Twig beetles, *Pityophthorus* spp. (Coleoptera: Scolytidae), as vectors of the pitch canker pathogen in California

Andrew J Storer[1]

School of Forest Resources and Environmental Science, Michigan Technological University, Houghton, Michigan 49931, United States of America

David L Wood

Division of Insect Biology, University of California, Berkeley, California 94720, United States of America

Thomas R Gordon

Department of Plant Pathology, University of California, Davis, California 95616, United States of America

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Abstract—Twig beetles in the genus *Pityophthorus* Eichhoff are known to be associated with the pitch canker pathogen, *Fusarium circinatum*, in California. Phoresy of the pathogen on these species has been reported to occur when insects emerge from diseased branches and when they infest disease-free, cut branch tips. To demonstrate that twig beetles can vector the pathogen, studies of phoresy and transmission were conducted in a native Monterey pine, *Pinus radiata* D. Don (Pinaceae), forest. Phoresy was confirmed for both *Pityophthorus setosus* Blackman and *Pityophthorus carmeli* Swaine, and *P. setosus* was shown to vector the pitch canker pathogen when contaminated with fungal spores and caged onto Monterey pine branches. When attractive baits were used to increase visitation to Monterey pines by *P. setosus*, baited trees were more likely to develop pitch canker than unbaited trees even though the beetles did not tunnel into the host to develop egg galleries. Therefore, twig beetles are competent as vectors of the pitch canker pathogen, and their vectoring activity, though requiring a wound, does not require that they establish egg galleries in the host.

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Résumé—On sait que les scolytes du genre *Pityophthorus* Eichhoff sont associés à l'agent pathogène du chancre poisseux, *Fusarium circinatum*, en Californie. La littérature rapporte que la phorésie du pathogène sur les insectes a lieu lorsque les insectes émergent de branches affectées et lorsqu'ils infectent les bouts coupés de branches saines. Nous avons mené des études de la phorésie et de la transmission du pathogène dans une forêt indigène de pins de Monterey, *Pinus radiata* D. Don (Pinaceae), pour démontrer que les scolytes peuvent servir de vecteurs au pathogène. Nous confirmons la phorésie tant chez *Pityophthorus setosus* Blackman que chez *Pityophthorus carmeli* Swaine; *P. setosus* peut servir de vecteur de l'agent pathogène du chancre poisseux lorsqu'il est contaminé avec des spores du champignon et gardé dans des cages placées sur les branches du pin de Monterey. Lorsque nous utilisons des appâts pour augmenter les visites de *P. setosus* aux pins de Monterey, les arbres porteurs d'appâts sont plus susceptibles de développer l'infection au chancre

[1] Corresponding author (e-mail: storer@mtu.edu).

poisseux que les arbres sans appât, même si les coléoptères ne creusent pas dans l'hôte pour y construire des galeries de ponte. Ces scolytes sont donc des vecteurs efficaces de l'agent pathogène du chancre poisseux et leur activité comme vecteurs exige la présence d'une blessure sur l'hôte, mais ne requiert pas qu'ils y creusent des galeries de ponte.

[Traduit par la Rédaction]

Introduction

The pathogen that causes pitch canker of pines and other conifers, *Fusarium circinatum* (Nirenberg and O'Donnell, 1998) (= *Fusarium subglutinans* (Wollenweb. *et* Reinking) P.E. Nelson, T.A. Toussoun *et* Marasas f. sp. *pini* (Correll *et al.* 1991)), was first identified in California in 1986 (McCain *et al.* 1987) and was previously known from the southeastern United States (Hepting and Roth 1946). Pitch canker is a prevalent disease of Monterey pine, *Pinus radiata* D. Don (Pinaceae), in many coastal counties of California (Gordon *et al.* 2001), and disease progression has been described in both ornamental plantings and native forests (Storer *et al.* 2002; Wikler *et al.* 2003). The disease affects Monterey pines in all three native stands of this species in California, as well as in landscape plantings. It also affects other pines and Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco (Pinaceae). Symptoms progress over a period of several years, from individual infected branch tips to multiple infected branch tips and cankers on large branches and the main stem of the tree (Storer *et al.* 2002). Tree mortality is frequently associated with infestation by bark beetles.

