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Authors: J.D. Bookwalter, J.J. Riggins, J.F.D. Dean, V.C. Mastro, L.R. Schimleck, et. al.

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Colonization and Development of *Sirex noctilio* (Hymenoptera: Siricidae) in Bolts of a Native Pine Host and Six Species of Pine Grown in the Southeastern United States[1]

J.D. Bookwalter[2], J.J. Riggins[3], J.F.D. Dean[3], V.C. Mastro[4], L.R. Schimleck[5], B.T. Sullivan[6], and K.J.K. Gandhi

University of Georgia, D.B. Warnell School of Forestry and Natural Resources, 180 E Green Street,
Athens, Georgia 30602, USA

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Abstract *Sirex noctilio* F. (Hymenoptera: Siricidae) is a major exotic pest of pines (*Pinus* spp.) in the Southern Hemisphere and has become established in northeastern North America. We investigated the suitability of bolts of six economically and ecologically important U.S. pine species grown in the southeastern United States, including eastern white (*P. strobus* L.), loblolly (*P. taeda* L.), longleaf (*P. palustris* Miller), shortleaf (*P. echinata* Miller), slash (*P. elliottii* Engelmann), and Virginia (*P. virginiana* Miller) pines and its native Eurasian host, Scots pine (*P. sylvestris* L.), for *S. noctilio* reproduction. The properties of wood and resin of different pine species were also analyzed for possible correlates to *S. noctilio*'s colonization and reproductive success on bolts. *Sirex noctilio* completed development on bolts within 4 mo of oviposition activities. Among the seven pine species, *S. noctilio* completed development in eastern white, Scots, and Virginia pines. Females tended to drill less on bolts with higher area and density of resin canals, as well as higher first 10-ring and radial strip-specific gravity. The resin of eastern white and Virginia pines had distinct extractive profiles, and eastern white pine may have two 3-carene chemotypes in the southeastern region.

Key Words bolts, exotic species, *Pinus*, *Sirex noctilio*, southeastern United States

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Sirex noctilio F. (Hymenoptera: Siricidae) is a Palearctic stem-boring pest of pine (*Pinus* spp. L.) trees that is now established in the northeastern United States and southeastern Canada. Since its initial discovery in 2004, *S. noctilio* has been reported in Connecticut, Massachusetts, Michigan, New Jersey, New York, Ohio, Ontario, Pennsylvania, Quebec, and Vermont (National Agricultural Pest Information System 2017). *Sirex noctilio* is a major exotic pest of nonnative pine plantations in Australia, New Zealand, South Africa, and South America (Morgan and Stewart

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[2] Corresponding author (email: J.bookwalter@creaf.uab.cat), Autonomous University of Barcelona, Ecological and Forestry Applications Research Centre, Edifici C. E-08193 Bellaterra, Spain.

[3] Mississippi State University, Department of Biochemistry, Molecular Biology, Entomology, & Plant Pathology, Mailstop 9655, Mississippi State, MS 39762, USA.

[4] Otis Laboratory, USDA-APHIS-PPQ-CPHST (retired), 1398 W. Truck Rd, Buzzards Bay, MA 02542, USA.

[5] Oregon State University, Wood Science and Engineering, Oregon State University, 119 Richardson Hall, Corvallis, OR 97331, USA.

[6] United States Department of Agriculture, Southern Research Station, Alexandria Forestry Center, 2500 Shreveport Highway, Pineville, LA 71360, USA.

1966, Aguilar and Lanfranco 1988, Tribe 1995, Carnegie et al. 2005). This insect is native to northern Asia, Europe, and northern Africa where it is a secondary colonizer of pine trees, especially those damaged by abiotic or biotic agents (e.g., drought or insects) or both (Coutts 1965, Madden 1975, Spradbery and Kirk 1978, Lombardero et al. 2016). In the northeastern United States and southeastern Canada regions, *S. noctilio* acts as a secondary colonizer but can also be the primary agent of tree mortality in unhealthy and unmanaged pine forests (Dodds et al. 2010, 2014, Haavik et al. 2016).

Sirex noctilio kills trees via oviposition activity when females inject a phytotoxic mucus containing a venom glycopeptide called noctilisin and fungal spores of *Amylostereum areolatum* (Fr.) Boidin into the sapwood of suitable trees (Ciesla 2003, Bordeaux et al. 2014). The phytotoxic mucus likely conditions the tree for fungal development by enhancing respiration and transpiration and inhibiting translocation, which results in an increased release of volatiles and water loss from bark tissue (Coutts 1969, Madden 1977, Bordeaux et al. 2014). In this weakened state, the fungal spores subsequently germinate to yield a white rot mycelium that is hypothesized to act as an external gut for the developing larvae (Rawlings 1948, Gilmour 1965, Madden 1981, Thompson et al. 2014).

