Sirex noctilio in North America: the effect of stem-injection timing on the attractiveness and suitability of trap trees

Kelley E. Zylstra
USDA APHIS PPQ, kelley.e.zylstra@aphis.usda.gov

Kevin J. Dodds
U.S. Forest Service

Joseph A. Francese
USDA APHIS PPQ

Victor Mastro
USDA APHIS PPQ

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Sirex noctilio in North America: the effect of stem-injection timing on the attractiveness and suitability of trap trees

Kelley E. Zylstra, Kevin J. Dodds∗, Joseph A. Francese† and Victor Mastro†

USDA APHIS PPQ, 374 Northern Lights Drive, North Syracuse, NY 13212, U.S.A., ∗U.S. Forest Service, Northeastern Area State and Private Forestry, 271 Mast Road, Durham, NH 03824, U.S.A. and †USDA APHIS PPQ, 1398 West Truck Road, Buzzards Bay, MA 02542, U.S.A.

Abstract

1 *Sirex noctilio* Fabricius, an invasive woodwasp responsible for severe economic damage to pine industries in the southern hemisphere, is now established in the northeastern U.S.A. and portions of eastern Canada.

2 Parts of North America are considered to be high risk for *S. noctilio* invasion. Effective detection tools, including trap trees, are needed to monitor and survey *S. noctilio* populations.

3 The present study was conducted to determine the optimal time to chemically stress a tree when aiming to attract the most *S. noctilio* to the host substrate, as well as to determine which timing produced the most adult progeny. Both of these measures (host attraction and host suitability for development) support the main objectives of the study by offering improved methods for monitoring and management of *S. noctilio*.

4 Red pine (*Pinus resinosa*) and Scots pine (*Pinus sylvestris*) were treated with Dicamba at three time intervals. Multiple funnel lindgren traps were placed on these trees and, at the end of the flight season, the treatment trees were felled and brought into the laboratory. The number of *S. noctilio* caught in the traps (host attraction) and the number of *S. noctilio* emerged from the treated trees (host suitability) were determined.

5 Optimal timing of the chemical girdle was dependent on host species. Significantly more female *S. noctilio* were captured on trap trees prepared 1 month before flight (red pine and Scots pine) or prepared at flight (Scots pine) compared with other treatments. There were also significantly more females reared from Scots pine trap trees prepared at flight and red pine trap trees prepared 1 month before and/or at flight.

6 By the beginning of August, most (79%) of the *S. noctilio* for the flight season were caught in the traps at the trap trees. The sex ratio (males : females) was closer to 1 : 1 than previously reported in studies from other countries.

7 The results obtained in the present study demonstrate that timing is important when creating a trap tree with herbicide in North America, whether for the purpose of detection or as part of a biological control effort.

Keywords Detection, girdling, Hymenoptera, invasive species, *Pinus*, *Sirex noctilio*, Siricidae, survey, trap trees.

Introduction

Sirex noctilio Fabricius is a woodwasp (Hymenoptera: Siricidae) native to Eurasia, which was recently detected and found to be established in the northeastern U.S.A. and parts of eastern Canada. First detected in the U.S.A. in the autumn of 2004 in New York State near the port of Oswego on Lake Ontario (Hoebeke *et al.*, 2005), *S. noctilio* has subsequently been found over a large geographic area, including parts of Michigan, Pennsylvania, Vermont and Ontario (Dodds & de Groot, in press). *Sirex noctilio* is generally described as a secondary species

Correspondence: Kelley E. Zylstra; Tel.: +1 315 455 7352; fax: +1 315 455 7361; e-mail: kelley.e.zylstra@aphis.usda.gov

colonizing weakened or dying trees in its native range but is most notable as a primary cause of pine tree death in exotic, mainly North American pine (*Pinus* spp., L.) plantations in the southern hemisphere (Rawlings, 1948; Mucha, 1967; Madden, 1988; Tribe, 1995; Iede *et al*., 1998; Carnegie *et al*., 2005, 2006). Adding to the complexities in understanding the pestilent behaviour of *S. noctilio*, in the southern hemisphere (where the bulk of research has come from), *S. noctilio* and *P. radiata* are exotic species compared with the northern hemisphere where they are both native, thus presenting potentially different environments and challenges in monitoring and control.

