir experiment

The colonization rate of Monterey pine

branches was relatively low in this experiment compared with the rate observed in the Monterey pine – Bishop pine experiment at Pebble Beach. Fifty-one percent of Monterey pine branches and 28.3% of Douglas-fir branches were colonized by *Pityophthorus* spp. Three percent of Monterey pine branches ($n = 60$) colonized by *Pityophthorus* spp. were also colonized by *E. punctulatus*. The colonization rate of *E. punctulatus* on Douglas-fir branches that were already colonized by *Pityophthorus* spp. was about 2%.

Monterey pine branches yielded a significantly higher number of *Pityophthorus* spp. than Douglas-fir branches (Table 2), whereas mean emergence did not vary between tree species. The branch \times tree interaction effect on mean numbers of *Pityophthorus* spp. was not significant.

The mean abundance of *Pityophthorus* spp. varied significantly (Table 2), suggesting that individual species showed significant variation in their abundance. Again *P. setosus* was the most abundant species (61%), followed by *P. nitidulus* and *P. carmeli*. Furthermore, *Pityophthorus* spp. \times branch, *Pityophthorus* spp. \times tree, and *Pityophthorus* spp. \times branch \times tree interaction effects were significant (Table 2). Monterey pine branches placed on either Douglas-fir or Monterey pines yielded significantly higher numbers of *P. setosus* than other treatments ($F_{3,116} = 3.01$, $P = 0.033$). Mean emergence of *P. nitidulus* from Douglas-fir branch tips placed on Douglas-fir trees was significantly higher than mean emergence from Monterey branch tips placed on Douglas-fir trees and Douglas-fir branches placed on Monterey pine trees ($F_{3,116} = 3.11$, $P = 0.03$).

Monterey–knobcone pine experiment

Colonization of Monterey pines by *Pityophthorus* spp. in this experiment was lower than that in any other experiment. Twenty-seven percent of knobcone pine branches and 20.2% of Monterey pine branches were colonized by *Pityophthorus* spp. Thirteen percent of knobcone pine branches ($n = 60$) colonized by *Pityophthorus* spp. were also colonized by *E. punctulatus*. The colonization rate of Monterey pine branches by both *Pityophthorus* spp. and *E. punctulatus* was 5.0%.

There were significant branch, tree, and *Pityophthorus* spp. effects on the mean numbers of *Pityophthorus* beetles emerged (Table 2). Colonization by *Pityophthorus* spp. was

significantly higher on knobcone pine branches than on Monterey pine branches. Moreover, knobcone pines were superior to Monterey pines for *Pityophthorus* spp. colonization. However, the branch \times tree interaction was not significant (Table 2).

Abundance of *Pityophthorus* spp. varied among the four combinations, and *P. nitidulus* was the most abundant species (90%), followed by *P. setosus* and *P. carmeli* (Table 3). Furthermore, there were significant *Pityophthorus* spp. \times branch interaction effects, and only *P. nitidulus* showed a significant difference in emergence from branch tips, perhaps because it was the most abundant species emerged. Knobcone pine branch tips placed on Monterey pines yielded significantly higher numbers of *P. nitidulus* than other treatments ($F_{3,116} = 2.96$, $P = 0.035$) (Table 3).

