Effects of Forest Type and Management on Native Wood Wasp Abundance (Hymenoptera: Siricidae) in Mississippi, United States

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J. Econ. Entomol. 107(3): 1142–1149 (2014); DOI: http://dx.doi.org/10.1603/EC14023

ABSTRACT The United States has a rich fauna of native Siricidae (wood wasps), but they are rarely studied because they have limited economic impact. In 2004, a non-native wood-boring pest, *Sirex noctilio* F., was found established in North America. Because *S. noctilio* is an economically important pest in pine plantations throughout the Southern Hemisphere, interest in the ecology of American native wood wasp populations has increased. A study was conducted during fall 2011 to investigate the effects of forest stand type and characteristics on native wood wasp abundance, and to describe their flight phenology in northeastern Mississippi. In total, 609 native wood wasps were captured, consisting of 608 *Sirex nigricornis* F. and one *Urocerus cressoni* Norton. There were significant treatment and location effects that influenced wood wasp abundance. The flight period of wood wasps captured in our study (October–December) was similar to studies in the southeastern United States, but differed from results in Minnesota and the northeastern United States (June–October). Wood wasp abundance was significantly correlated with higher basal area, smaller tree diameter at breast height, and shorter trees, all indicators of forest stand stress. It appears proper silvicultural management of pine plantations may reduce native wood wasp population abundance in the southeastern United States, as it does to *S. noctilio* in the Southern Hemisphere. We propose implementing management models used for the southern pine beetle to reduce stand hazard of future infestations of native and invasive wood wasps.

KEY WORDS flight phenology, forest management, Siricidae, stand hazard

Siricids, commonly called wood wasps or horntails (Hymenoptera: Siricidae), are xylophagous insects that help decompose woody material in temperate forest ecosystems (Hall 1968, Spradbery and Kirk 1978). Worldwide, 122 species of wood wasps in 10 extant genera are known; the Americas contain 33 species in 7 genera (Schiff et al. 2012). The family Siricidae is composed of two subfamilies. The subfamily Siricinae oviposit into gymnosperms and harbor fungi in the genus *Amylostereum* Boidin; the subfamily Tremicinae use angiosperms as hosts and vector *Cerrena* Gray fungus (Tabata and Abe 1995, Schiff et al. 2006). Wood wasps are rarely studied in their natural habitat because of their limited economic impacts and relatively cryptic lifestyle. However, global interest in wood wasps has increased as the Eurasian wood wasp, *Sirex noctilio* F., has been introduced via solid wood packing materials throughout the Southern Hemisphere, where it has caused significant damage (up to 90% mortality) to pine plantations (Neumann et al. 1987, Morgan 1989, Tribe and Cillie 2004).

More recently, *S. noctilio* has arrived in North America (Hoebeke et al. 2005, Carnegie et al. 2006); it was detected in Oswego County, NY, in 2004, and the following summer in Ontario, Canada (Hoebeke et al. 2005, de Groot et al. 2006). In North America, *S. noctilio* is currently not a serious pest (Dodds et al. 2010). However, it is predicted to cause significant economic loss if it becomes established in southeastern and northwestern North America (Haugen et al. 1990, Hoebeke et al. 2005, Yemshanov et al. 2009, Ryan et al. 2012). Potential ecological concerns revolving around *S. noctilio* in North America include infestations in longleaf pine (*Pinus palustrus* Miller) stands, an endangered ecosystem in the southeastern United States (Farjon 2013), and nontarget interactions of native wood wasps with a nematode, *Deladenus siricidicola* Bedding, proposed as a biological control agent (Morris et al. 2012). One way of improving our predictions of how *S. noctilio* will behave in North America is to better understand the ecology and biology of the native wood wasp communities and what factors prevent these populations from reaching outbreak status.