Female *S. noctilio* carry a symbiotic fungus, *Amylostereum areolatum* (Fr.) (Clark, 1933; Talbot, 1964; Gaut, 1969), in mycangia, which are specialized sacs located at the base of the ovipositor (Spradberry, 1973). A pair of mucus glands in the abdomen of the female produces a secretion that prepares the host tree for colonization by the fungus. The female begins the process of ovipositing on the host tree by drilling several radiating holes from the initial puncture point where fungal spores, mucus and (but not always) eggs are deposited. The developing larvae then feed on the fungus when mining through the sapwood. The majority of *S. noctilio* have a 1-year lifecycle, although some larvae take more than 1 year to fully develop in areas where the pest is currently distributed in North America (P. de Groot, personal communication). It is the combined action of the mucus and fungus that eventually kills the host tree (Coutts, 1969). Although the levels of tree mortality that *S. noctilio* will cause in North America remain unknown, the development of effective survey methods, including trap trees, is an important step for determining its current range, providing early detection in new areas, and as a release mechanism for the biological control agent *Beddingia siricidicola*.

The use of trap trees (or lure trees) was developed in Australia to make the detection of *S. noctilio* more efficient (Madden, 1971; Madden & Irvine, 1971). The serendipitous discovery that *S. noctilio* was attracted to chemically-stressed trees resulted in a strong survey tool for detecting low level populations (Minko, 1981). *Sirex noctilio* preferentially colonizes trees in a weakened condition (Neumann & Minko, 1981) and this biological characteristic makes artificially stressing trees to attract dispersing adults an effective survey tool. Trap trees, created by basal stem-injections using Dicamba (3,6-dichloro-2-methoxybenzoic acid) were further developed into a component of integrated pest management in Australia (Neumann *et al*., 1982). This established trap trees as an improved method for detecting *S. noctilio* in commercial forests, at the same time as providing a release point for *B. siricidicola* (Bedding & Aukhurst, 1974; Neumann *et al*., 1982). Trap trees have subsequently become a critical component of integrated pest management programmes targeting *S. noctilio* throughout the southern hemisphere.

Because of the logistical complexities of setting trap trees (e.g. private property access, legal liability), detection efforts with respect to *S. noctilio* in North America have relied upon semiochemical-baited multiple funnel or intercept panel traps (Dodds & de Groot, in press). Stem-injected (chemically girdled) trap trees could provide a more reliable detection method for *S. noctilio* in North America, although their use has not been tested in this continent. Compared with the southern hemisphere's commercial, non-native forests, North American forests have diverse insect and fungal communities that may compete for stressed trees (i.e. trap trees), potentially limiting their effectiveness in the detection of *S. noctilio* and management efforts if not timed appropriately.

In the northeastern U.S.A., *S. noctilio* flight starts at the beginning of July and continues throughout September. Because other pine-inhabiting native and exotic insects are active in the early spring through much of the summer, there was a concern these species and associated fungi would compete for trap tree resources with *S. noctilio*. In addition to the concern regarding native organisms, it was important to determine the maximum time before flight that trap trees could be set to allow natural resource managers to have the most time possible to spread out workloads throughout the season. Therefore, we developed a study to determine the optimal time of year to stem-inject (chemically girdle) trap trees and evaluate attraction for S. *noctilio* in the northeastern U.S.A. The most effective of the three girdling times was determined by measuring *S. noctilio* attraction to trees and reproductive success within those trees for two species of pine (*Pinus resinosa* A. and *Pinus sylvestris* L.). The optimal time was determined by how successful the trap tree was at attracting *S. noctilio* (host attraction), as well as how suitable the trap tree was for the development of progeny (host suitability). It was also important to examine how suitable the host substrate is for the development of the progeny because trap trees that can support more larvae increase the number of release points for the spread of *B. siricidicola*, thus making management efforts more effective.

Materials and methods

Study sites

Seven Scots pine (*P. sylvestris*) and eight red pine (*P. resinosa*) sites, as well as one mixed Scots/red pine site, were chosen within an 80 km radius of Syracuse, New York, in Onondaga and Oswego counties. At the latter field site, the two host species were not intermixed within the site but were planted as two different stands, and each stand was separated by at least 300 m. Each field site was at least 1 ha in size with stands dominated by either *P. resinosa* or *P. sylvestris.* Most sites were even-aged (approximately 30–40 years old) pure stands, overstocked, and generally unmanaged subsequent to stand initiation (Table 1). In most cases, each site contained only one replicate of the treatments. However, there were two sites that contained two replicates, one of which contained both a red pine and Scots pine replicate (the mixed species site described above), where each replicate was separated by at least 100 m. There was also one site that contained three replicates, each separated by at least 100 m. A total of ten replicates of the study were conducted in Scots pine and ten in red pine. With the exception of the one mixed site described above, there were no other sites where treatments were mixed between the species.