Sirex noctilio can use a range of conifer trees as hosts, especially pines planted off-site (Taylor 1981). In the Southern Hemisphere, *S. noctilio* colonizes introduced North American pine species, including jack (*P. banksiana* Lambert), loblolly (*P. taeda* L.), longleaf (*P. palustris* Miller), radiata (*P. radiata* D. Don), shortleaf (*P. echinata* Miller), and slash (*P. elliottii* Engelmann) pines (Maderni 1996, Klasmer et al. 2000). In North America, *S. noctilio* has been found in eastern white (P. strobus L.), jack, red (*P. resinosa* Aiton), and Scots (*P. sylvestris* L.) pines (Dodds and de Groot 2012). Experiments using freshly cut logs suggest varying levels of insect responses; for example, Haavik et al. (2017) reported that Scots pine, red pine, and jack pine were perceived by *S. noctilio* females as optimal hosts, whereas eastern white pine was perceived as suboptimal. However, eastern white pine was found to be a suitable larval host, whereas jack pine was found to be the least suitable larval host (Haavik et al. 2017). *Sirex noctilio* surveys in forest stands also show differing levels of susceptibility among pine species (Maderni 1996, Dodds et al. 2010, Lombardero et al. 2016) and *S. noctilio* emergence (Ryan et al. 2012, Zylstra and Mastro 2012, Foelker 2016). Such varying levels of *S. noctilio* responses could be due to the physical and chemical properties of the trees in addition to levels of tree stress and other environmental factors. For example, females tend to drill shorter oviposition tunnels and lay single eggs when rings are narrow and when wood is denser (Coutts 1965). In contrast, in trees that have wider rings (less dense wood) or have rings that are less lignified (as in fast growing trees), the female will commonly drill with the entire length of her ovipositor and lay two eggs (Coutts 1965). However, Madden (1974) found no differences in *S. noctilio* drilling with respect to wood density in *P. radiata*. Secondary defensive compounds, such as monoterpenes and sesquiterpenes, present in the resin of host pines may also drive *S. noctilio* colonization (Kile and Turnbull 1974). In the field, lures baited with a 70% α-pinene and 30% β-pinene monoterpene ratio have shown some success in attracting *S. noctilio* (Bashford 2008).

Sirex noctilio is not yet detected in the southeastern United States. However, the potential for its introduction and consequent impact, especially in unmanaged natural stands resulting from abandoned agricultural fields, appears high in this region (Hoebeke et al. 2005). Our research objectives were, therefore, to (a) assess the responses (colonization and progeny development) of *S. noctilio* in bolts of six pine species (eastern white, loblolly, longleaf, slash, shortleaf, and Virginia [*P. virginiana* Mill.] pines) grown in the southeastern United States, as well as a native host (Scots pine); and (b) elucidate differences in physical and chemical properties of the xylem of these seven pine species that may be correlated with the development of *S. noctilio*. Pine bolts instead of trees were used in this study, as *S. noctilio* is not yet detected in the southeastern United States, and there are relatively few or no southeastern pine species growing in the northeastern region. Bolts have also been successfully used in other studies on siricid bioassays, including those on *S. noctilio* (e.g., Coutts and Dolezal 1969, Ryan et al. 2012, Hartshorn et al. 2015, Myers et al. 2014, and Haavik et al. 2017).

Materials and Methods

***Sirex noctilio* development in response to pine species.** In May 2010, three trees each of eastern white, shortleaf, and Virginia pines were felled at Dawsonville Forest, Dawsonville, GA (N 34°27′0″, W 84°13′39″); three trees each of loblolly, longleaf, and slash pine were felled in Bartram Forest, Milledgeville, GA (N 33°1′7″, W 83°12′17″); and three Scots pine trees were felled in Heiberg Memorial Forest, NY (N 42°46′8″, W 76°4′54″). A 0.75-m long bolt was cut from each tree, and Waxlor® sealant (Willamette Valley, Co., Eugene, OR) was painted on the ends immediately. Dominant trees within a stand were chosen for the experiments. All bolts were 19–28 cm in diameter because our preliminary work indicated that *S. noctilio* emergence was greatest from large-sized (18.3–26-cm diameter) bolts (Dinkins 2011). Bolts from Georgia were then transported to Syracuse, NY. These southeastern bolts were exposed to insects within 5–6 d of cutting and those of Scots pine within 2–3 d of cutting. Felled or cut pine trees remain susceptible to attacks by *S. noctilio* for ∼14 d and, hence, differences in cutting times would not impact their responses (Madden 1971). Tops of the bolts were scratched to allow the release of volatiles before insect introduction. All experimental insects were obtained from the USDA, Animal and Plant Health Inspection Service (USDA-APHIS) laboratory in Syracuse. Insects used in the study were reared from bolts cut from naturally infested trees across the Syracuse area.

A screen house (4.1 × 2.3 × 2.2 m) was set up inside a ventilated greenhouse (with ventilation fans and open windows), and each pine bolt (21 bolts total) was stood on end within a randomly assigned square on a grid marked on the floor of the screen house. The temperature in the greenhouse was 17.2–34.3°C with 59%–75% relative humidity. Newly emerged adults of *S. noctilio* (44 females and 59 males) were placed in the center of the screen house at 0915 h. At 0915 h on day 2, a second set of newly emerged adults (12 females and 26 males) was released in the same manner in the screen house. Four observations at 15-min intervals were recorded during the first hour following the introduction of each set of insects. Additionally, observations were taken of each bolt at 2-h intervals three times daily beginning at 1315 h over 3 d. After 3 d, the majority of adults in the screen house had died.

Subsequent to these tests, bolts were enclosed individually in a fiberglass screen and stacked at right angles to each other to optimize space on pallets adjacent to a cluster of mature hardwoods at the border of the USDA-APHIS laboratory experiment station. A large black plastic tarp ($\sim$36-m^2 size) was draped and secured over the bolts. However, progeny began to emerge in early August 2010, and bolts were moved into a rearing facility inside rearing barrels in November 2010 to capture the rest of the emerging insects. In December 2010, the total numbers of round exit holes created by emerging insects and their diameters (as the size of emerging insects may indicate host quality [Madden 1974]) were recorded. Exit holes were used as a measure of the number of emerged progeny because some adults chewed through the fiberglass. Afterward, the bolts were split to find all nonemergent larvae and pupae. The sex of the larvae was determined by using presence (female) or absence (male) of a third ventral sclerite on the ninth abominable segment (Rawlings 1953).