The introduction of *S. noctilio* has spurred research efforts in North America concerning wood wasp taxonomy (Schiff et al. 2006, 2012), its parasitoid complex (Eager et al. 2011, Coyle and Gandhi 2012, Standley et al. 2012), silvicultural control efforts (Dodds et al. 2007, 2010; Zylstra et al. 2010), and the composition of

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Table 1. Definitions of stand types used in study

Forest stand type	Definition
Unthinned loblolly pine plantation	A stand that is aged at least 10 yr old and has not received any silvicultural thinning.
Thinned loblolly pine plantation	A stand that is aged at least 10 yr old and has received at least one silvicultural thinning.
Old growth (mature) forest	Mature forests contain these structural components: supercanopy trees, canopy trees, understory trees, shrubs and saplings, decaying wood, ground cover, organic litter, pits and mounds, cavity trees, and snags. Stands will be aged >60 yr old.
Mixed pine–hardwood forest	Pine–hardwood stands contain 30–50% hardwood and 51–69% pine in the main canopy. Stands are not aged >50 yr old.

native wood wasp and wood-boring insect competitors in North America (Ryan et al. 2011,2012; Coyle et al. 2012; Dodds et al. 2012; Barnes et al. 2014). However, the effects of forest management practices on *S. noctilio* or native wood wasp abundance have yet to be determined in North America. Because *S. noctilio* is not currently present in the southeastern United States, it is unknown how stand characteristics and management practices might impact its distribution, abundance, and behavior. However, *Sirex nigricornis* F. is a native species whose ecosystem niche in America appears similar to that of *S. noctilio* in its native range in Europe. By understanding how *S. nigricornis* populations are affected by management practices, predictions can be made on how *S. noctilio* might behave if introduced into the southeastern United States forests.

The objectives of this study were threefold: 1) to investigate what effect forest stand type and management practices have on native wood wasp abundance; 2) to determine what forest stand characteristics (i.e., tree diameter, age, and height) are correlated with native wood wasp abundance; and 3) to compare wood wasp flight activity in northeastern Mississippi to other studies performed throughout the United States (Coyle et al. 2012, Keeler 2012, Schiff et al. 2012, Barnes et al. 2014).

Materials and Methods

Forest Stand Types. This study was conducted in four forest stand types: unthinned pine plantation, thinned pine plantation, mixed hardwood–pine forest, and old growth forest (Table 1). The age of each forest was determined from known planting dates for each forest stand or in one location was determined by coring trees. Sixteen stands (four stand types each having four locations) were selected in northeastern Mississippi (Fig. 1) based on the definitions in Table 1. Pine plantations consisted of *Pinus taeda* L. (loblolly pine), which was also the dominant pine species found in mixed and old growth forests. *Pinus echinata* Miller (shortleaf pine) occurred in low numbers throughout mixed and old growth forests.

Insect Trapping. Three Lindgren multiple-funnel traps (Lindgren 1983; Synergy Semiochemical Corp., Burnaby, BC, Canada) were dispersed at each of the 16 sites (48 traps in total). Each trap location was arbitrarily selected within the stand and traps were hung at breast height (≈1.7 m). Traps were separated by a distance of at least 150 m. Traps were placed on the week of 28 September 2011 and removed the week of 21 December 2011. Collection cups contained a mixture of 50/50 Prestone Low Tox Antifreeze/Coolant (Prestone Products Corp., Danbury, CT) and water.

A recent study found that standard *Sirex* lures (comprising 70:30 α/β-pinene blend) were relatively ineffective attractants for native wood wasps in the southeastern United States (Barnes 2012, Barnes et al. 2014); thus, a recently developed trapping method was used for this study. A polypropylene mesh bag (55.9 by 45.7 cm; U-Line product # S-14435, Pleasant Prairie, WI) was filled with small diameter (≈75–100 mm) pine slash partially stripped of its bark and hung parallel to the funnel trap (hereafter called pine lure). Insects were collected weekly, and pine lures were replaced every 14 d.

Captured wood wasps were identified using Schiff et al. (2006), with the only exception being that according to recent changes in the Siricidae taxonomy (Schiff et al. 2012), *Sirex edwardsii* Brulle was treated as *S. nigricornis* F. Voucher specimens from the study were deposited into the Mississippi Entomological Museum at Mississippi State University.

