Suitability of Pines and Other Conifers as Hosts for the Invasive Mediterranean Pine Engraver (Coleoptera: Scolytidae) in North America

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J. Econ. Entomol. 101(3): 829–837 (2008)

ABSTRACT The invasive Mediterranean pine engraver, *Orthotomicus erosus* (Wollaston) (Coleoptera: Scolytidae), was detected in North America in 2004, and it is currently distributed in the southern Central Valley of California. It originates from the Mediterranean region, the Middle East, and Asia, and it reproduces on pines (*Pinus* spp.). To identify potentially vulnerable native and adventive hosts in North America, no-choice host range tests were conducted in the laboratory on 22 conifer species. The beetle reproduced on four pines from its native Eurasian range—Aleppo, Canary Island, Italian stone, and Scots pines; 11 native North American pines—eastern white, grey, jack, Jeffrey, loblolly, Monterey, ponderosa, red, Sierra lodgepole, singleleaf pinyon, and sugar pines; and four native nonpines—Douglas-fir, black and white spruce, and tamarack. Among nonpines, fewer progeny developed and they were of smaller size on Douglas-fir and tamarack, but sex ratios of progeny were nearly 1:1 on all hosts. Last, beetles did not develop on white fir, incense cedar, and coast redwood. With loblolly pine, the first new adults emerged 42 d after parental females were introduced into host logs at temperatures of 20–33°C and 523.5 or 334.7 accumulated degree-days based on lower development thresholds of 13.6 or 18°C, respectively.

KEY WORDS bark beetle, distribution, host range, invasive species, *Pinus*

The Mediterranean pine engraver, *Orthotomicus erosus* (Wollaston) (Coleoptera: Scolytidae), was first detected in North America in May 2004 in Fresno, CA, during an exotic woodborer and bark beetle survey by the California Department of Food and Agriculture (Lee et al. 2005; Penrose et al., unpublished data). This beetle may have been accidentally introduced to the United States by trade. Between 1985 and 2000, *O. erosus* was intercepted at U.S. ports-of-entry 385 times, primarily associated with crating materials used to carry tiles, marble, and granite from Spain, Italy, China, Turkey, and Portugal (Haack 2001). Since the initial discovery, *O. erosus* has not been detected outside of California in North America. It is prevalent in the southern Central Valley of California (Fresno, Kern, Kings, Madera, Merced, and Tulare counties) where it has been caught in baited Lindgren flight traps, and where beetles or vacant galleries have been found on dead or dying pine trees or woody debris (Lee et al. 2005, Penrose et al., unpublished data). Although one or two *O. erosus* have been captured in flight traps in the Los Angeles Basin, inland valleys along the Central Coast, and northern Central Valley of California, populations in those areas are suspected to be low, because beetles have not been found with additional trapping or during visual inspection of pine debris.

O. erosus is native to the Mediterranean, Middle East, central Asia, and China (Mendel and Halperin 1982; Yin et al. 1984; Wood and Bright 1992; Bright and Skidmore 1997, 2002). This cosmopolitan pest invaded Chile in 1986 (Ciesla 1988), South Africa in 1968 (Geertsema 1979), and Swaziland in 1983 (Bevan 1984). In its native range, *O. erosus* has been reported on Armand pine, *Pinus armandii* Franchet; Turkish red pine, *Pinus brutia* Ten.; Canary Island pine, *Pinus canariensis* Smith; Aleppo pine, *Pinus halepensis* Mill.; *Pinus kesiya* Royle ex Gordon [*Pinus khasya* Royle], Chinese red pine, *Pinus massoniana* Lambert; Austrian pine, *Pinus nigra* Arnold; maritime pine, *Pinus pinaster* Ait.; Italian stone pine, *Pinus pinea* L.; Scots pine, *Pinus sylvestris;* southern Chinese pine, *Pinus tabuliformis* Carrière; and Yunnan pine, *Pinus yunnanensis* Franchet (Yin et al. 1984, Jiang et al. 1992, Wood and Bright 1992, Bright and Skidmore 1997, 2002). Nearctic and neotropic pines also have been attacked when they have been planted within the native or adventive range of *O. erosus.* These species include Caribbean pine, *Pinus caribaea* Morelet; shortleaf pine, *Pinus echinata* Mill.; slash pine, *Pinus elliottii* Engelm.; Mexican

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weeping pine, *Pinus patula* Scheide & Deppe ex Schlech. & Cham.; Monterey pine, *Pinus radiata* D. Don; eastern white pine, *Pinus strobus* L.; and loblolly pine, *Pinus taeda* L. (Bevan 1984, Eglitis 2000). *O. erosus* also has been reported on nonpine conifers: Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco; spruce (*Picea* spp.); fir (*Abies* spp.); cypress (*Cupressus* spp.); and cedar (*Cedrus* spp.), although these have been considered cases of maturation feeding or overwintering sites (Grüne 1979; Mendel and Halperin 1982; Wood and Bright 1992; Bright and Skidmore 1997, 2002; Eglitis 2000).