A predominant mode of transmission of the pitch canker pathogen in California is through feeding activities of insects that either vector the pathogen or create wounds through which the pathogen can enter the tree. The California five-spined ips, *Ips paraconfusus* Lanier, 1970 (Coleoptera: Scolytidae) (Fox *et al.* 1991), the Monterey pine cone beetle, *Conophthorus radiatae* Hopkins, 1915 (Coleoptera: Scolytidae), and the deathwatch beetle, *Ernobius punctulatus* (LeConte, 1859) (Coleoptera: Anobiidae) (Hoover *et al.* 1996) can vector the pathogen. The spittlebug, *Aphrophora canadensis* Walley, 1928 (Hemiptera: Cercopidae), has also been associated with the pathogen and disease, probably by providing infection courts from its feeding activities (Storer *et al.* 1998). Twig beetles carrying the pathogen have been reared and dissected from diseased branch tips (Hoover *et al.* 1996; McNee *et al.* 2002) and have emerged from non-diseased branch tips cut from trees and hung in their canopy to sample these beetles (Dallara 1997).

In the absence of pitch canker, twig beetles breed in shade-suppressed and broken branches and in branches on recently dead trees (Furniss and Carolin 1977). Twig beetles rarely cause mortality of trees or even individual branches. In the presence of pitch canker, twig beetles breed in diseased branch tips in all parts of the tree canopy. Twig beetle species infesting Monterey pine in the coastal counties of central California include *Pityophthorus setosus* Blackman, 1928, *P. nitidulus* (Mannerheim, 1843), *P. carmeli* Swaine, 1918, and *P. tuberculatus* Eichhoff, 1878 (Dallara 1997). On the Monterey peninsula, *P. setosus* and *P. carmeli* are the two most common species, accounting for over 70% of emerged twig beetles (McNee *et al.* 2002). In this study, *P. setosus* was used because a selective bait is known for this species, and consistently high trap catches can be obtained with this bait (Dallara *et al.* 2000).

To evaluate whether twig beetles are vectors of the pitch canker pathogen, we (*i*) assessed the occurrence of phoresy of the pitch canker pathogen on two species of twig beetles on the Monterey peninsula, California, (*ii*) determined whether transmission of the pathogen by one species, *P. setosus*, occurs under controlled conditions, (*iii*) determined whether trees baited with *P. setosus* pheromones are more likely to develop pitch canker symptoms than unbaited trees, and (*iv*) evaluated whether transmission of the pathogen to baited trees is dependent upon tree resistance or susceptibility to the pathogen.

Methods

Phoresy of the pitch canker pathogen on *P. setosus* and *P. carmeli*

Twig beetles were sampled using Lindgren multiple funnel traps (Lindgren 1983) baited with pheromone components. Traps were baited with pityol to selectively trap *P. setosus* (Dallara *et al.* 2000). Conophthorin was added to the pityol baits to selectively trap *P. carmeli* (Dallara *et al.* 2000). In September 1999, traps were established at three locations on the Monterey peninsula in Monterey Co., California, two of which had trees with pitch canker (Indian Village and Spanish Bay) and one of which was considered free of pitch canker at the time of the study (Jacks Peak). Two traps targeting each insect species were placed at each location to collect sufficient beetles to assess the occurrence of phoresy of the pathogen on the insects at each location. Traps were emptied on three occasions after 1–6 days of trapping. Insects caught in the traps were counted, and samples of up to 50 beetles from each trap were plated on agar medium selective for *Fusarium* spp. The composition of this medium was as described by Correll *et al.* (1991), with the following modifications: (*i*) the concentration of pentachloronitrobenzene was reduced from 1.0 to 0.2 g/L, (*ii*) choroneb and triadimefon were eliminated, and (*iii*) 300 ppm of streptomycin was used instead of ampicillin and rifampicin. Colonies growing on the medium were determined to be *F. circinatum* (Nirenberg and O'Donnell 1998) based on colony morphology as viewed under a dissecting microscope. Features discernible at this level of magnification, principally the disposition of conidia on aerial microconidiophores, have been shown to be diagnostic of *F. circinatum* (Gordon *et al.* 1996). The significance of differences in phoresy rates between the two species was evaluated using G tests on data from each site on each date and for all dates combined.