Forest Stand Measurements. Fixed-radius circular plots (0.04 or 0.02 ha based on total acreage; Avery and Burkhart 2002) were conducted at all 16 locations, and geographically referenced using Garmin GPSmap 60CSx (Garmin, Olathe, KS). Diameter at breast height (cm) (DBH), height of two dominant or codominant pines (to the nearest 0.1 m), and tree species were recorded for all trees >7.62 cm (3 inches) DBH within plots. A TruPulse 200 rangefinder (Laser Technology Inc., Centennial, CO) was used to record tree heights. The number of standing dead pines was also recorded within plots. Pine basal area (PBA) and hardwood (deciduous) basal area (HBA) were calculated for each location based on the DBH measurements acquired from the plots.

Data Analyses. Relative abundance of wood wasps (log (wood wasps + 1)) in each treatment were analyzed using a generalized linear model (GLM) in R statistical software (R version 3.0, R Foundation for Statistical Computing, Vienna, Austria). Wood wasp count data were grouped from the three traps per location ($n = 16$) and summed across the 12-wk trapping period. Stand location had a significant effect on wood wasp abundance, with more northern sites in Holly Springs National Forest, Potts Camp, MS, yielding significantly more wood wasps ($F_{1, 14} = 18.31$; $P = <0.005$; Fig. 2). Therefore, the northern locations ($n = 4$) were analyzed separately from the central locations

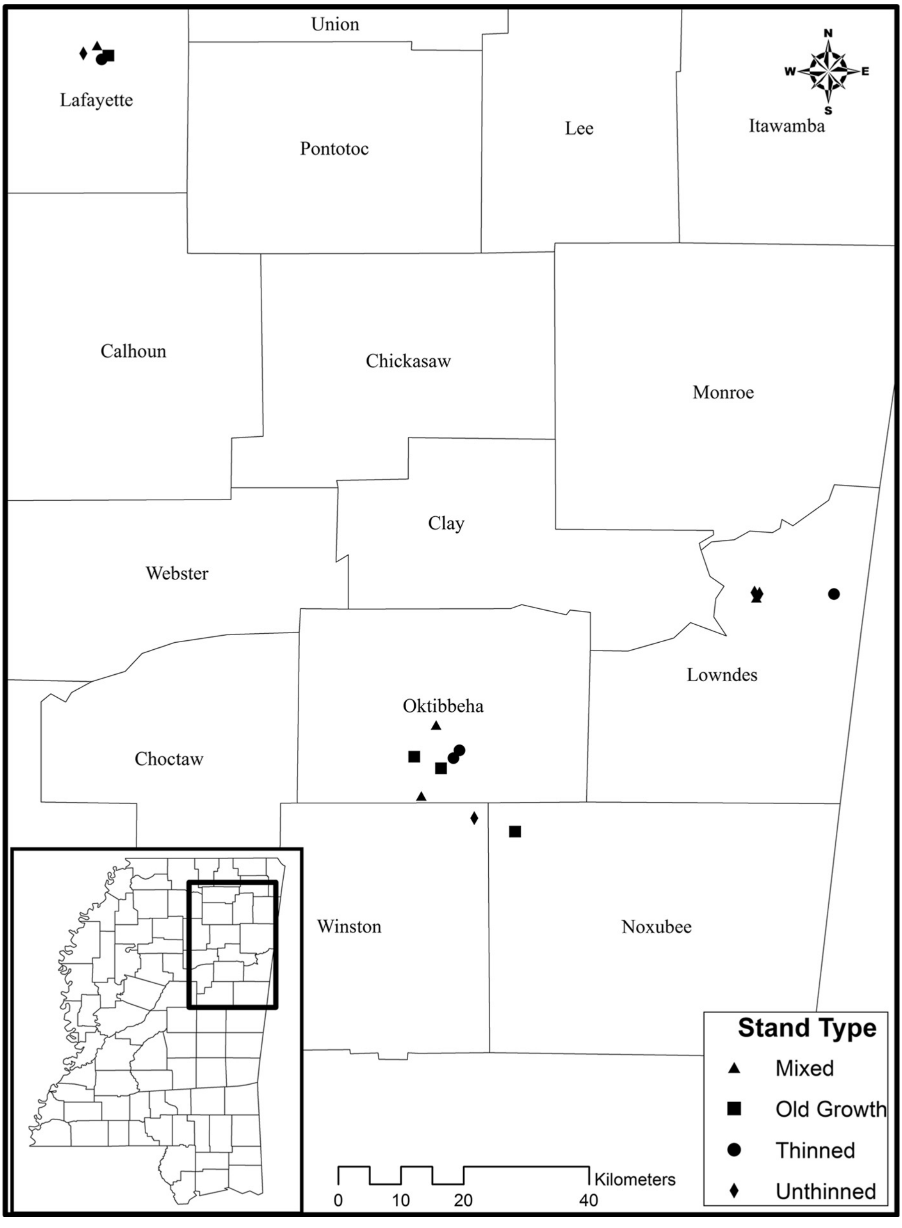

Fig. 1. Map displaying locations of wood wasp trapping in four different forest stand types, autumn 2011. Inserted map is of Mississippi.