Like many bark beetles, *O. erosus* is a secondary pest infesting standing trees under stress, recently fallen trees, or broken branches (Bevan 1984). Jiang et al. (1992) reported that *O. erosus* colonized healthy *P. massoniana* and caused a 20% loss of standing pines in the Zhejiang University Forest in China. *O. erosus* also has killed large numbers of *P. brutia* and *P. halepensis* in Israel after drought (Mendel and Halperin 1982), and *P. elliottii, P. pinaster* [*P. maritima*], and *P. radiata* in South Africa after fire (Baylis et al. 1986). Besides direct injury to pine trees, *O. erosus* can vector fungal pathogens. In South Africa, spores of *Ophiostoma ips* (Rumb.) Nannf., the causative agent of bluestain fungus, were found on 60% of 665 adult beetles or galleries on trap logs of *P. elliottii* and *P. patula;* spores of *Leptographium lundbergii* Lagerb. & Melin were also found on a few samples (Zhou et al. 2001). Spores of *Graphium pseudormiticum* Mouton & Wingfield have been found with *O. erosus* on unspecified pine logs (Mouton et al. 1994). In California, *O. erosus* overwintering in *P. canariensis* and *P. halepensis* carried spores of *Ophiostoma ips* (T. Harrington, unpublished data).

The North American establishment of *O. erosus* is likely relatively recent. This species was not reported in the last major systematic treatments of the California fauna (Bright and Stark 1973, Wood 1982, Wood and Bright 1992). In time this beetle may become prevalent in other regions of California and spread through North America if climatic factors and other conditions are favorable. *O. erosus* may spread easily because native and ornamental pines are present throughout California and North America, green waste is abundant and can harbor large scolytid populations, and firewood is often moved within and between states. The primary objective of this study was to identify conifers potentially vulnerable to *O. erosus* by testing its physiological host range on native and ornamental conifers frequently planted in the United States. Previous host range records represent observations from trees or trap logs; this study will be the first to quantify and compare various host range parameters among host species. Another objective was to determine the development time of this North American *O. erosus* population on loblolly pine, *P. taeda,* an economically important pine located in a climatically suitable area where *O. erosus* could establish.

Materials and Methods

Host materials were collected in 2005 and 2006 by felling live trees in California, Louisiana, Minnesota, and Nevada (Table 1). Small logs ≈9–13 cm in diameter and 60 cm in length were stored at 4°C before testing to preserve phloem moisture. Five separate trials were conducted according to availability of host materials and newly emerged beetles (Table 1). All beetles were reared from naturally infested pine logs (30 cm in diameter; *P. halepensis, P. pinea,* or *P. sylvestris*) collected on various dates from green waste piles in Tulare Co. Infested logs were transferred into large outdoor emergence boxes (Browne 1972) exposed to ambient conditions at the Kearney Research and Education Center in Parlier, CA (Fresno Co.). Newly emerged beetles exited the rearing box via a plastic tube leading to a glass jar in a refrigerator where beetles were stored until experimentation.

Test logs were cut into 25–35-cm-long bolts to yield 1,000 cm^2 of bark surface area and waxed on the ends. For each log, three males were inserted into separate 2-mm-diameter holes drilled into the phloem spaced at least 15 cm apart. Males were secured in the holes for 24 h by stapling metal screening over the hole. During the first day, males could feed, excavate a nuptial chamber, and start producing aggregation pheromone. The next day, we recorded the appearance of frass to confirm feeding, inserted two females per hole, and secured all three beetles in each gallery with metal screening so that they could mate and initiate brood production. Thus, each test log had three sets of one male: two females, or nine beetles total. Each test log was reared indoors at ambient conditions in an individually aerated and sealed black plastic 18.9-L (5-gallon) paint bucket with a glass collection jar at the bottom. Four to five buckets were connected together by mesh-covered polyvinyl chloride pipes, and a bathroom ceiling fan was connected to the pipes to force air from one end to ventilate the containers and retard fungal growth. The position of the buckets relative to the fan was alternated twice a week. Data loggers were placed inside two buckets to monitor temperature and humidity (HOBOware, Bourne, MA).

Collection jars were checked daily or every few days for emerging beetles, and test trials ended when emergence rates declined. At this time, all test logs were stored at 4°C to halt development until test logs could be debarked with the remaining beetles collected. Parental beetles were dead, and darker in color and were not counted. All adult progeny were frozen, sexed, and measured from anterior tip of pronotum to posterior tip of elytra. The head of the beetle was not measured as part of body length because the head could be protracted or retracted. Egg galleries were counted, but due to the general degradation of the phloem, gallery length and larval galleries were not compared. During tests, emerging beetles were found to move in and out of the collection jar and back into the test log. Due to the potential for progeny to reenter the log, collection records from jars may not

Table 1. Sources of conifer hosts and beetles, no. of logs tested, trial dates, and mean temperature and humidity during trial or by month if ambient indoor temperatures were changing