Physical wood properties of bioassayed trees. Several physical attributes were assessed for each sample used in the previous experiment. Disks (3 cm thick) were cut from each tree immediately above and below the bolts used in the experiment. These disks were stored at <0°C in plastic bags until two 2-cm-wide radial strips from pith to bark could be cut from opposite sides of each disk. Using these radial strips, the specific gravity of latewood and earlywood was measured for each ring from each tree by using a direct scanning X-ray densitometer (QTRS-01X, Quintek Measurement Systems, Knoxville, TN) as described by Jordan et al. (2008). Specific gravity was computed for the basal area-weighted radial strip as well as for the first (or outer) 10 rings. An average specific gravity measurement for one radial strip from the top disk and one radial strip from the bottom disk from each tree was used for subsequent analyses.

To determine the density and area of resin canals, a radial strip from each top disk and bottom disk was dried at 39.4°C for 48 h, and then sanded using a belt sander and fine sandpaper. A square with an area of 1 cm^2 was selected using the cambium as one edge of the square. The total area and number of latewood resin canals within the selected area were respectively measured and counted using Image Pro (version 4.5 for Windows, Media Cybernetics, Inc., Rockville, MD) (Nair et al. 2009). An average of the resin canal area and density from each pair of radial strips was used for analyses.

Resin properties of bioassayed trees. In July 2010, we analyzed the monoterpene and sesquiterpene compositions of the resin of six of the seven tree species (Scots pine was excluded) investigated in the insect development experiment. Resin was sampled from trees of the same diameter class and located adjacent to those felled for the insect development experiment. In general, resin was collected with a prefabricated resin sampler (Karsky et al. 2004) in conjunction with a 15-ml capacity polypropylene centrifuge tube reservoir. Samplers were inserted into a $\sim$2.5-cm diameter hole cut with a cork borer through the bark to the xylem face and located at a height of 1.4 m. Exuded resin was collected for 24 h into the centrifuge tube that was then capped and stored at <0°C until analyzed. Two samples were collected on opposite sides of 8 trees of each species, for a total of 96 samples. This sampling procedure was adequate for loblolly, longleaf, shortleaf, and slash but not for all eastern white or Virginia pines because their resin crystalized on the wound. For the latter species, in September 2010, resin was collected for 24 h in 1-mm internal diameter glass capillaries inserted into punctures made through the bark. Otherwise, procedures were identical to those with the resin samplers. Capillaries were subsequently placed in glass scintillation vials, capped, and stored at <0°C until analyzed. Previous studies indicate that the seasonal variability of bole terpene composition in conifers is either very low or stabilizes after the first 5 yr of radial growth, and, therefore, we are confident that July and September samples are comparable (von Rudloff 1975, Schmitt et al. 1988, Jactel et al. 1996, Mita et al. 2002).

For composition analyses, resin aliquots (1 μl) were withdrawn using a Drummond micropipette and dissolved in 1 ml of high performance liquid chromatography-grade hexane (spiked with 35 μg heptyl acetate) in a 1.5-ml capacity glass vial. For samples collected into centrifuge tubes, the 1-μl subsample was taken from the tip of a clean Pasteur pipette that had been dipped into the resin. For resin collected into glass capillaries, the capillary was scored and broken and the subsample drawn from resin exposed at the broken end of the capillary.

Samples (1 μl) were analyzed on a Hewlett-Packard G1800C GCD coupled gas chromatograph-mass spectrometer (GC-MS) fitted with an HP-INNOWax capillary column (Agilent Technologies, Wilmington, DE; 60 m × 0.25 mm × 0.25-μm film). The GC-MS oven program was 40°C for 1 min, 16°C/min to 80°C, then 7°C/min to 230°C, and then held at 230°C for the final 10 min to purge the column. Samples were injected in splitmode, and carrier gas (helium) was programmed for a constant flow of 1.0 ml/min. Compounds in the samples were identified by comparing their mass spectra and retention times to those of authentic standards obtained from commercial suppliers (Sigma-Aldrich, Milwaukee, WI; Fluka, Buchs, Switzerland; Acros Organics, Geel, Belgium). Retention time and mass spectral data for β-phellandrene were obtained by analyzing dipentene LPX (Millennium, Jacksonville, FL), a turpentine fraction that contains a high concentration of β-phellandrene. Single ion chromatogram peak areas were normalized relative to the peak area of the internal standard, and these normalized peak areas were converted to quantities with a calibration curve obtained from analysis of serial dilutions of authentic standards of known concentrations.

Statistical analyses of responses of parental *S. noctilio* to pine bolts. Colonization data consisted of insects counts (walking or drilling) per bolt. These data were nonnormal, and normality could not be achieved using transformations. Differences in the responses of *S. noctilio* among pine species were, therefore, analyzed by regression by using a Poisson distribution (PROC GENMOD, error = poisson) (Zar 1999, SAS Institute 2004). Sample size was considered the number of times the bolts were checked multiplied by the number of host species multiplied by the number of replications (bolts) of host species. To account for variation in bolt sizes within a category, the surface area (m^2) of each bolt available to *S. noctilio* (minus the area of one cut end because the bolts were vertical) was tested as a covariate in the Poisson test. To control for the number of insects released in the screen house, the log of the number of insects released was used as an offset. To determine the possible differences in the behavior of males and females, interactions between sex and pine species were also tested.

There was both an overabundance of zeros and relatively large values in the colonization data. The data were found to be overdispersed relative to the Poisson distribution, and an overdispersion parameter (PSCALE) was inserted into the model. This parameter generally increased the standard errors and made it more difficult to detect significant differences within the groups. The parameterization method was set so that the beta estimates determined differences in the effect of each nonreference level compared with the average effect over all levels (PARAM=EFFECT, SAS Institute 2004).

Statistical analyses of progeny of *S. noctilio*. The volume (m^3) of the bolt was tested as a possible covariate in the Poisson test to control for confounding variables in the emergence data. The parameterization method, including the PSCALE option, was set the same as for the parental data. Progeny data (number of exit holes) were analyzed using a Poisson regression by using number of exit holes per bolt. Data for the diameter of exit holes were normal, and significant differences among exit hole data were found by analysis of variance (ANOVA) tests, followed by Tukey tests.