Transmission of *F. circinatum* by *P. setosus* to Monterey pine in field caging studies

A spore suspension was prepared from *F. circinatum* isolate FSP17 (Gordon *et al.* 1996), which was originally collected from the Monterey peninsula. Colonies were grown on potato dextrose agar for 10 days, then flooded with water and scraped with a microscope slide to remove microconidia and other structures. The resulting suspension was filtered through cheesecloth, and the concentration of the spore suspension was determined using a hemacytometer and then adjusted to 4.6×10^7 spores/mL (Gordon *et al.* 1998). The suspension was determined to be 100% viable before and after use by plating aliquots onto *Fusarium*-selective medium and counting the resulting colonies.

In August 1997, 10 branches were selected on each of 10 trees at a field site on Huckleberry Hill on the Monterey peninsula. Branches were within 2 m of the ground, had live needles, and were on trees that had no symptoms of pitch canker. The trees had regenerated following a wildfire in 1987 and were selected to be 20 m from each other to reduce the chance that they originated from the same seed tree. Three locations at least 15 cm apart were marked on each branch using Wite-Out® correction fluid. Cages for beetles were then placed onto the branches 1 cm proximal to these marks. Cages consisted of a 0.5 cm long piece of a plastic drinking straw (inside diameter 6 mm) with the end cut to maximize contact of the edges of the straw with the branch and therefore reduce the chance of beetle escape. Cages were retained on the branch using adhesive tape. On each branch, one cage was left empty, one cage contained a beetle contaminated with *F. circinatum*, and the third cage contained a beetle treated with sterile water. The relative positions of these three treatments were random on each branch. *Pityophthorus setosus* to be used in transmission studies were caught in pityol-baited traps at Spanish Bay, Monterey Co., 3 days prior to the establishment of the study. Contaminated beetles were produced by immersing them in the *F. circinatum* spore suspension, then removing and drying them using filter papers.

Following establishment of the experiment, the spore load of *F. circinatum* on treated beetles was determined by vortexing individual beetles not used in the experiment with 1 mL of sterilized water for 30 s. The water was then spread over *Fusarium*-selective medium. This process was repeated three times for each beetle. After 5 days, *F. circinatum* colonies growing on the medium were counted.

Branches were removed from trees in February 1998. All cage sites on the branches were dissected, and any lesions evident in the phloem were measured. Phloem tissue was excised from all cage locations, surface-sterilized with 0.5% sodium hypochlorite for 2 min, and plated onto *Fusarium*-selective medium to determine the presence of the pitch canker pathogen. Any dead beetles found in the cages were also plated onto the selective medium.

Differences in lesion length among treatments and among trees were tested using analysis of variance. Differences among the three treatments were subsequently tested using Tukey's HSD test. Relationships between the presence or absence of visible wounds, presence or absence of lesions, recovery of *F. circinatum*, and treatment were tested using log-linear analyses followed by *G* tests to make comparisons among treatments (Sokal and Rohlf 1981).

Transmission of *F. circinatum* to Monterey pines by *P. setosus* attracted to trees using pheromones

Six-year-old potted Monterey pines derived from clonal material from trees of known resistance or susceptibility to the pitch canker pathogen (Storer *et al.* 1999) were placed in groups in an outdoor nursery on the Monterey peninsula in June 2000. Groups of six trees were selected at random such that each group contained two susceptible trees, two resistant trees, and two trees of intermediate susceptibility, based on the original data from the parent trees of the clones (Storer *et al.* 1999). Eight such groups were placed 10 m apart from each other in the nursery. Trees from four groups selected at random were baited using pityol to attract *P. setosus*; trees in the remaining four groups were left unbaited. In baited groups, a microcentrifuge tube containing 5 μl of pityol was attached halfway up the main stem adjacent to an aluminum tree number tag. The volatile pheromone was released by piercing a hole in the top of the tube using a number 2 insect pin. Baits were periodically renewed to maintain a high density of visiting *P. setosus* potentially carrying the pitch canker pathogen. The residual activity of the pityol baits was high, as beetles were seen walking on the trees prior to renewal of baits each time the baits were replaced. Trees were maintained in pots and watered as needed for the duration of the experiment.

After 3 years of baiting, we counted the number of beads of resin on branches within 15 cm of the bait on each tree in the baited groups. These beads were considered to be indicative of wounding and (or) possible pitch canker infection. For the groups of trees without bait, we counted the number of beads of resin on branches within 15 cm of the aluminum tree number tag. Trees were then dissected at all points where symptoms characteristic of pitch canker were evident. These symptoms included areas of resinosis on the main stem or branches, or branch tips that had died or had wilting needles and associated resinosis. Subsamples of symptomatic tissues were returned to the laboratory and plated on *Fusarium*-selective medium. These samples included all those for which there was any doubt as to whether the symptoms were associated with pitch canker. Colonies were identified as those of the pitch canker pathogen using a dissecting microscope as described previously.