Girdling treatments

Each treatment group consisted of three adjacent trees of the same species and similar diameter at breast height (DBH),

Table 1 Stand attributes, estimates of *Sirex noctilio* activity and adult sex ratios from study sites located in central New York

Host species	Site number	Average DBH	Trees (ha)	Total stand BA (m^2/ha)	*Sirex* killed BA (m^2/ha)	% of dead pine BA killed By Sirex	Number of *Sirex* killed trees (ha)	Sex ratio of *Sirex noctilio*/site (male : female)
Red pine	1	30.9	894	49.2	0.93	51.7	16	1 : 1
Red pine	2	22.3	1219	37.7	1.6	41.7	81	1.6 : 1
Red pine	3 + 4	20.2	1430	47.1	0.5	14.5	33	2.3 : 1
Red pine	5	23.9	1202	49.5	0	0	0	2 : 1
Red pine	6	20.9	1479	50.7	0	0	0	2.1 : 1
Red pine	7	21.4	1219	48.5	0	0	0	3.8 : 1
Red pine	8	26.9	1154	52.3	0.5	7.9	33	1 : 1
Red pine	9	27.9	926	51.8	0	0	0	3.7 : 1
Red pine	10	20.1	1381	46.1	0	0	0	1 : 1
Scots pine	11	22.9	1040	38	0.9	16.4	49	4.6 : 1
Scots pine	12	20.2	1251	40.1	4	59	163	1.9 : 1
Scots pine	13	19.6	1137	36.6	0.4	10.1	49	3 : 1
Scots pine	14	20	1007	32.8	0.8	9.1	33	9.9 : 1
Scots pine	15	–	–	–	–	–	–	5.2 : 1
Scots pine	16	18	1089	28.7	2.7	41.6	146	3.7 : 1
Scots pine	17	20.1	1024	33.4	1.3	45.1	33	—
Scots pine	18	23.2	1023	45.3	0.6	13.9	49	3.2 : 1
Scots pine	19	22.9	894	36.8	0.6	32.1	33	5.8 : 1
Scots pine	20	21.6	1284	51	0.5	4	33	3.7 : 1

DBH, diameter at breast height; BA, basal area.
Sites 3 and 4, 5 and 18, and 14, 15 and 16 are combined replicates on the same geographic field site.
Zero females and five males emerged out of material sampled from site #17.

which all received the same treatment. Each treatment group was assigned one of four treatments: (i) nongirdled control; (ii) girdled 3 months (2–6 April 2007) prior to the anticipated *S. noctilio* flight; (iii) girdled 1 month (3–8 June 2007) before flight; and (iv) girdled at the time of anticipated flight (9–13 July 2007). Treatment groups are hereafter referred to as the control, April, June and July girdles. Each treatment group was spaced approximately 50 m apart within a site. Whenever possible, suppressed and overtopped trees were selected for use as trap trees. However, in many stands, these trees were not available and larger intermediate and codominant trees were used as trap trees.

Holes were drilled (approximately 5–10 cm deep, depending on diameter of the tree) every 10 cm around the circumference of each tree at an approximate height of 46 cm, using a gas-powered drill (Stihl Inc., Virginia Beach, Virginia) fitted with a drill bit 30.5 cm long × 1.3 cm in diameter (Irwin Industrial tools, Dewitt, Nebraska). Holes were drilled at approximately 45° angles to act as reservoirs for herbicide and provide an uptake point. We stem-injected 4.0 mL of a 1 : 1 solution of water to Banvel® (48.2% dimethylamine salt of Dicamba) (BASF Corp., Florham Park, New Jersey) into each drilled hole. The approximate amount of active ingredient (A.I.) injected into each hole was 0.96 mL; 1.04 g, which was the amount used in preliminary studies (V. Mastro, unpublished data). No drill holes or herbicide treatment were applied to the control trees.

Tree and stand assessments

Prior to girdling, DBH was measured and photos of the crowns of each treatment group were also taken from a fixed point approximately equidistant from each tree. Only trees that appeared to be healthy (i.e. green crowns, no other woodboring or bark beetle activity present, etc.) upon visual inspection were chosen as study trees. Attention was also given to choosing trees of approximately the same DBH. Assessments of the trees' appearance were made monthly throughout the study to track the overall health or decline of the study trees. For each assessment, crown colour (green, yellow, red, brown), insect activity (bark beetles and cerambycids), and any symptoms or signs of *S. noctilio* (resin beading, adults) were recorded. To maintain consistency throughout the sampling period, one person was responsible for all tree evaluations. Photographs of the treatment group crowns were taken from the fixed point at each assessment to document treatment effects at 1-month intervals from the beginning until the end of the study.

Fixed radius plots (8 m in radius) were used to estimate forest stand characteristics from each site. The number of plots varied among sites because of size constraints but at least four plots were placed in each stand. In each plot, tree species, DBH, crown class, tree health (i.e. living or dead) and the presence of *S. noctilio* in trees were recorded. Plot level data was expanded to a per hectare basis for comparison among sites, employing methods similar to those previously described by Husch *et al*. (2003).