Host[a]/beetle	Source	*n*	Trial dates	Temp, humidity
White fir, *Abies concolor* (Gond. & Glend.) Hildebr	2 Aug. 2005, McCloud Flats near Pilgrim Creek Road, Shasta-Trinity National Forest, Shasta Co., CA, 41° 18′36″ N, 122° 02′24″ W	7	Trial 1, 8 Aug.–22 Nov. 2005	Aug., 27.0°C, 78.5% RH
Sierra lodgepole pine, *Pinus contorta murrayana* (Balf.) Critch	2 Aug. 2005, near Highway 44, Lassen National Forest, Lassen Co., CA, 40° 30′ 00″ N, 121° 00′ 00″ W	7		Sept., 25.4°C, 59.9% RH
Jeffrey pine, *Pinus jeffreyi* Balf	Same as *P. contorta murrayana*	7		Oct., 22.8°C, 80.9% RH
Sugar pine, *Pinus lambertiana* Dougl	2 Aug. 2005, near Highway 89, Shasta-Trinity National Forest, Shasta Co., CA, 41° 15′ 00″ N 122° 05′24″ W	7		Nov., 19.6°C, 90.7% RH
Ponderosa pine, *Pinus ponderosa* Dougl. ex Laws	2 Aug. 2005, McCloud Flats near Pilgrim Creek Rd., Shasta-Trinity National Forest, Shasta Co., CA, 41° 21′36″ N 122° 03′36″ W	7		
Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco	Same as *A. concolor*	5		
Orthotomicus erosus beetles	Emerged ≈2 Aug. 2005 from infested *P. halepensis* logs collected from Valley Oaks Golf Course, Tulare Co., CA on 15 July 2005, 36° 19′35″ N, 119° 23′06″ W			
Canary Island pine, *Pinus canariensis* Smith	Nov. 2005, Kings River County Club, Tulare Co., CA, 36° 31′08″ N, 119° 30′14″ W	4	Trial 2, 2 Dec. 2005–21 April 2006	18.5°C, 86.8% RH thermostat-controlled room
Scots pine, *P. sylvestris* L	Same as *P. canariensis*	4		
Orthotomicus erosus beetles	Emerged ≈26 Nov. 2005 from infested *P. halepensis* logs collected from Valley Oaks Golf Course, Tulare Co., CA on 6 Oct. 2005, 36° 19′35″ N, 119° 23′06″ W			
Tamarack, *Larix laricina* (Du Roi) Koch	3 April 2006, University of Minnesota North Central Research and Outreach Center, Grand Rapids, Itasca Co., MN, 47° 14′57″ N 93° 29′33″ W	4	Trial 3, 25 April–19 July 2006	April, 21.8°C, 59.7% RH
White spruce, *Picea glauca* (Moench) Voss	Same as *Larix laricina*	4		May, 23.7°C, 66.4% RH
Black spruce, *Picea mariana* (Mill.) B.S.P	Same as *Larix laricina*	4		June, 27.3°C, 82% RH
Jack pine, *Pinus banksiana* Lamb	Same as *Larix laricina*	4		July, 28.7°C, 65.6% RH
Aleppo pine, *Pinus halepensis* Mill	Jan. 2006, J St., Davis, Yolo Co., CA, 38° 33′25″ N, 121° 44′26″ W	4		
Monterey pine, *P. radiata* Don	15 Mar. 2006, Salinas Municipal Golf Course, Salinas, Monterey Co, CA, 36° 40′09″ N, 121° 37′10″ W	5		
Red pine, *P. resinosa* Ait	Same as *L. laricina*	4		
Grey pine, *P. sabiniana* Douglas ex Don	24 April 2006, Highway 16 near Cache Creek and Bear Creek confluence, Yolo Co., CA, 38° 55′22″ N, 122° 19′49″ W	5		
Eastern white pine, *P. strobus* L	Same as *L. laricina*	4		
Orthotomicus erosus beetles	Emerged ≈19 April 2006 from infested *P. sylvestris* logs collected from Kings River Country Club, Tulare Co., CA on 22 Nov. 2005, 36° 31′08″ N, 119° 30′14″ W			
Incense cedar, *Calocedrus decurrens* (Torr.) Florin	4 May 2006, Blodgett Forest, El Dorado Co., CA, 38° 54′31″ N 120° 38′57″ W	5	Trial 4, 16 May–7 Aug. 2006	May, 23.7°C, 66.4% RH June (see trial 3)
Loblolly pine, *Pinus taeda* L	8 May 2006, Camp Livingston, near Ball, Rapides Co., LA, 31°26′26“N 92°22′48”W	5		July, 29.5°C, 63.1% RH
Orthotomicus erosus beetles	Emerged ≈10 May 2006 from infested *P. sylvestris* logs collected from Kings River Country Club, Tulare Co., CA on 22 Nov. 2005, 36° 31′08″ N, 119°30′14″ W			Aug., 27.5°C, 55.4% RH
Singleleaf pinyon pine, *Pinus monophylla* Torr. & Frem	22 Aug. 2006, Brunswick Canyon Road, west side of Pinenut Mountains, Carson City Co., NV, 39° 10′14″ N, 119° 41′39″ W	5	Trial 5, 31 Aug.–17 Nov. 2006	Sept., 25.7°C, 86.8% RH
Italian stone pine, *Pinus pinea* L	2 Aug. 2006, Valley Oaks Golf Course, Visalia, Tulare Co., CA, 36° 19′35“N, 119° 23′06″ W	4		Oct., 23.3°C, 67% RH
Coast redwood, *Sequoia sempervirens* Lamb	15 Aug. 2006, Russell Reserve, Happy Valley Road, Lafayette, Contra Costa Co., CA, 37° 54′57″ N 122° 09′46″ W	5		Nov., 22.1°C, 43.1% RH
Orthotomicus erosus beetles	Emerged ≈31 Aug. 2006 from infested *P. pinea* logs collected from Valley Oaks Golf Course, Tulare Co., CA on 28 July 2006, 36° 19′35″ N, 119° 23′06″ W			

[a] *Pinus* nomenclature based on Price et al. (1998).