Statistical analyses of wood and resin properties of bioassayed trees. Differences in wood properties between the pine species were assessed using ANOVA and posthoc Tukey tests. Data were not normal and were log transformed to achieve normality before analyses. Correlations of physical wood properties (i.e., tree age, surface area of bolt, specific gravity in the first 10 rings of each tree, radial strip specific gravity, and density and total area of resin canals) on *S. noctilio*'s behavior (only drilling females) were examined individually in a Poisson regression model by using Type III Sum of Squares and Wald's 95% confidence limits.

Resin composition data (calculated as the weight proportion of each resin component within the sum of measured resin components) could not be normalized by transformations and were analyzed using Kruskal–Wallis tests. These were followed by nonparametric Tukey-type multiple comparisons by using the Dunn equation for standard errors, as tied ranks and unequal sample sizes were present (Zar 1999). To test for differences in the composition of resin recovered by the two collection techniques, we similarly used Kruskal–Wallis tests, followed by the Dunn method. To account for multiple testing in the differences of resin extraction analysis, the Holm variation of the Bonferroni correction was used to control for Type I error (Holm 1979).

The resin composition of sampled pine species was also compared by using nonmetric multidimensional scaling (NMS) (McCune and Mefford 1999, McCune and Grace 2002). As the coefficient of variation was $>100\%$, data were log transformed before analyses. Initial NMS was conducted with six axes, 50 runs of real data, stability criterion of 0.0005, 15 iterations for stability with a maximum of 250 iterations, and 0.20 steps down in dimensionality. The NMS scree plot assessed the final number of dimensions, and a plot of stress versus number of iterations was assessed for the stability of the model. The final NMS was conducted using the same parameters as above, except only two dimensions and one run of real data, and no step down in dimensionality were used. The final instability of the model was 0.00039, and the final stress for two-dimensional solution was 8.54. For clarity, an ordination plot was created using means and standard errors of ordination points along two hypothetical axes for each of the pine species.

Results

Responses of *S. noctilio* to bolts of seven pine species. Eastern white, Scots, and slash pine bolts had 2–4 times higher counts of males than other pine species ($\chi^2_6 = 12.85$, $P = 0.045$) (Fig. 1A). Three to 10 times higher counts of nondrilling females were recorded on eastern white and Virginia pine bolts than other pine species ($\chi^2_6 = 18.91$, $P = 0.004$) (Fig. 1B). Female *S. noctilio* were observed drilling on all pine species but had two times higher drilling counts on eastern white, Scots, and Virginia pines ($\chi^2_6 = 101.4$, $P < 0.001$) (Fig. 1C).

Progeny began emerging about 4 mo after oviposition. Progeny were produced only in bolts of eastern white, Scots, and Virginia pines, so only these species were included in further analyses. A total of 66 adults, 5 larvae, and 0 pupae were produced in all bolts. About five times more exit holes per bolt were found on Scots compared with eastern white and Virginia pines ($\chi^2_2 = 12.12$; $P = 0.002$) (Fig. 2). There were no differences in exit hole diameters among pine species ($P > 0.05$), and exit hole diameters ranged from 1.5 mm to 4.6 mm.

Wood properties of bioassayed trees. There were no significant differences in surface area among the bolts of seven pine species used in 2010 ($P = 0.214$) (Table 1). However, tree age varied significantly between pine species ($F = 10.54$; df = 6, 14; $P < 0.001$). The oldest trees were longleaf pine (67.2 ± 16.2 yr) and the youngest were slash pine (16.5 ± 2.0 yr). Eastern white pine had the lowest first 10-ring and radial strip specific gravity, followed by Scots and Virginia pines. Tukey tests showed that the first 10-ring specific gravity of eastern white pine was different from all other species, except Scots pine ($F = 10.27$; df = 6, 14; $P < 0.001$). The mean radial strip specific gravity of eastern white pine was significantly lower than that of other species, except Scots and Virginia pines ($F = 10.54$; df = 6, 14; $P < 0.001$). Bolts from eastern white pine had the lowest resin canal density; however, Tukey tests showed that the differences from slash pine were only marginally significant ($F = 2.88$; df = 6, 14; $P < 0.049$).

For drilling females, the effect of bolt surface area on activity was positive ($\chi^2_1 = 14.88$, $P < 0.001$). There was a negative relationship between female drilling and the first 10-ring specific gravity ($\chi^2_1 = 60.82$, $P < 0.001$), radial strip specific gravity ($\chi^2_1 = 51.01$, $P < 0.001$), mean area of resin canals ($\chi^2_1 = 94.30$, $P < 0.001$), and density of resin canals ($\chi^2_1 = 22.82$, $P < 0.001$). There was no significant relationship between progeny development (number of exit holes) of *S. noctilio* and tree age, specific gravity of the radial strip and first 10 rings, resin canal density, or resin canal area of each bolt (*P* values ranged from 0.112 to 0.906). There was a positive relationship between progeny development (number of exit holes) and bolt surface area ($\chi^2_1 = 5.09$, $P = 0.024$).