($N = 12$) in the GLM. The wood wasp abundance data were overdispersed, so a quasi-Poisson error distribution was utilized to address this (ver Hoef and Boveng 2007).

R statistical software was also used to run linear and multiple regression models to analyze the relationship between wood wasp abundance (log (wood wasps + 1)) and the stand variables collected from the fixed-radius circular plots: 1) mean tree height, 2) PBA, 3) HBA, 4) age of stand, 5) mean number of dead pines, and 6) mean pine DBH. Wood wasp count was summed across weeks for each trap ($N = 48$).

Results

Wood Wasp Abundance. In total, 609 wood wasps were captured throughout the 12-wk study, all female. Collected species consisted of 608 *S. nigricornis* and one *Urocerus cressoni* Norton. No non-native wood wasps (e.g., *S. noctilio* or *Eriotremex formosanus* Matsumura) were captured in this survey. Sixty-nine percent of traps captured at least one wood wasp per week (396 of 576 counts). All traps except one captured at least 1 wood wasp during the study.

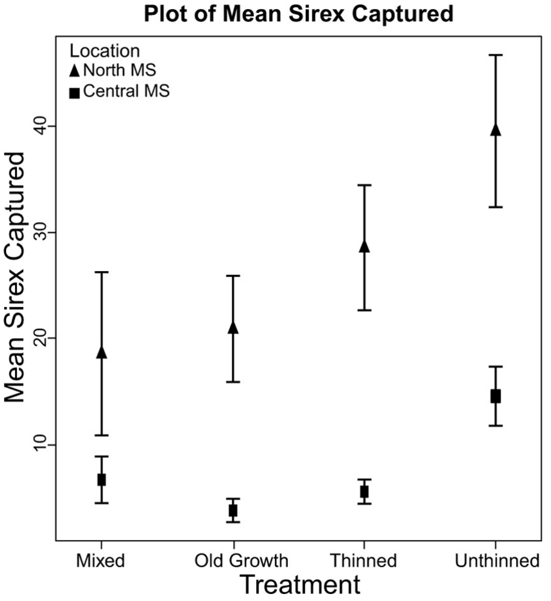

Fig. 2. Mean wood wasps (±SEM) captured per trap over 12 wk in northeastern Mississippi, fall 2011.

The GLM analysis revealed that treatment and northern spatial location had significant effects on wood wasp abundance (Table 2). Mean wood wasp abundance was ≈1.9-fold greater in unthinned pine plantations than thinned pine plantations, ≈2.2-fold greater than in mixed pine-hardwood forests, and 2.6-fold greater than in old growth forests.

Wood Wasp Flight Phenology. *S. nigricornis* was captured from 5 October to 17 December 2011. Peak wood wasp flight period (Fig. 3) occurred from late October through mid-November with 435 wood wasps caught (71% of total wood wasps captured) between all forest stand types, respectively. A single specimen of *U. cressoni* was collected during the week of 15–22 October at the Holly Springs National Forest in an unthinned pine plantation.