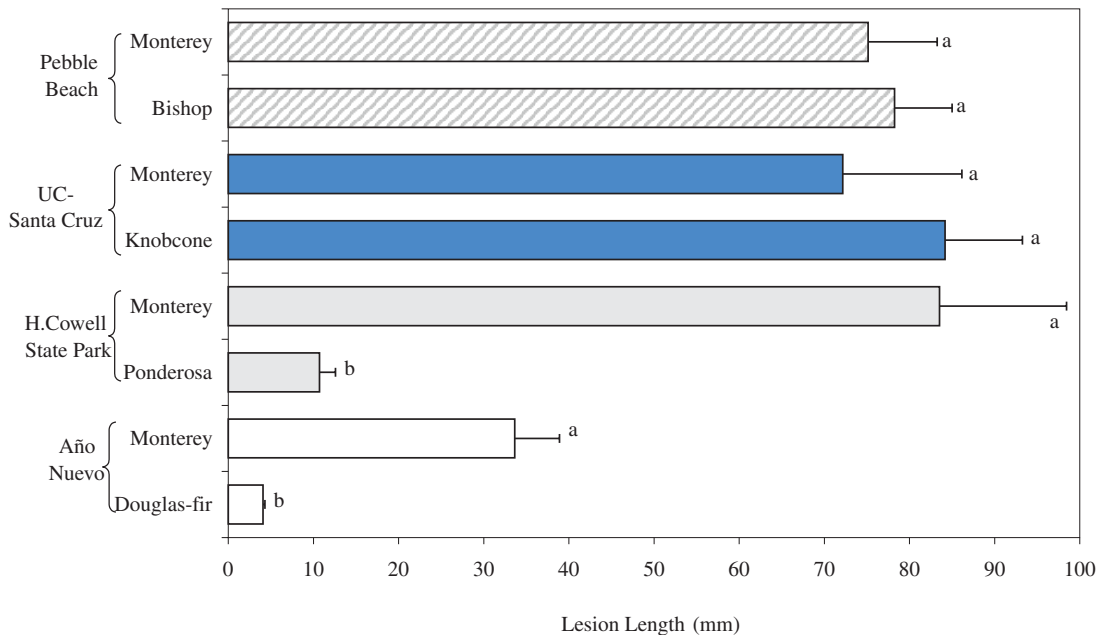
Fungal isolation

Fusarium circinatum was not isolated from adult progeny emerged or dissected from any of the cut branch tips.

Fungal inoculation

Mean lesion lengths on branches of four pairs of host species varied significantly only between Monterey and ponderosa pines ($F_{1,18} = 67.2$, $P < 0.0001$) and between Monterey pine and Douglas-fir ($F_{1,20} = 67.2$, $P < 0.0001$) (Fig. 1), and in each case Monterey pine produced a significantly longer lesion than the other host. Lesion length on Monterey pine varied from 6 to 134 mm, whereas lesion lengths ranged from 37 to 128 mm for Bishop pine, 35 to 185 mm for knobcone pine, 3 to 35 mm for ponderosa pine, and 3 to 6 mm for Douglas-fir. When mean lesion lengths of Monterey pines at all sites were pooled and compared with those of the other host trees, Douglas-fir and ponderosa pine exhibited the shortest lesion lengths among all species ($F_{4,18} = 48.95$, $P < 0.0001$). There were no significant differences in mean lesion lengths among Monterey, Bishop, and knobcone pines. Comparisons of mean lesion lengths among locations indicated that Monterey pines at Año Nuevo State Reserve had shorter lesions than Monterey pines at the other three sites ($F_{3,18} = 5.55$, $P = 0.0071$). Similarly, mean lesion length on planted Monterey pines (78.04 ± 8.23 mm) was significantly greater than that on naturally occurring Monterey pines (50.24 ± 7.23 mm) ($F_{1,19} = 6.43$, $P = 0.0202$). Isolations from all branch

Fig. 1. Mean lesion lengths of four pairs of conifer species (Monterey, Bishop, knobcone, and ponderosa pines and Douglas-fir) artificially inoculated with *Fusarium circinatum* in central, coastal California. The species were paired at four different sites (Pebble Beach, University of California Santa Cruz, Henry Cowell State Park, and Año Nuevo State Reserve). On each tree, three individual branch tips were inoculated with 500 spores on 1 July 2003, and branch tips were cut and brought to the laboratory to measure the lesion lengths on 24 January 2004. Differences in mean lesion length among tree species were tested using one-way ANOVA (Proc Mixed, SAS Institute Inc. 1996). For each site, means followed by the same letter are not significantly different.



tips with lesions <0.3 mm in length indicated that the pathogen did not survive; however, fungi survived on a subset of branch tips with lesions >0.03 mm long.