Chemical properties of bioassayed trees. Volatile constituents detected in the resin samples included 15 monoterpenes (bornyl acetate, camphene, 3-carene, ρ-cymene, limonene, myrcene, α-phellandrene, β-phellandrene, α-pinene, β-pinene, sabinene, α-terpinene, γ-terpinene, terpinolene, and tricyclene), two hydrocarbon sesquiterpenes (β-caryophyllene and α-humulene), and one phenylpropanoid (4-allylanisole) (Table 2). No significant differences were found between the July and September samples taken from eastern white and Virginia pines in relative

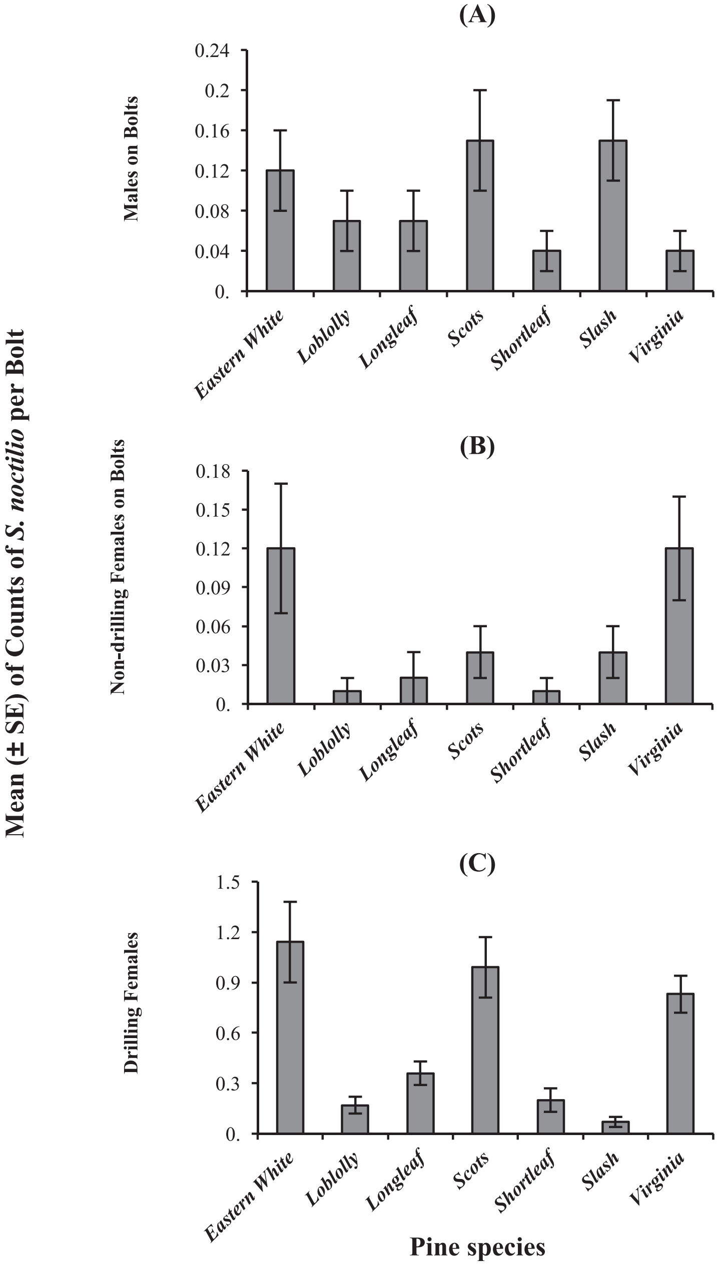

Fig. 1. Mean (± standard error [SE]) counts of *S. noctilio* (A) males, (B) nondrilling females, and (C) drilling females observed on bolts.

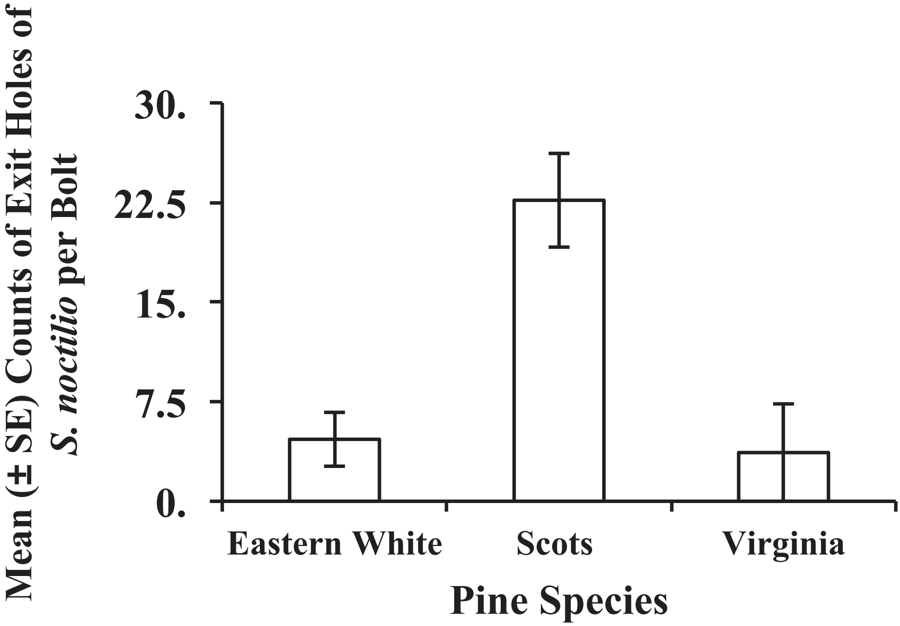

Fig. 2. Mean (± SE) numbers of exit holes of progeny of *S. noctilio* per bolt.

composition for any compound (Holm–Bonferroni correction, $\alpha = 0.003$ for both species; $P = 0.057$–0.909 [eastern white pine]; $P = 0.077$–0.688 [Virginia pine]).