Forest Stand Characteristics. Forest stand characteristics (Table 3) were significantly correlated with wood wasp abundance using linear regression, but the low R^2 values means limited predictive power. PBA was significantly positively correlated with wood wasp abundance ($R^2_{adj} = 0.08$; $F_{1,46} = 5.283$; $P = 0.0261$). Tree height was significantly negatively correlated with wood wasp abundance ($R^2_{adj} = 0.13$; $F_{1,46} = 8.06$; $P = 0.007$). DBH was also negatively correlated with wood wasp abundance, although not quite significantly ($R^2_{adj} = 0.05$, $F_{1,46} = 3.71$; $P = 0.06$). There was no significant relationship with age ($R^2_{adj} = -0.002$; $F_{1,46} = 0.88$; $P = 0.35$), number of dead trees ($R^2_{adj} = 0.03$; $F_{1,46} = 2.58$; $P = 0.12$), and HBA ($R^2_{adj} = -0.01$; $F_{1,46} = 0.52$; $P = 0.47$). Multiple regression analysis of tree height, DBH, and PBA displayed the highest correlation of combined factors ($R^2_{adj} = 0.18$; $F_{3,44} = 4.54$; $P = 0.007$). Figure 4 displays the relationship between *S. nigricornis* abundance and these variables.

Table 2. Analysis of variance of GLM of wood wasps captured in Mississippi

	df	Deviance	Residual df	Residual deviation	F	Pr (>F)
Null			15	387.88		
Treatment	3	86.01	12	301.86	3.94	0.04
North	1	226.27	11	75.59	31.07	<0.001

Discussion

S. nigricornis abundance was highest in stands with greater PBA, smaller DBH, and shorter trees. PBA in all unthinned stands exceeded the recommended stocking density for *P. taeda* (<23.0 square meter per hectare) in the southeastern United States (Burkhart et al. 1986), and in three of the four stands, contained patches of standing dead pines. All thinned stands were composed of >75% pine, and all unthinned stands were >40% pine by total basal area. However, two of the unthinned stands contained numerous small DBH (7.6–10.1 cm) deciduous trees (e.g., *Liquidambar styraciflua* L. and *Carya* spp.) in stand edges, influencing overall stand composition. All old growth and mixed stands were composed of ≤40% pine and a mean pine DBH > 30 cm. Dodds et al. (2010) found that *S. noctilio* was scarce in *Pinus resinosa* Aiton stands with a mean DBH ≥ 30 cm in New York and Ontario, consistent with our findings for *S. nigricornis.* Stand composition and stocking density influenced the abundance of *S. nigricornis* in a manner similar to reports of *S. noctilio* in the northeastern United States (Dodds et al. 2010) and the Southern Hemisphere (Haugen et al. 1990).

Although not measured in this study, we observed that wood wasp capture may have been influenced by adjacent stands (≈0.5–3 km) and pine slash left on the forest floor after precommercial thinning. Composition of adjacent forest stands has been correlated with severity of attack and abundance of pest species in other studies (i.e., Kouki et al. 1997, Jactel et al. 2002). Jactel and Brockerhoff 2007 determined that monoculture stands were affected by higher herbivory rates than the same species from diverse stands in a meta-analysis of 119 studies (see also Castagneyrol et al. 2013). In the current study, we anecdotally observed that funnel traps in mixed and old growth stands that were closer to adjacent stands consisting of pine monocultures appeared to have increased captures of *S. nigricornis.* Perkins and Matlack (2002) suggest that human-mediated landscape transformation has created larger and more continuous pathways for pests to spread, and recommend that plantations be separated with nonhost barriers. It was also noted that high volumes of pine slash, left after a precommercial thinning, covered much of the forest floor in the thinned stand at Holly Springs National Forest, which is one possible reason why *S. nigricornis* abundance there was three times higher than other thinned stands. Wood wasps are xylophagous; if large volumes