Differences in the number of resin beads within 15 cm of the bait or aluminum tag between baited and unbaited trees and between resistance categories were tested using analysis of variance followed by Tukey's HSD tests. Interactions between the presence of pitch canker, presence of baits, and the resistance categories of the trees were tested using log-linear analyses followed by G tests.

Results

Phoresy of the pitch canker pathogen on *P. setosus* and *P. carmeli*

Both *P. setosus* and *P. carmeli* were found carrying the pitch canker pathogen at the Indian Village and Spanish Bay sites (Table 1) but not at the Jacks Peak site, where pitch canker was not known to occur. On all dates at Spanish Bay and Indian Village, *P. carmeli* were significantly more likely to carry the pathogen than *P. setosus* (Table 1).

Transmission of *F. circinatum* by *P. setosus* to Monterey pine in field caging studies

The mean (±SE) spore load on beetles that were contaminated with *F. circinatum* prior to caging onto Monterey pine branches was 51.7 (±9.8) propagules/beetle. The mean (±SE) number of propagules removed from each insect declined with each sequential vortex in water from 41.4 (±11.9) after the first vortex to 6.4 (±2.0) after the second vortex and 3.9 (±1.0) after the third vortex. Propagules were recovered from all 20 beetles used in the test (3–146 propagules/beetle).

There were no differences in lesion length among trees ($F_{9,299} = 1.44$, $P = 0.126$), and no interaction between trees and treatments was evident ($F_{18,299} = 1.29$, $P = 0.192$). Differences in lesion length between branch locations without beetles and those with non-contaminated or contaminated beetles were significant, but differences between branch locations with non-contaminated caged beetles and those with contaminated caged beetles were not significant (Table 2).

The pitch canker pathogen was not isolated from all lesions, but the mean length of lesions from which pitch canker was isolated (6.15 ± 0.78 mm) was greater than that of lesions from which the pathogen was not isolated (3.72 ± 0.47 mm) ($F_{1,73} = 7.05$, $P = 0.010$).

The incidences of wounds and lesions were higher on branch sites where beetles were caged than on those where they were absent. The pitch canker pathogen was recovered more frequently from branch sites with contaminated beetles than from branch sites with non-contaminated beetles or no beetles (Table 2). Branch sites with visible wounds were more likely to have lesions (69.0%, $n = 71$) than branch sites that were unwounded (10.5%, $n = 229$), independent of treatment (log-linear analysis; $P < 0.001$).

Dead beetles were found in 24 of the 100 cages containing contaminated beetles, and in 22 of the 100 cages containing non-contaminated beetles. The pathogen was recovered from 91.7% of the contaminated beetles, and from 9.1% of non-contaminated beetles.

TABLE 1. Phoresy of *Fusarium circinatum* on *Pityophthorus* spp. trapped at baited Lindgren multiple funnel traps on the Monterey Peninsula, California, in 1999.

		Site					
		Indian Village		Spanish Bay		Jacks Peak*	
Date	Species	*N*	Phoresy, % (*n*)	*N*	Phoresy, % (*n*)	*N*	Phoresy, % (*n*)
9 Sept.	*P. setosus*	278	0.00 (100)*a*	104	0.00 (53)*a*	9	0.00 (9)*a*
	P. carmeli	45	6.67 (45)*b*	147	8.45 (71)*b*	3	0.00 (3)*a*
10 Sept.	*P. setosus*	376	2.00 (100)*a*	63	0.00 (62)*a*	31	0.00 (31)*a*
	P. carmeli	31	12.90 (31)*b*	142	14.29 (70)*b*	9	0.00 (9)*a*
16 Sept.	*P. setosus*	2053	4.00 (100)*a*	1510	2.00 (100)*a*	1305	0.00 (100)*a*
	P. carmeli	124	12.32 (73)*b*	447	17.00 (100)*b*	20	0.00 (20)*a*
All dates	*P. setosus*	2707	2.00 (300)*a*	1677	0.93 (215)*a*	1345	0.00 (140)*a*
	P. carmeli	200	10.74 (149)*b*	736	13.69 (241)*b*	32	0.00 (32)*a*

NOTE: *N*, number of insects trapped; phoresy, percentage of beetles carrying the pitch canker pathogen (number in parentheses (*n*) is the number of beetles plated). Phoresy rates (%) at each site on each date, and at each site for all dates combined, followed by different lowercase letters are different (*G* test; $P < 0.05$).
*Pitch canker was not known to occur at this site in 1999.