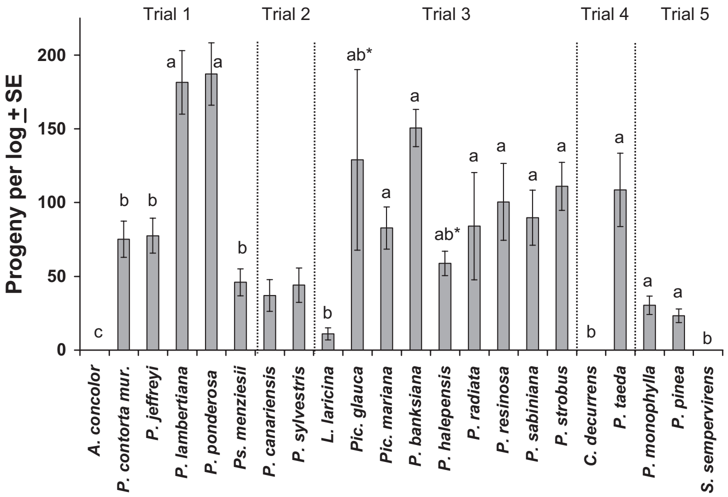

Fig. 1. Mean number (back-transformed data) of adult progeny produced per log per host species (letters denote significant differences by Tukey HSD on $\log_{10}$-transformed data within a trial group). Analysis of variance (ANOVA) trial 1: $F = 203$, df = 5, 34, $P < 0.001$; trial 2: $F = 0.16$, df = 1, 6, $P = 0.699$; trial 3: $F = 3.5$, df = 8, 29, $P = 0.006$; trial 4: $F = 83.4$, df = 1, 8, $P < 0.001$; and trial 5, $F = 69.6$, df = 2, 11, $P < 0.001$. *, $\log_{10}$-transformed data in trial 3 have a different trend where *Pic. glauca* and *P. halepensis* had the second and third lowest means.

accurately reflect emergence time. Therefore, mean emergence times were not analyzed, and only the first day that progeny occurred in collection jars was noted as the possible start of emergence. Progeny reentering the log would be unlikely to reproduce because the phloem was mostly degraded, dried, colonized by fungus, and unsuitable at that time.

For each trial, the effect of host species on the following dependent variables was tested: number of males producing frass after 1 d, total number of adult progeny ($\log_{10}$ transformed), proportion of females among progeny (arc-sine transformed, and weighted by beetle sample size), body length of males and females (weighted by sample size), and number of galleries per log where the log was the experimental unit (SAS Institute 1999). Body length was measured because larger size has been associated with greater fitness among bark beetles, such as laying more eggs, dispersing farther, and producing more antiaggregation pheromones to reduce competition (Pureswaran and Borden 2003). Each dependent variable of each trial was analyzed separately, because beetles were obtained from different sources and rearing conditions varied during trials. Multiple comparisons among host species were evaluated by Tukey's honestly significant difference (HSD) if the treatment effect was significant, $\alpha = 0.05$. For each host species, a one-sided t-test evaluated whether the number of progeny was greater than nine (the number of parents initially introduced) to determine whether the population increased. A two-sided t-test determined whether the proportion of female progeny differed from 0.5.

The number of degree-days (DD) required for development was determined on *P. taeda*, an economically important pine species (pulp production) that grows in the southeastern United States where the climate is likely amenable to *O. erosus*. Between 30 and 45 d, *P. taeda* logs were removed from their sealed rearing buckets and inspected daily for new exit holes on the bark surface and any adult progeny not in the collection jar. Degree-days were calculated between introduction of the parental female to when the first new exit holes or adult progeny were detected by using a single sine method with daily minimum and maximum temperatures and vertical cut-off (UC IPM 2007), an upper developmental threshold of 39°C, and lower threshold of 13.6 or 18°C. A lower threshold of 13.6°C is a theoretical point at which no development should occur based on a developmental equation (fig. 6 in Mendel and Halperin 1982). We also used a conservative threshold of 18°C, the lowest observed temperature at which larvae would complete their development (Mendel and Halperin 1982). Voucher specimens from all hosts were deposited at the Oregon State Arthopod Museum (accession 00226), University of California Davis Bohart Museum, and the California Academy of Sciences.