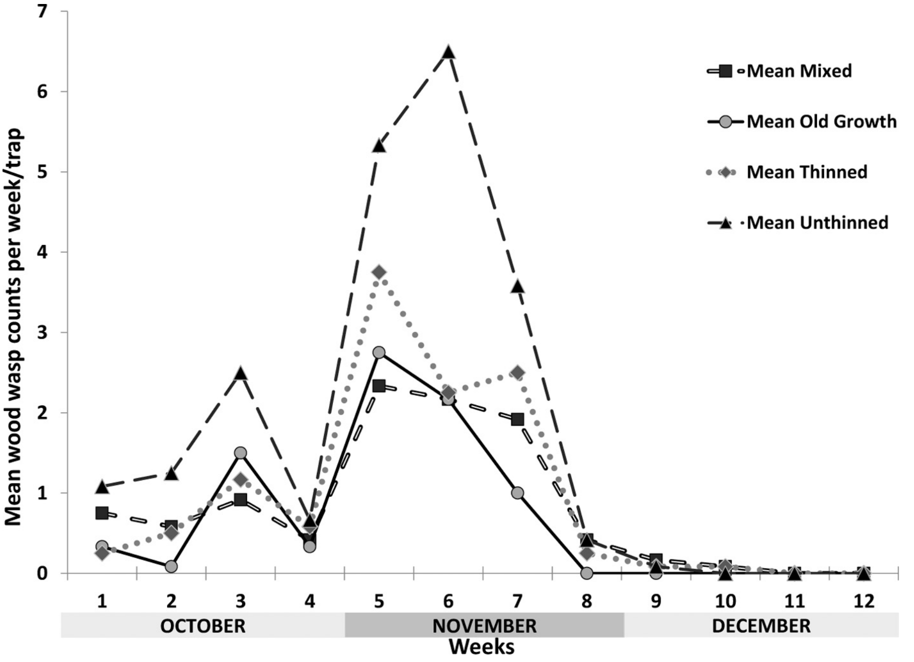

Fig. 3. Model-based estimate phenology curve of *S. nigricornis* based on actual mean capture.

of slash remain after a thinning treatment, conditions may be conducive to population increases.

Peak flight period for *S. nigricornis* in northeastern Mississippi was late October through mid-November; however, wood wasps were captured from 5 October 2011through 17 December 2011. Flight phenology of *S. nigricornis* in Mississippi were consistent with data reported from Arkansas (Keeler 2012) and Georgia (Barnes 2012), but differ from prior studies. Coyle et al. (2012) reported that *S. nigricornis* flight activity occurred from late June to late October in Minnesota. Schiff et al. (2012) report the flight activity of *S. nigricornis* ranges from late July to early October, based on 893 field-collected specimens from across the United States.

Knowing the flight phenology of *S. noctilio* is important for efficient deployment of management techniques, such as trap trees (Zylstra et al. 2010), and to understand the competitive interactions that may be occurring (Ryan et al. 2011). Currently, the flight period of *S. noctilio* in the northeastern United States is from early July through September (Zylstra et al. 2010). The effect of latitude in North America on *S. noctilio* flight activity in the southern and western portions of the continent is unknown. Cumulative degree–day models have been developed for *S. noctilio* in Ontario, Canada (flight period from early July to mid September) and for *S. nigricornis* in Louisiana (flight period from early October to late November) (Haavik et al. 2013). In South Africa, where seasons are reversed, *S. noctilio* flight phenology ranges from mid-November through April and peaks in March (equivalent to September in the Northern Hemisphere), in agreement with findings from Australia (Tribe and Cillie 2004).

The use of pine lures was successful in attracting *S. nigricornis* females in northeastern Mississippi. Apart from rearing specimens from infested host material (Barnes 2012), collecting methods for wood wasps are not highly effective, especially for male specimens (Smith and Schiff 2002, Schiff et al. 2012). Pine lures may be a tool that could be used to monitor wood wasp populations and to detect the presence of the invasive *S. noctilio.* This technique would be difficult for large-scale monitoring programs because of the labor and financial costs needed to produce the lures. In fact, the

Table 3. Means (±SEM) of wood wasps captured and forest stand characteristics of each stand type

Stand type	Σ WW caught	Stand age	μ pine DBH (cm)	% pine	PBA (m^2)	TBA (m^2)	μ tree ht (m^2)	μ no. dead pine
Unthinned	1.78 ± 0.29	15.25 ± 2.52	20.90 ± 1.94	68.5 ± 10.44	32.98 ± 2.68	37.78 ± 2.45	18.14 ± 0.71	3.43 ± 1.47
Thinned	0.95 ± 0.19	21.5 ± 1.19	23.38 ± 1.39	88 ± 5.12	15.49 ± 2.59	16.53 ± 2.77	19.26 ± 31.06	1.04 ± 0.49
Mixed	0.81 ± 0.15	47.75 ± 2.29	37.18 ± 3.25	23 ± 4.95	11.15 ± 2.01	23.42 ± 4.13	31.06 ± 1.85	0.28 ± 0.12
Old growth	0.68 ± 0.14	86.75 ± 14.65	47.06 ± 3.95	22.5 ± 6.46	14.79 ± 4.63	30.12 ± 2.09	33.21 ± 2.22	0.05 ± 0.03

Σ, total summation; μ, mean of the characteristic per circular plot; WW, wood wasp; DBH, diameter at breast height; PBA, pine basal area; TBA, total basal area.