TABLE 2. Incidence of wounding, pitch canker symptoms (lesions), and pathogen isolation from *Pinus radiata* branches that had *Pityophthorus setosus* contaminated with *Fusarium circinatum*, non-contaminated *P. setosus,* or no *P. setosus* caged onto them.

		Percentage of branches		
Treatment	Mean lesion length, mm (SE = 0.25)	Wounded	With lesions	With *F. circinatum*
Contaminated insects	1.86*a*	35.0*a*	40.0*a*	31.0*a*
Non-contaminated insects	1.33*a*	34.0*a*	32.0*a*	8.0*b*
No insects	0.06*b*	2.0*b*	1.0*b*	8.0*b*

NOTE: Insects were caged onto branches in August 1997, and branches were assessed in February 1998. In all cases, n = 100. Means or percentages in the same column followed by different lowercase letters are different (ANOVA and log-linear analysis, respectively; $P < 0.05$).

Transmission of *F. circinatum* to Monterey pines by *P. setosus* attracted to trees using pheromones

All subsamples of tissues showing suspected pitch canker symptoms tested positive for *F. circinatum*. In no case did twig beetles tunnel into trees and establish galleries. Two trees in the resistant category died during the study. Neither of these trees had symptoms of pitch canker and they were therefore omitted from the analyses. There was no interaction between the baiting status of trees and tree resistance for the number of beads of resin per tree ($F_{2,45} = 0.50$, $P = 0.608$) or for the number of cankers per tree ($F_{2,45} = 2.18$, $P = 0.127$). There was no difference in the mean number of beads of resin or in the mean number of cankers between resistance categories of trees, independently of baiting status (number of beads of resin, $F_{2,45} = 0.08$, $P = 0.921$; cankers, $F_{2,45} = 1.20$, $P = 0.313$). There were significantly more beads of resin and pitch canker symptoms on trees that had been baited than on trees that had not been baited (Table 3). This effect was independent of the resistance category of the trees. The proportion of trees with beads of resin did not differ significantly between the baited group and the non-baited group, but trees with baits were more likely to develop one or more pitch canker symptoms (Table 3). The proportion of trees with at least one pitch canker

Table 3. Incidence of resin beads and pitch canker symptoms on potted *Pinus radiata* with and without baits attractive to *Pityophthorus setosus* attached to them for a 3-year period starting in June 2000.

	No. of resin beads/tree, mean ± SE	No. of *F. circinatum* cankers/tree, mean ± SE	Percentage of trees with resin beads	Percentage of trees with pitch canker
Baited trees	8.13±1.20	3.21±0.42	91.7 (n = 24)	91.7 (n = 24)
Non-baited trees	3.91±1.26	1.18±0.44	81.8 (n = 22)	54.5 (n = 22)
P value for difference	0.022	0.001	0.583	0.003

Note: Resin beads were counted within 15 cm of the location of bait deployment or a comparable location on non-baited trees.

symptom was dependent on the resistance category of the tree (log-linear analysis; P < 0.019). More susceptible trees (93.8%, n = 16) than resistant trees (50.0%, n = 14) developed pitch canker (G test; P < 0.05), independent of whether they were baited. Trees in the intermediate resistance category were no more likely to develop pitch canker symptoms (73.3%, n = 15) than trees in the other two categories.

Discussion

The twig beetle *P. setosus* is capable of transmitting the pitch canker pathogen, *F. circinatum*, to Monterey pine when caged onto branches and when attracted to trees using baits. In addition, growth chamber experiments showed that wounds induced by *P. setosus* became infected by the pitch canker pathogen (Sakamoto *et al.* 2001). These results confirm that *P. setosus* carries the pitch canker pathogen in native stands of Monterey pine. Therefore, according to Leach's postulates (Leach 1940), *P. setosus* is a vector of the pitch canker pathogen because this species is associated with non-diseased hosts (Furniss and Carolin 1977) and diseased hosts (McNee *et al.* 2002), carries the pathogen, and is capable of transmitting the pathogen in controlled tests.