Results

Beetle Characteristics. From the analysis of the total number of adult progeny, *O. erosus* developed on all pine species, *L. laricina*, *Pic. glauca*, *Pic. mariana*, and *Ps. menziesii*, but not on *A. concolor*, *C. decurrens*, or *S. sempervirens* (Fig. 1). For hosts in which development occurred, the number of progeny significantly exceeded nine, except for *L. laricina* (Table 2). The presence of frass at 1 d suggested that males mined in the phloem of logs from all species except for *Pic. glauca* (Table 2). That progeny developed from *Pic. glauca* indicates that males eventually mined the phloem after 1 d, or the frass was not pushed out and as visible as in the other hosts. Males were more likely to mine the phloem of *P. jeffreyi* than *P. ponderosa* in

Table 2. Effect of host species on various reproductive parameters with separate ANOVA and Tukey means comparisons for each trial and dependent variable, and *t*-tests for each host

Host	Means, Tukey comparisons, and ANOVA tests						*t*-tests for each host				
	Frass[a]	Prop. female[b]	Male length (mm)[c]	Female length (mm)[d]	First emergence (d)[e]	Galleries per log[f]	df	Progeny > 9		Prop. female 0.5	
								t	*P*	*t*	*P*
Trial 1											
Abies concolor	2.29ab	na[g]	na	na	na	na					
Pinus contorta Mur.	2ab	0.536	3.82c	3.77b	41	3.9b	6	5.38	<0.001	1.88	0.109
Pinus jeffreyi	3a	0.490	3.96a	3.94a	41	5.4a	6	5.8	<0.001	0.782	0.464
Pinus lambertiana	2.14ab	0.470	3.95ab	3.90a	41	5.7a	6	8.02	<0.001	0.584	0.580
Pinus ponderosa	1.71b	0.513	3.95a	3.94a	41	3.9b	6	8.39	<0.001	0.683	0.520
Pseudotsuga menziesii	2.8ab	0.534	3.84bc	3.78b	43	5.4a	4	4.04	0.008	0.931	0.404
Trial 2											
Pinus canariensis	2.25	0.546	4.08	4.02	98	Na	3	2.60	0.040	1.45	0.244
Pinus sylvestris	3	0.485	4.04	3.95	98	2.0	3	2.99	0.029	0.269	0.806
Trial 3											
Larix laricina	1.75ab	0.436	3.83bc	3.71b	83	2.3c	3	0.49	0.329	0.625	0.576
Picea glauca	0.25b	0.381	3.98ab	3.88b	79	5.3b	3	2.88	0.032	0.932	0.420
Picea mariana	2ab	0.487	3.89b	3.83b	57	4.3b	3	5.17	0.007	0.540	0.627
Pinus banksiana	2.25ab	0.494	3.87b	3.85b	57	3.3bc	3	11.2	0.007	0.564	0.612
Pinus halepensis	2.25ab	0.510	3.91abc	3.89ab	57	3.5bc	3	3.0	0.020	0.873	0.432
Pinus radiata	1.8ab	0.482	4.06a	3.99a	57	3.8bc	4	5.73	0.023	0.641	0.557
Pinus resinosa	2.75a	0.503	3.84c	3.84b	57	4.5b	3	3.52	0.019	0.132	0.903
Pinus sabiniana	2.8a	0.464	3.89bc	3.85b	57	5.8ab	4	4.37	0.006	0.878	0.429
Pinus strobus	3a	0.470	3.96ab	3.89ab	57	4.0b	3	6.27	0.004	0.620	0.579
Trial 4											
Calocedrus decurrens	2.8	na	Na	na	na	Na					
Pinus taeda	2.6	0.499	3.84	3.95	42	4.8	4	4.01	0.008	0.038	0.972
Trial 5											
Pinus monophylla	2.4	0.532	3.89	3.77	63	2.4	4	3.45	0.013	1.76	0.153
Pinus pinea	3	0.423	3.88	3.82	55	4.0	3	3.12	0.026	0.835	0.451
Sequoia sempervirens	2.8	na	Na	na	na	Na					

[a] Number of introduced parental males out of three per log that produced visible frass at 1 d, ANOVA tests on frass outcome for trial 1: $F = 4.2$, df = 5, 34, $P = 0.0085$; trial 2: $F = 2.5$, df = 1, 6, $P = 0.17$; trial 3: $F = 3.8$, df = 8, 29, $P = 0.0038$; trial 4, $F = 0.20$, df = 1, 8, $P = 0.67$; and trial 5: $F = 4.7$, df = 2, 11, $P = 0.068$.

[b] Proportion of female progeny for trial 1: $F = 0.71$, df = 4, 28, $P = 0.59$; trial 2: $F = 0.61$, df = 1, 6, $P = 0.46$; trial 3: $F = 0.10$, df = 8, 29, $P = 0.99$; and trail 5: $F = 0.74$, df = 1, 7, $P = 0.42$.

[c] Male thoracic and elytral length for trial 1: $F = 9.7$, df = 4, 28, $P < 0.001$; trial 2: $F = 0.25$, df = 1, 6, $P = 0.63$; trial 3: $F = 8.3$, df = 8, 29, $P < 0.001$; and trial 5: $F = 0.05$, df = 1, 7, $P = 0.83$.

[d] Female thoracic and elytral length for trial 1: $F = 14.3$, df = 4, 28, $P < 0.001$; trial 2: $F = 5.3$, df = 1, 6, $P = 0.062$; trial 3: $F = 4.8$, df = 8, 28, $P < 0.001$; and trial 5) $F = 0.02$, df = 1, 7, $P = 0.88$.