There was considerable variation in resin volatile composition within and among pine species. Kruskal–Wallis tests indicated that the percent of 4-allylanisole in the eastern white and Virginia pines was lower than in other species ($\chi^2_5 = 42.6$, $P < 0.001$); however, nonparametric posthoc tests showed that eastern white (0.08% ± 0.03%), slash (2.66% ± 0.72%), and shortleaf pines (5.36% ± 0.88%) were not different from each other (Table 2). Virginia and eastern white pine resin contained the largest percentage of sabinene, with eastern white pine resin containing 4.7 and Virginia pine containing 1.3 times the percent in slash pine, which was the next highest species ($\chi^2_5 = 36.09$, $P < 0.001$). The mean percent of six hydrocarbon monoterpenes (3-carene, α-phellandrene, sabinene, α-terpinene, γ-terpinene, and terpinolene) and two hydrocarbon sesquiterpenes (β-caryophyllene and α-humulene) in eastern white pine resin were marginally higher (0.01%–0.1%) than in other species. Posthoc tests also found few significant differences among the samples (3-carene, $\chi^2_5 = 31.49$, $P < 0.001$; β-caryophyllene, $\chi^2_5 = 35.49$, $P < 0.001$; α-humulene, $\chi^2_5 = 31.79$, $P < 0.001$; α-phellandrene, $\chi^2_5 = 36.03$, $P < 0.001$; sabinene, $\chi^2_5 = 36.09$, $P < 0.001$; α-terpinene, $\chi^2_5 = 29.00$, $P < 0.001$; γ-terpinene, $\chi^2_5 = 32.83$, $P < 0.001$; and terpinolene, $\chi^2_5 = 41.88$, $P < 0.001$) (Table 2). Although the mean percent of 3-carene in the resin from eastern white pine was 10.87% ± 2.27%, no other species contained more than 0.01% (Table 2). Three of the 10 resin samples taken from eastern white pines had very little (<0.02%) 3-carene.

Table 1. Means (± SE) of surface area, age, radial strip specific gravity, first ten-ring specific gravity, and resin canal density and size among the seven species of pines.

	Physical Wood Properties					
Pine Species	**Surface Area (m^2)**	**Age (years)***	**Radial Strip Specific Gravity***	**First 10-Ring Specific Gravity***	**Resin Canal Density* (#/cm^2)**	**Resin Canal Area (mm^2/cm^2)**
Eastern White	0.169 (0.015)	23.33 (1.093)cd	0.385 (0.019)d	0.333 (0.016)c	23.50 (4.924)b	123.1 (30.65)
Loblolly	0.164 (0.005)	31.83 (2.315)bc	0.499 (0.009)ab	0.466 (0.026)ab	41.33 (1.965)ab	200.7 (12.75)
Longleaf	0.153 (0.003)	67.17 (16.16)a	0.540 (0.011)a	0.541 (0.018)a	44.83 (2.682)ab	230.5 (23.78)
Scots	0.186 (0.005)	36.67 (4.086)abc	0.417 (0.010)cd	0.386 (0.015)cb	49.67 (8.085)ab	123.6 (23.74)
Shortleaf	0.184 (0.016)	46.00 (2.291)ab	0.467 (0.025)abc	0.437 (0.037)ab	45.33 (10.70)ab	169.0 (41.74)
Slash	0.161 (0.002)	16.50 (2.021)d	0.492 (0.020)abc	0.486 (0.008)ab	59.83 (5.645)a	227.9 (20.50)
Virginia	0.174 (0.009)	22.50 (0.500)cd	0.440 (0.013)bcd	0.429 (0.010)ab	50.50 (11.36)ab	147.5 (22.66)

* Significant differences among pine species within each column. These differences in physical wood properties were found by ANOVA. Among the pine species, means followed by the same number did not differ significantly (Tukey test, $\alpha = 0.05$).

NMS results support the Kruskal–Wallis analyses by indicating qualitative differences in the percentages of resin volatile constituents in eastern white pine as compared with those of the other species (first axis $R^2 = 0.29$; second axis, $R^2 = 0.97$). Standard error bars for eastern white pine did not overlap with any other species (Fig. 3). Resin volatile constituents of Virginia pine were also substantially different from other species, although on a different scale than for eastern white pine, with the standard error bars of shortleaf and Virginia pines slightly overlapping (Fig. 3). There were minimal differences in the total blend of resin volatile constituents among longleaf, shortleaf, and slash pines (Fig. 3).

Discussion

The following four major trends were observed: (1) *S. noctilio* responded differently to pine bolts, with more females drilling on eastern white, Scots, and Virginia pines; (2) *S. noctilio* completed development only in eastern white, Scots, and Virginia pine bolts; (3) there was a negative relationship between specific gravity of wood and the number and area of resin canals and oviposition drilling; and (4) eastern white pine had a distinct resin volatile composition compared with other pines.

The progeny of *S. noctilio* began emerging about 4 mo after the bolts were exposed to *S. noctilio*. This is 6–8 mo before the 1-yr life cycle typically documented in other parts of the world (Taylor 1978). *Sirex noctilio* development appears to depend on the condition of the symbiotic fungus *A. areolatum*, whereas the growth of fungus depends directly on conditions in the tree. The optimum temperature for growth of the fungus is 24°C and lower temperatures and higher humidity retard growth (Madden 1981). We hypothesize that the higher temperatures under the tarp tent in which the bolts were stored may have accelerated larval development but were not high enough to kill the progeny. Although results are mixed over the importance of humidity as a driving mechanism for early emergence of *S. noctilio* (Rawlings 1948, 1951, 1953, Madden 1981), higher temperatures have been shown to speed up *Sirex* spp. development and shorten life cycles in the laboratory. For example, *S. juvencus* L. completed its typical 2-yr life cycle in as little as 7 mo when reared from bolts kept indoors at 22°C (Stillwell 1966), whereas bolts kept outside in a recent study supported a typical 1-yr life cycle (Haavik et al. 2017). Other factors affecting *S. noctilio* development time may include the size of the bolts, as Neumann and Minko (1981) recorded a 2–3.5-mo life cycle of *S. noctilio* on smaller diameter pine stems. However, Haavik et al. (2017) documented a 1-yr life cycle on ~6–8-cm diameter bolts.