Pityophthorus carmeli was more likely to carry the pathogen than *P. setosus* at the sites and on the dates where and when it was sampled, which suggests that this species has habits that make it more likely to acquire the pathogen. These habits may include moving around under the bark of infected branch tips prior to emerging, thereby increasing the likelihood of contacting propagules of the pathogen. Population size estimates suggest that *P. carmeli* is about as common as *P. setosus* at some sites and more common than *P. setosus* at other sites (McNee *et al.* 2002). Therefore, *P. carmeli* may be a more important vector of the pathogen than *P. setosus*. Since a lower proportion of *P. setosus* carry the pathogen compared with *P. carmeli*, the non-contaminated *P. setosus* used in the transmission study were less likely to be naturally carrying the pathogen than would have been the case if *P. carmeli* had been used. Pityol is highly selective for *P. setosus*, and thus the higher incidence of disease on the baited potted trees is a result of higher visitation rates and resultant wounding by *P. setosus*.

The high variation in the mean number of pitch canker infections per tree resulted in no significant difference for this measure between resistance categories. However, when trees were categorized as with or without pitch canker, resistant trees were found to be less likely to develop pitch canker than susceptible trees. Previous work to characterize tree resistance (Gordon *et al.* 1998; Storer *et al.* 1999) used inoculations of mechanical wounds to induce lesions. Trees that sustained no lesions or only small lesions were then assigned to a resistant category. It was not clear whether the feeding activities of beetles would influence the ability of a tree to resist infection by the pitch canker pathogen. The extent to which tree resistance will be durable in the field in the long term remains to be seen. However, the decreased likelihood of twig beetle vectored infection of resistant trees, along with observations of acquired resistance in trees challenged by the pathogen (Bonello *et al.* 2001*a*), is encouraging.

Host volatiles from cut branches are not attractive to twig beetles (Bonello *et al.* 2001*b*). This suggests that host finding by twig beetles is through random searching and feeding initiation to determine whether a host is suitable for colonization. This has been referred to as exploratory feeding (Gordon *et al.* 2001), though it remains unclear whether feeding actually takes place or if wounds are made without ingestion of host material. Vectoring of the pathogen may occur during this exploratory feeding phase. The increased incidence of pitch canker on pheromone-baited trees is strong evidence of this exploratory feeding behavior on branches prior to host colonization.

Many twig beetle species have multiple hosts and likely contribute to the transmission of pitch canker to species other than Monterey pine. The host range of *P. setosus* is apparently limited to Monterey pine and Bishop pine, *Pinus muricata* D. Don (Bright and Stark 1973). Native stands of both species are found on the Monterey peninsula, and both have pitch canker. The extent to which beetles emerging from one host species act as a vector of the pathogen to another host species is not known. The host range of *P. carmeli* includes Bishop pine, Torrey pine (*Pinus torreyana* Parry *ex* Carr.), and Coulter pine (*Pinus coulteri* D. Don) (Bright and Stark 1973). Both Torrey pine and Coulter pine are recorded hosts of the pitch canker pathogen (Storer *et al.* 1994) but their native distributions do not coincide with that of Monterey pine. The extensive planting of Monterey pine as landscape trees may provide corridors whereby the pitch canker pathogen can be moved into native stands of both Torrey and Coulter pine. The native range of Torrey pine is limited to one small mainland native stand and the spread of pitch canker may threaten the existence of this species. However, observations of Torrey pine and Coulter pine in ornamental plantings suggest that the effect of pitch canker on these species is limited. Another twig beetle species, *P. nitidulus*, has a host range that includes all Pinaceae species (Bright and Stark 1973). Therefore, this species has the potential to facilitate the movement of pitch canker into many parts of California where it currently does not occur, including inland portions of the state. Pitch canker is almost entirely restricted to coastal locations in California, and it is suggested that this is due to abiotic constraints on the infection process (Gordon *et al.* 2001; Wikler *et al.* 2003). Such constraints might preclude transmission of the pathogen to trees in inland locations through the feeding activities of *P. nitidulus*. The continued absence of pitch canker from most inland portions of the state supports this hypothesis.

The relative importance of the different twig beetle species in the movement of pitch canker within and between stands and between host species, as well as their importance compared with other known vectors of the pathogen, is still largely unknown. Further study is needed to determine the relative importance of these insect vectors so that efforts to reduce disease may include consideration of which vector species pose the greatest risk of transmitting pitch canker.

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