[e] Not tested due to uncertainty of observations. First emergence was based on when progeny first appeared in collection jars for most hosts except for *P. taeda*, which was based on the appearance of progeny or exit holes.

[f] Galleries per log for trial 1: $F = 5.0$, df = 4, 28, $P = 0.0036$; trial 3: $F = 6.4$, df = 8, 27, $P < 0.001$; and trial 5: $F = 4.3$, df = 1.7, $P = 0.076$.

[g] Not applicable.

trial 1, and *P. resinosa*, *P. sabiniana*, and *P. strobus* in trial 3. The proportion of female progeny ranged from 0.38 in *Pic. glauca* to 0.546 in *P. canariensis,* but the sex ratio never significantly deviated from 1:1 for all hosts (Table 2). The body length of males ranged from 3.82 mm in *P. contorta murrayana* to 4.08 mm in *P. canariensis,* and females ranged from 3.71 mm in *L. larcina* to 4.02 mm in *P. canariensis* (Table 2). In trial 1, body lengths of males and females were greater from *P. jeffreyi,* and *P. ponderosa* compared with *P. contorta murrayana* and *Ps. menziesii.* In trial 3, progeny size was greatest with *P. radiata* and smallest with *L. laricina.*

The first detection of progeny from test logs varied from 41 d in trial 1 when temperatures were highest to 98 d in trial 2 when temperatures were lowest (Table 2). Development was closely monitored in *P. taeda* logs where parental females were introduced 17 May 2006 and new progeny or exit holes were first observed 42 d later, after 523.5 or 334.7 accumulated degree-days (threshold 13.6–39 or 18–39°C, respectively). The temperature ranged from 20 to 33°C, with a mean of 25.8°C; mean humidity was 79.4% RH.

Gallery Characteristics. The number of "overall galleries" per log ranged from 2.3 to 5.8 (Table 2) when three were expected because three parental sets (one male:two females) were introduced per log. An overall gallery should have a nuptial chamber in the center and two egg galleries extending in opposite directions (Mendel and Halperin 1982). Most logs had more than three overall galleries, suggesting that parental beetles initiated secondary galleries once primary galleries were completed. Because nuptial chambers were not always identifiable to distinguish individual egg galleries, overall galleries were compared and not individual egg galleries. It was possible that some observed galleries may have included only one mated female; hence, one egg gallery. Due to observational limitations, the gallery data are used for qualitative comparisons across hosts. Typical gallery lengths and larval mines have been well characterized by Mendel and Halperin (1982) and Mendel (1983). In trial 1, there were more galleries per log in *P. jeffreyi*, *P. lambertiana*, *Ps. menziesii* (5.4–5.7) compared with *P. contorta murrayana* and *P. ponderosa* (3.9). In trial 3, *P. sabiniana* had more galleries per log than *L. laricina* (5.8 versus 2.3).

Discussion

Host Suitability. In no-choice laboratory tests, *O. erosus* developed on all 15 *Pinus* spp., *Ps. menziesii*, *Pic. glauca*, and *Pic. mariana*, and marginally on *L. laricina.* Depending on the trial, parental beetles were from naturally infested *P. halepensis*, *P. pinea*, or *P. sylvestris* logs, which may have affected the ability of progeny to develop on other host species in the experiment. Yet, in trials 1, 3, and 4, progeny developed in large numbers on nonparental hosts. Notably, our physiological host range tests may not reflect preference and colonization behavior in the field. To better understand the impact of *O. erosus*, choice-tests in the field are needed, as well as assays for oviposition rates, larval and adult survival, and emerging adult fertility, such as were conducted for other wood- and bark-boring beetles (Hanks et al. 1995, Eager et al. 2004, Faccoli 2007). Nevertheless, our laboratory results are consistent with field observations. In preliminary trials, freshly cut logs of *P. monophylla*, *P. ponderosa*, and *P. radiata* were colonized by *O. erosus* after being placed in infested areas of California from late June to late July 2007 (J.C.L., unpublished data). In California, we have observed *O. erosus* beetles, galleries, and signs of complete development on dying trees, stumps, or debris from *P. canariensis*, *P. halepensis*, *P. pinea*, *P. radiata*, *P. sabiniana*, *P. sylvestris*, and *Cedrus deodara* (Roxb.) Don, although the latter species was not tested in the laboratory (Lee et al. 2005; Penrose et al., unpublished data).