Discussion

Pityophthorus spp. have been shown to colonize pitch canker infected branches (McNee *et al.* 2002), to make feeding wounds and introduce the pathogen into these wounds under controlled conditions (Sakamoto *et al.* 2001; Storer *et al.* 2004), and to vector the pathogen into non-infected hosts baited with pheromones of these beetles in the field (Storer *et al.* 2004). Thus, *Pityophthorus* spp. are potentially important vectors of *F. circinatum* into new hosts and new locations (Storer *et al.* 1997, 2004; McNee *et al.* 2002).

Infestation of asymptomatic cut branches by *Pityophthorus* spp. usually takes 4–5 weeks in the field, and an additional 2–3 weeks is required for reemergence of parental adults from

branches under controlled environmental conditions (20 ± 2 °C, ambient humidity, 16L:8D) (Dallara 1997). In the current study, most parental adults likely reemerged from the infested cut branches in the field, before they were brought to the laboratory. Beetles emerged in the laboratory were likely their offspring, which would have a low probability of carrying the pathogen because the branches they colonized were not infected by pitch canker. The absence of *F. circinatum* infested beetles in our study is consistent with the low frequency of isolation of *F. circinatum* from parental *Pityophthorus* spp. emerged from asymptomatic cut branches reported by McNee *et al.* (2002) (0.0%) and Dallara (1997) (2.5%). In contrast, the frequency of isolation was 17% when progeny emerged from symptomatic branch tips (McNee *et al.* 2002). The strong association of *F. circinatum* with beetles emerging from symptomatic branches suggests that infected host material greatly increases the probability of transmission to uninfected hosts (Dwinell

and Tidwell 1987; McNee *et al.* 2002) and the chance of inter- or intraspecific transmission of inoculum (Hoover *et al.* 1995, 1996).

A low phoresy rate has also been shown for other insect-vectorized pathosystems (Juzwik and French 1983). Such vectors may still play an important role in the epidemiology of a disease if their populations are high and (or) they effectively locate and colonize infected hosts (Harrington *et al.* 1985). Conversely, poor host location behaviors, as suggested by the findings of Bonello *et al.* (2001), may enhance the role of twig beetles as vectors if they routinely wound numerous branches (Sakamoto *et al.* 2001) before finding a suitable host.

All species of *Pityophthorus* identified in this study were more abundant on the Monterey Peninsula than at the other locations where experiments were conducted. The greater abundance of *Pityophthorus* spp., particularly *P. setosus*, on the Monterey Peninsula is probably due in part to higher densities of infected host trees at this location. Infection by *F. circinatum* weakens tree branches, consequently increasing the availability of resources used by these beetles, which may in turn transfer the pathogen to new hosts and new locations. In fact, the high colonization rate of *Pityophthorus* spp. on Bishop pine branches in the current study may reflect the high incidence of pitch canker on this pine species on the Monterey Peninsula. Similarly, the low colonization rate of Monterey and knobcone pines relative to the other species pairs at the other sites indicates low vector populations in some portions of Santa Cruz Co. (McNee *et al.* 2002).

Attraction and concentration of vectors on host trees can be another key factor determining disease progression and infection of new hosts. In previous work, higher colonization rates of *Pityophthorus* spp. were demonstrated on pitch canker infected branches than on uninfected branches (Bonello *et al.* 2001; McNee *et al.* 2002). Moreover, Bonello *et al.* (2001) indicated that discrimination of dead and dying branches by *Pityophthorus* spp. likely occurs after the beetles land on the host tree. Attraction of *P. setosus* to healthy Monterey pines baited with the pheromone of *P. setosus* increased the pitch canker infection rate compared with nearby unbaited trees (Storer *et al.* 2004). In the current study, *P. setosus* preferentially colonized Monterey pine branches over ponderosa pine or Douglas-fir branches, whereas *P. nitidulus* colonized knobcone pine

branches more frequently than Monterey pine branches. The number of *P. setosus* emerging from cut branches was too low to evaluate preferences between Monterey and knobcone pines.