Both male and female *S. noctilio* varied in their responses to different pine bolts when exposed to them simultaneously. Males of *S. noctilio* were most often found on Scots and slash pine bolts, whereas females were most often found on eastern white, Scots, and Virginia pine bolts. It may not be surprising that male and female *S. noctilio* showed differing responses to bolts, as they exhibit different flying behaviors in the forest setting. Males, when active, engage in short, swarming flights in the upper branches. Females, in contrast, fly into the canopy primarily to mate before searching for suitable hosts (Morgan and Stewart 1966, Madden 1988). The antennal morphology of males and females differ, as females have 7% more chemoreceptors, which may aid females in detecting suitable hosts in which

Table 2. Mean percentage (± SE) of individual compounds within the total volatile terpenoid composition of resin of each pine species sampled in 2010.

Terpenoid Volatile	Pine Species[a]			
	Eastern White	Loblolly	Longleaf	Shortleaf
4-allylanisole*	0.08 (0.03)bc	6.13 (1.48)a	4.36 (0.35)a	5.36 (0.88)a
bornyl acetate*	0.02 (0.01)d	0.34 (0.08)abcd	0.02 (0.01)ac	0.18 (0.05)ad
camphene*	1.16 (0.06)bc	1.38 (0.12)b	0.94 (0.03)ac	0.87 (0.03)a
3-carene*	10.9 (2.72)b	0.00 (0.00)a	0.00 (0.00)ab	0.00 (0.00)a
β-caryophyllene*	1.26 (0.56)a	0.03 (0.01)ac	0.03 (0.01)bc	0.12 (0.04)ab
ρ-cymene*	0.04 (0.01)a	0.02 (0.00)ab	0.02 (0.00)ab	0.02 (0.00)ab
α-humulene*	0.19 (0.08)c	0.01 (0.00)abc	0.01 (0.00)a	0.03 (0.01)ac
limonene	1.00 (0.04)	1.64 (0.62)	0.85 (0.05)	2.23 (1.43)
myrcene*	1.30 (0.08)ab	3.02 (0.49)b	0.98 (0.05)a	1.07 (0.06)a
α-phellandrene*	0.05 (0.00)d	0.02 (0.01)bce	0.02 (0.00)ad	0.02 (0.00)ac
β-phellandrene*	4.81 (0.21)ab	4.80 (1.72)a	3.33 (0.34)a	4.57 (0.29)a
α-pinene*	53.3 (1.86)b	68.3 (2.95)ac	72.8 (2.50)a	60.5 (2.26)abc
β-pinene*	24.1 (2.00)a	13.5 (3.25)a	15.9 (2.26)a	24.5 (1.95)a
sabinene*	0.52 (0.08)c	0.06 (0.01)a	0.06 (0.02)a	0.09 (0.01)ab
α-terpinene*	0.06 (0.00)a	0.02 (0.00)a	0.02 (0.00)a	0.01 (0.00)ab
γ-terpinene*	0.10 (0.02)ab	0.04 (0.00)ab	0.04 (0.00)a	0.02 (0.00)abc
terpinolene*	0.95 (0.00)a	0.21 (0.00)a	0.20 (0.00)a	0.14 (0.00)ab
tricyclene*	0.14 (0.06)bc	0.49 (0.06)a	0.41 (0.04)a	0.24 (0.06)abc

* Significant differences within rows using Kruskal-Wallis Tests. Means with the same letters are not significantly different among pine species (nonparametric Tukey-type test).

[a] eastern white, $n = 10$; loblolly, $n = 7$; longleaf, $n = 8$; shortleaf, $n = 7$; slash, $n = 7$; Virginia, $n = 12$.

to lay eggs (Crook et al. 2008). Trapping studies of siricids have also indicated that only females are caught when traps are baited with pine billets, monoterpenes, or ethanol or are placed adjacent to lures filled with pine slash or girdled trees in the forest (Zylstra et al. 2010, Böröczky et al. 2012, Barnes et al. 2014, Chase et al. 2014).

Three times greater numbers of *S. noctilio* females were found drilling on eastern white, Scots, and Virginia pine bolts than other pines. Correspondingly, progeny emerged only from these three species, with the most exit holes from Scots pine bolts. Haavik et al. (2017) also introduced *S. noctilio* to caged bolts and documented higher numbers of eggs oviposited in Scots than white pine, and no

Table 2. Extended.

Pine Species[a]			
Slash	**Virginia**	χ^2_5	***P* value**
2.66 (0.72)ac	0.00 (0.00)b	42.6	<0.001
0.20 (0.13)ab	0.03 (0.01)b	22.8	<0.001
1.19 (0.12)abc	1.10 (0.06)abc	20.6	0.001
0.00 (0.00)a	0.00 (0.00)a	31.7	<0.001
0.02 (0.00)bc	0.00 (0.00)b	35.5	<0.001
0.02 (0.00)ab	0.01 (0.00)b	25.3	0.001
0.00 (0.00)abc	0.00 (0.00)b	31.8	<0.001
1.00 (0.04)	0.97 (0.02)	8.59	0.127
3.75 (0.51)b	1.16 (0.03)a	36.5	<0.001
0.02 (0.00)ae	0.03 (0.00)ac	36.0	<0.001
4.06 (0.31)a	7.65 (0.36)b	29.1	<0.001
64.1 (1.76)abc	59.7 (2.49)bc	24.8	0.002
22.1 (1.64)a	28.8 (2.33)a	20.0	<0.001
0.11 (0.02)ab	0.14 (0.01)bc	36.1	<0.001
0.01 (0.00)ab	0.01 (0.10)b	29.0	<0.001
0.03 (0.00)abc	0.01 (0.00)c	32.8	<0.001
0.18 (0.00)ab	0.08 (0.00)b	41.9	<0.001
0.51 (0.05)a	0.24 (0.02)c	32.7	<0.001

difference of *S. noctilio* emergence numbers between bolts of these two species. Böröczky et al. (2012) compared the attraction of chemically girdled Scots versus eastern white pines for *S. noctilio* in New York, and found that more females drilled on Scots than eastern white pine. They also did not find a big difference in the number of *S. noctilio* that emerged from the two species. Although *S. noctilio* did not emerge from bolts of other species, the other pines tested in our study (loblolly, longleaf, shortleaf, and slash) are known to be suitable tree hosts for this insect (e.g., Maderni 1996, Klasmer et al. 2000, Haavik et al. 2017). In this laboratory study, the insects were given choices between pine species that infrequently occur together in the same stands. Possibly, there was less insect activity on loblolly, longleaf, shortleaf, and slash pines because insects had more host options.