Our laboratory results are also consistent with collection records from other countries for *P. canariensis*, *P. halepensis*, *P. pinea*, *P. radiata*, *P. sylvestris*, *P. strobus* and *P. taeda* (Bevan 1984, Eglitis 2000). Our studies show reproductive capability on *Ps. menziesii*, *Pic. glauca*, and *Pic. mariana*, whereas previous reports have considered *Ps. menziesii* and *Picea* spp. as "occasional hosts" for maturation feeding or overwintering (Eglitis 2000). This study is the first record of development of *O. erosus* on *L. laricina*, and it confirms that *O. erosus* cannot reproduce on *A. concolor*, although *Abies* spp. have, like *Ps. menziesii* and *Picea* spp., been listed as occasional hosts for maturation feeding (Eglitis 2000). *O. erosus* cannot develop on *C. decurrens* or *S. sempervirens*, valuable trees in California for specialized timber products. Although no statistical comparison can be made directly across all 22 species, *Ps. menziesii* seemed less suitable than *P. contorta murrayana*, *P. jeffreyi*, *P. lambertiana*, and *P. ponderosa* in trial 1. Fewer and smaller progeny emerged from *Ps. menziesii.* In trial 3, *O. erosus* reproduced on *Pic. glauca* and *Pic. mariana* equally well as on the *Pinus* spp., but *O. erosus* developed poorly on *L. laricina* versus *Pinus* and *Picea* spp. *L. laricina* yielded smaller progeny, fewer galleries, and progeny production did not exceed the number of parental beetles first introduced.

The proportions of female progeny on all hosts in our trials were similar. They did not deviate from 0.5, assuming sex ratios are equal. However, for species with polygynous pairing, a slight female bias may exist for emerging adults. Tribe (1990) found 0.545 *O. erosus* females on trap *P. radiata* logs, and Cameron and Borden (1967) found 0.541 *Ips confusus* (LeConte) (now *Ips paraconfusus* Lanier) females on *P. ponderosa* logs and branches (slash).

After monitoring *O. erosus* development on *P. taeda*, 42 d elapsed between introduction of parental females and emergence of the first progeny under a mean temperature of 25.8°C and 79.4% RH, and 523.5 or 334.7 accumulated degree-days with a lower threshold of 13.6 or 18°C, respectively. Exact dates of oviposition were unknown in this study, but females have been observed to mate with the males shortly after entering the nuptial chamber, and can start ovipositing within 1.5 d at 36°C and 10 d at 18°C (Mendel and Halperin 1982). In trials conducted in Israel, only 16.5 d elapsed between parental female entrance to progeny emergence from *P. brutia* at a constant 36°C, and 369.6 or 297 degree-days (Mendel and Halperin 1982).

Potential Geographic Impacts. These physiological host range tests help identify potentially vulnerable conifers if *O. erosus* continues to spread through California and the United States. Coincidentally, *O. erosus* is abundant in the Central Valley of California where hosts from its native range, *P. canariensis*, *P. halepensis*, and *P. pinea* are widely planted in urban landscapes (Seybold et al. 2006) (Fig. 2a). Should *O. erosus* expand its range to the Sierra Nevada, Coastal, and Transverse mountain ranges, it would likely encounter and reproduce in native *P. sabiniana*, which encircles the Central Valley at foothill elevations ≈500–1,000 m (Fig. 2a). At higher elevations, *O. erosus* could potentially reproduce in native populations of *P. contorta murrayana*, *P. jeffreyi*, *P. lambertiana*, and *P. ponderosa*, although harsher high elevation climates may restrain its invasion into these ecotones. We suspect that *O. erosus* may spread easily to the Los Angeles Basin and Inland Empire regions of California where the weather is warm and exotic *Pinus* spp. are planted widely (Fig. 2a). Native *P. monophylla* on the Tehachapi mountain range could provide a potential pathway for population movement southward. Should *O. erosus* spread to coastal locations, it will threaten *P. radiata* in native stands, as well as those planted along highway corridors and in urban and periurban landscapes. For example, adventive *P. radiata* provides 8% of canopy cover in San Francisco (Maco et al. 2003). Plantations of *P. radiata* in Chile and South Africa have been damaged by *O. erosus* (Baylis et al. 1986, Ciesla 1988).