Monterey and knobcone pine branches on the University of California Santa Cruz campus had the lowest colonization by twig beetles in the current study. This might suggest that other insects colonize these two species and perhaps transmit *F. circinatum* to healthy branches (Fox *et al.* 1990a, 1991; Hoover *et al.* 1996). The current study focused only on the association of twig beetles with *F. circinatum* infected Monterey pines and other conifer species. However, Fox *et al.* (1990a, 1991) demonstrated colonization of slash and killed branches infected by *F. circinatum* and transmission of the pathogen by engraver beetles (*Ips paraconfusus* Lanier, *Ips mexicanus* (Hopkins), and *Ips plastographus maritimus* Lanier). Many species of conifers, including those tested in this study, occur in the same habitat as Monterey pines and share many wood-inhabiting beetle species, including those bark beetles reported to be associated with diseased Monterey pines.

Development of lesions on different host trees in the current study is similar to the frequency of natural infection observed on these hosts in the field. Douglas-fir and ponderosa pine, which are rarely infected in the field, also had the smallest mean lesion sizes, and no foliar symptoms developed in response to inoculation. This suggests that Douglas-fir and ponderosa pine are less susceptible to *F. circinatum* than Monterey, Bishop, or knobcone pines. Currently we do not know whether increased spore loads would have any effect on the lesion length on such resistant trees as Douglas-fir and ponderosa pine. Previously, Gordon *et al.* (1998b) reported that susceptible Monterey pines inoculated with 2500 spores produced longer lesions than those inoculated with lower spore loads (25–250), whereas more resistant species, such as *Pinus canariensis* C. Smith and *Pinus thunbergiana* Franco, had short lesions even at the highest spore load.

Mean lesion length in Monterey pines varied among sites. Monterey pines in Año Nuevo State Reserve sustained significantly shorter lesions than trees of this species at other sites. Other studies have also shown differences in canker development between Monterey pines at different locations in California (Correll *et al.* 1991; Gordon *et al.* 1998a; Storer *et al.* 1999),

as well as interactions between the pathogen and environmental factors (Gordon *et al.* 1998a). Our study further suggests that susceptibility of Monterey pines to the pitch canker pathogen was greater in adventive stands than in naturally occurring stands, which supports an earlier report (Storer *et al.* 1999). This view is also consistent with the behavior of the disease in the southeastern United States, where pitch canker was problematic in plantations and seed orchards but not in wildland situations (Dwinell *et al.* 1985).

In summary, the current study indicates that several species of *Pityophthorus* are associated with each of the five host trees and suggests that other insect species may colonize these hosts, particularly knobcone pines and Douglas-firs, because colonization rates of *Pityophthorus* spp. appear to be too low in these species. Pitch canker occurs in all three native stands of Monterey pines in California and in each stand Monterey pines are mixed with other conifer species (Roy 1966), except in Cambria (Rogers 2002). All insect species known to carry *F. circinatum* inoculum in Monterey pines could transfer *F. circinatum* inoculum between Monterey pines and other conifers. Among *Pityophthorus* species, *P. carmeli* and *P. nitidulus* have the greatest potential to extend the distribution of *F. circinatum* because both species have wider geographical and host ranges than *P. setosus*, which is limited to a few hosts in central, coastal California (Bright 1981; Wood 1982; Wood and Bright 1992; Dallara 1997; Storer *et al.* 1997, 2004). Given the extent of the host range and the vector relationships of pitch canker in California and the western United States (Gordon *et al.* 1996; Storer *et al.* 1997), pitch canker has significant potential to alter the species composition of western forest ecosystems. Additional studies are needed to determine the vector efficiency of insect species associated with *F. circinatum* so the risk of transmitting the pathogen to susceptible hosts in other regions or countries can be reduced.

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