In general, bolts from eastern white, Scots, and Virginia pines had the lowest radial strip and first 10-ring specific gravity (although posthoc tests revealed that the

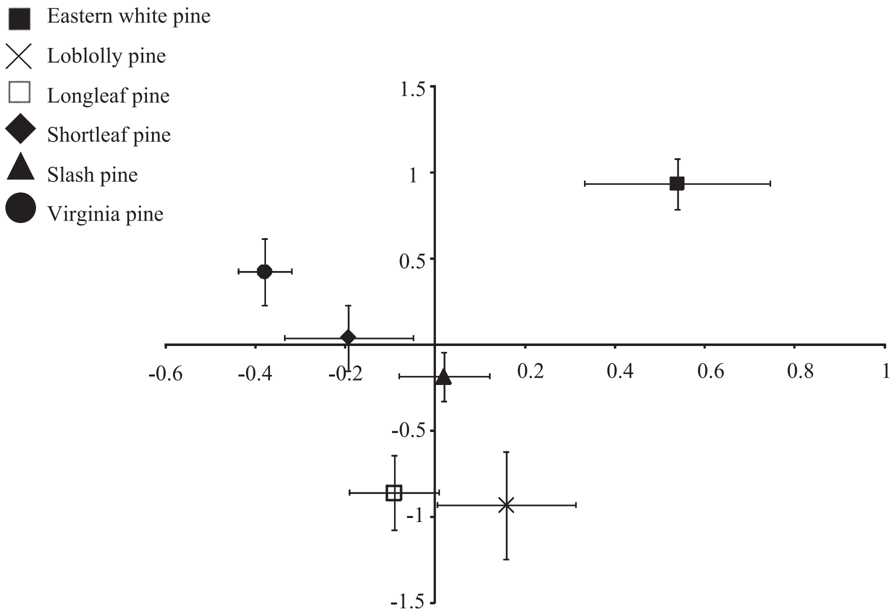

Fig. 3. Nonmetric multidimensional scaling (NMS) of the composition of volatile resin terpenoid constituents from six pine species.

radial strip and first 10-ring specific gravity of Scots and Virginia pines were not different from several of the other species). Furthermore, drilling by female *S. noctilio* was negatively correlated with these two attributes. Specific gravity can vary across the native range of tree species as a response to environmental conditions (Zamudio et al. 2002, Jokela et al. 2004, Jordan et al. 2008); however, relatively lower specific gravity values for eastern white, Scots, and Virginia pines as compared with longleaf, shortleaf, and slash pines have been reported previously (Barr 1918, Hoadley 1990, Bowyer et al. 2007). A few studies have looked at the effect of wood specific gravity or density on *S. noctilio* oviposition activities and the results are conflicting; when wood is less dense, females may drill deeper holes and lay multiple eggs (Coutts 1965), whereas Madden (1974) did not find any differences in *S. noctilio* drilling with respect to wood density. In agreement with Coutts (1965), our study indicates that *S. noctilio* could be deterred by wood with high specific gravity, perhaps because closer tree rings make drilling more difficult.

Chemical analyses of resin indicated that eastern white pines had a different profile of monoterpene and sesquiterpene compositions compared with other pine species occurring in the southeastern United States. Relatively larger percentages of specific hydrocarbon monoterpenes (3-carene, α-phellandrene, sabinene, α-terpinene, γ-terpinene, and terpinolene) and two hydrocarbon sesquiterpenes (β-caryophyllene and α-humulene) were found in eastern white pine resin. The disparity between eastern white pine and the other examined species is in agreement with phylogenetic analyses and other comparative systematic data that divide the genus *Pinus* into two discrete lineages: subgenus *Pinus* (includes loblolly, longleaf, shortleaf, Scots, slash, and Virginia pines) and subgenus *Strobus* (white pines) (Price et al. 1998). Resin samples from eastern white pine had a mean 100-fold higher percentage of 3-carene than the other pines in this study. However, 3 of the 10 samples taken from eastern white pines contained less than 0.02% of 3-carene, suggesting that they may have two chemotypes based on 3-carene content in resin, similar to the two chemotypes documented for Scots pines (Thoss et al. 2007, Böröczky et al. 2012). The resin chemistry of eastern white pines is known to be highly variable (Gerhold and Plank 1970, Gilmore and Jokela 1977). Scots pines from New York with a high 3-carene content were colonized in greater numbers by *S. noctilio* (Böröczky et al. 2012).

Overall, our results indicate that *S. noctilio* can reproduce in the bolts of three U.S. pines (eastern white, Scots, and Virginia pine) that occur in the southeastern United States, and they responded differentially to the seven tested pine species. More females drilled and progeny completed development on the bolts of eastern white, Scots, and Virginia pines. Wood properties appeared to be an important factor, as we documented a negative relationship between specific gravity of wood and resin canals with oviposition drilling. Eastern white pine had a distinct resin volatile composition, and two possible chemotypes with respect to 3-carene were detected in our study.

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