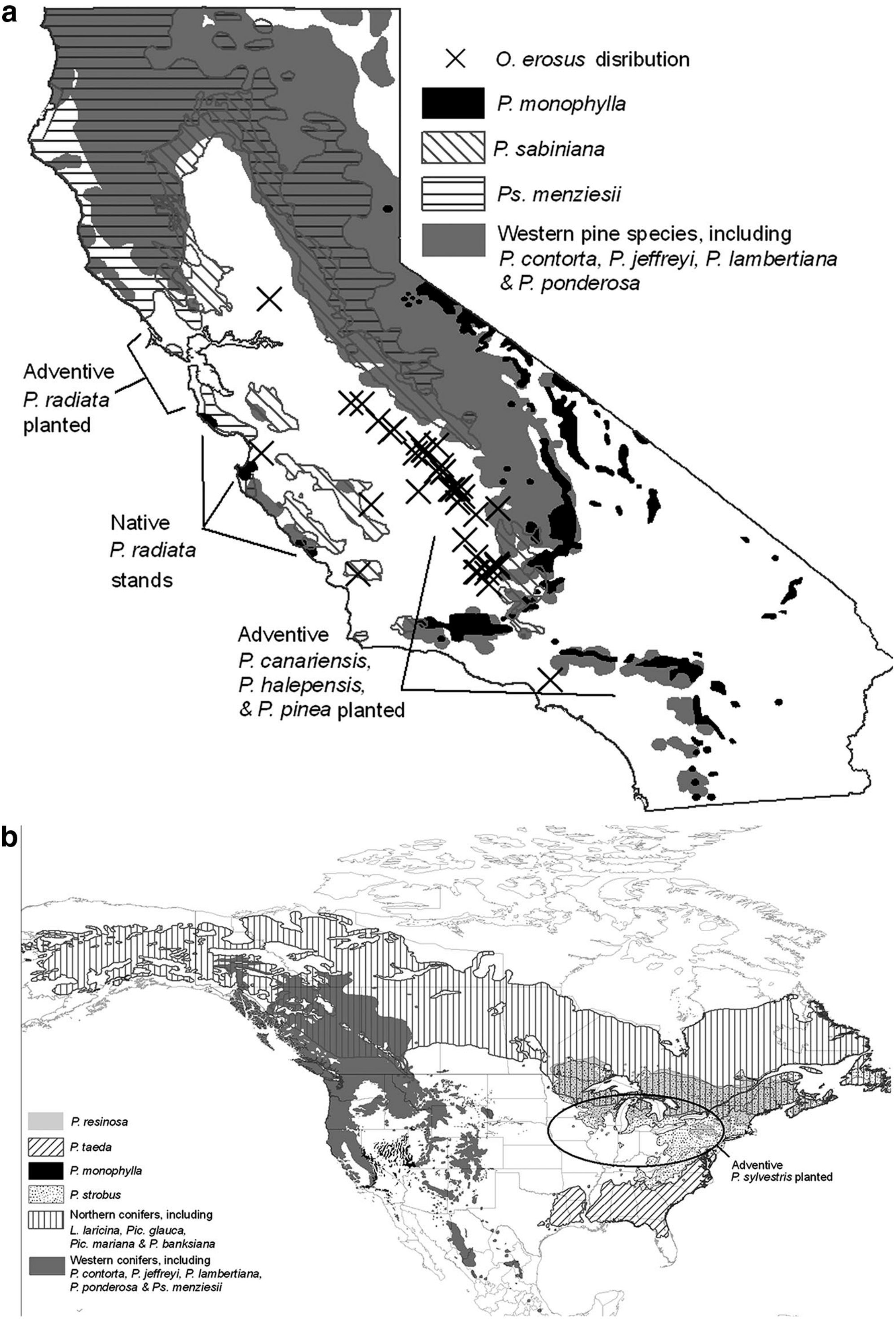

Fig. 2. Current distribution of *O. erosus* and approximate location of potentially vulnerable conifer hosts in California (a), and in the United States (b); many hosts occur at higher elevations and latitudes where *O. erosus* might not develop. California *Pinus* spp. distributions based on Griffin and Critchfield (1972), United States *Pinus* spp. distributions based on Critchfield and Little (1966), and nonpine conifer distributions based on Burns and Honkala (1990).

O. erosus could potentially affect *Pinus contorta, P. ponderosa,* and *Ps. menziesii* throughout the Pacific coast and Rocky Mountains (Fig. 2b), and *P. monophylla* in the arid regions of California and Nevada. In the north, *O. erosus* could potentially affect native *P. banksiana, P. resinosa, P. strobus,* and *Pic. glauca* and *Pic. mariana. P. sylvestris* is commonly planted in urban landscapes, rural properties, and Christmas tree plantations in the Northeast (Fig. 2b), and it has been colonized by *O. erosus* in its native range (Eglitis 2000) and in California (this study). However, the likelihood that *O. erosus* will establish in the northern regions should be lower than southern regions because of climate. Although *O. erosus* has been reported in England (Atkinson 1921), Finland (Siitonen 1990), and Sweden (Schroeder 1990), there is no evidence of established populations in those countries (Penrose, et al. unpublished data). In contrast, the warm weather of the southeastern United States may make it particularly vulnerable to invasion by *O. erosus.* There, *O. erosus* may reproduce on *P. strobus* in southern Appalachia and *P. taeda* planted widely throughout the southeastern United States. Overall, our host suitability tests demonstrate the potential for *O. erosus* to affect North America because many conifers tested were potentially suitable. However, further analysis of the short- and long-range dispersal of *O. erosus,* its cold tolerance, and climatic modeling would be needed to accurately project the ecological and economic impacts.

Acknowledgments

We thank Z. Heath for creating the host range maps; E. Espiritu, S. Hamud, and T. Young for laboratory assistance; D.-G. Liu for a critical review and translation of Chinese literature; and A. Eglitis, C. Millar, R. Venette, and A. Walters for comments on the manuscript. We thank R. Rice for acquiring infested pines in the field, and the following people for obtaining host species: H. Bertances, R. Borys, C. Fettig, D. W. Gilmore, M. Kroeze, T. O'Brien, R. Rice, W. Shepherd, and R. West. K. Daane provided rearing buckets and space for emergence cages at the Kearney Research and Education Center, Project 0705. Funding was provided by the University of California IPM Exotic/Invasive Pests and Diseases grant 05XU039, and USDA NRI CSREES postdoctoral grant 2006-35302-16611. We also thank D. Ullman, S. Padgett, L. Beneze, and C. Adan (Department of Entomology, University of California-Davis) for administrative support.

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Received 20 October 2007; accepted 6 February 2008.