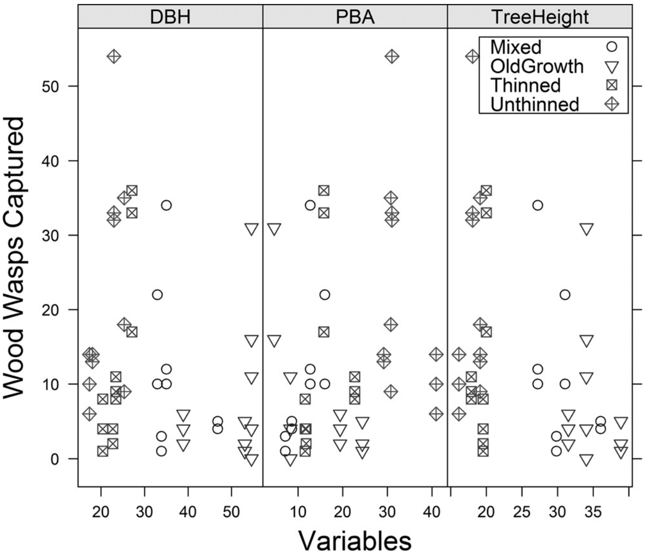

Fig. 4. Wood wasp abundance in Mississippi related to DBH, PBA, and tree height.

costs were so high that we were only able to complete one season of trapping. Although less effective, pairing synthetic lures with multiple funnel traps remains the most time- and cost-effective method for collecting wood wasps. Coyle et al. (2012) were able to catch 609 wood wasps over a 3-yr period in Minnesota using the standard *Sirex* lure. A male-produced pheromone has recently been reported that attracts both males and females, which may have applications in future field studies (Cooperband et al. 2012).

Management of pine plantations should focus on removing stressed trees, proper site selection (e.g., not planting coniferous trees in locations more suitable for deciduous trees), and reducing basal area to recommended density (i.e., *P. taeda* <23.0 square meter per hectare), thereby increasing stand vigor and reducing *S. noctilio* hazard (Burkhart et al. 1986, Dodds et al. 2007).

Fortunately, a silvicultural system that is widely practiced and understood in the southeastern United States is already in place for the southern pine beetle (*Dendroctonus frontalis* Zimmerman), a serious pest of pine plantations, and this may also serve as a useful default management plan for *S. noctilio.* Outbreaks of southern pine beetle, like those of *S. noctilio,* are associated with high stand density and reduced radial growth, both characteristics of poorly managed plantations (Coulson et al. 1974, Morgan 1989, Fettig et al. 2007). Silvicultural guidelines for reducing southern pine beetle hazard recommend thinning stands at a basal area between 16.1 square meter per hectare (70 square feet per acre) and 23.0 square meter per hectare (100 square feet per acre) in loblolly pine plantations (Brown et al. 1987, Belanger et al. 1993). Lower stand basal area increases individual tree vigor by reducing competition for sunlight, water, and nutrients. Preventing improper site selection and applying proper burning practices also reduce susceptibility of stands to insect attack (Guldin 2011). Guidelines for reducing southern pine beetle hazard are very similar to recommendations for *S. noctilio* management for pine plantations in the northeastern United States and the Southern Hemisphere (Haugen et al. 1990, Dodds et al. 2007). Land managers in the southeastern United States should adopt silvicultural practices associated with southern pine beetle prevention to reduce *S. noctilio* risk in pine plantations.

Acknowledgments

We thank Todd Mathews, Misty Booth, Bill Oswalt, and Richard Smith for assistance locating research forests; James Meeker and Wood Johnson for help with trap design; and Dave Kelly and Ecki Brockerhoff for reviewing earlier versions of the manuscript. This project was funded by U.S. Department of Agriculture–Forest Service Special Technology Development Program, the Mississippi Agricultural and Forestry Experiment Station, and the University of Georgia.

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Received 18 January 2014; accepted 19 April 2014.