Host attraction

On each tree of a treatment group, a 12-unit Lindgren multiple-funnel trap fitted with a wet collection cup was hung (with the top approximately 6 m above the ground and 0.3 m from the tree bole) to catch incoming *S. noctilio*. Preliminary trapping results using sticky panel traps suggested this was the optimal height to capture *S. noctilio* (K. E. Zylstra, unpublished data). Propylene glycol was used as preservative in the collection cup. Traps were hung from a total of 240 trees (20 replicates, four treatment groups of three trees with a trap each). Traps were checked once every 2 weeks from 26 June 2007 to 21 September 2007. At each visit, the contents of each trap cup were strained using a paint filter to separate captured insects from the collection liquid. Specimens from the collections were placed in a Whirl-Pak® sampling bag (Nasco, Fort Atkinson, Wisconsin) and covered with ethanol for preservation until identification and sorting could be conducted. Laboratory processing of trap samples comprised of sorting Siricidae and all suspect *S. noctilio* from other trap contents. All *Sirex* spp. were preliminarily identified and species were confirmed by E. R. Hoebeke (Cornell University, Ithaca, New York).

To compare the attraction of *S. noctilio* among treatments, trap catch was summed for each treatment group beginning with sampling period 9–23 July 2007 and ending at the conclusion of the study on 21 September 2007. Because the three trap trees that constituted a treatment group were not independent replicates, trap catches from each trap tree were combined to provide a total number for the group. Although trapping began before 9 July, these collections were not included in the analysis because the final girdle period did not occur until the week of 9 July. Data were analysed using a generalized linear mixed model (Proc GLIMMIX) via maximum likelihood estimation technique, and blocked by site. The Laplace likelihood approximation method was employed. Sites were a random factor and treatment was a fixed factor. Data were modelled using the negative binomial function with log link (SAS, version 9.2; SAS Institute, Cary, North Carolina). Tukey-Kramer honestly significant difference ($\alpha = 0.05$) was used to compare differences in *S. noctilio* caught between treatments. Flight phenology of *S. noctilio* in New York was also investigated using the trap catches. Trap catches were pooled from all treatments and depicted as the number of individuals captured in all traps during each sampling period.

Host suitability

At the end of the flight season, two of the three trees from each treatment group were randomly chosen for sub-sampling and felled during November 2007. Approximately ten billets (length 55 cm) from 1.8 m from the base of the tree to 9.1 m along the bole of each tree were brought to the APHIS PPQ laboratory (North Syracuse, New York) for insect rearing. This section of the tree was selected for sampling based on preliminary results suggesting this portion of the tree produced the most adults. The end of each billet was sealed with clear waxlor water-based paint (Willamette Valley Co., Eugene, Oregon) to prevent desiccation. All billets from one tree of each treatment group were immediately brought into the laboratory and placed into barrels for rearing. The billets from the second tree of each treatment group were left outside in a storage shelter under ambient winter and spring temperatures and later moved into the laboratory for rearing in May 2008.

The rearing laboratory was maintained under an LD 9 : 15 h photocycle at 21.1°C and approximately 50% relative humidity, using fluorescent overhead lights. Siricids began emerging in late February 2008, approximately 3 months after the infested material was brought into the laboratory. *Sirex noctilio* and native Siricidae were collected weekly from the barrels until no adults were found for several consecutive collections (late May). All species of siricids were identified and the sex of each *S. noctilio* recorded for determination of sex ratios from each site. The second tree from each treatment group was moved into the laboratory for emergence in early June. Siricid emergence from the second rotation started mid-June and continued until August in the laboratory. There was no evidence that *S. noctilio* had emerged from the second tree of each group before being placed into rearing barrels.

Statistical analysis for the emergence data was performed in a similar manner to the host attraction data. The number of females emerged from each treatment was analysed using a generalized linear model with sites as a random factor and treatment as a fixed factor. Tukey–Kramer honestly significant difference ($\alpha = 0.05$) was used to compare differences among the treatments. Student's t-test was used to compare the combined mean number of *S. noctilio* adult females trapped or emerged by host species.

Results

Tree and stand assessments

Qualitative assessment of trees demonstrated differences among the treatment groups for a number of variables. Both Scots and red pine showed an almost immediate response to herbicide treatment. Within 3–4 weeks, tree crowns began to fade and noticeable signs of tree stress were evident. Treatment trees girdled in April had crowns with no needles by the time that *S. noctilio* was in flight. These treatment trees were also most heavily colonized by bark beetles (Scolytinae) and longhorn beetles (Cerambycidae). We found that trees girdled 1 month before flight (June) showed the most symptoms of attack (i.e. resin beads), had the most *S. noctilio* females actively probing for host assessment and/or oviposition, and trees had brown crowns for the entirety of the flight season. Treatment trees girdled at the beginning of the flight period (i.e. July) had crowns that were just turning yellowish–brown by the end of July (at the approximate time of peak flight activity for *S. noctilio*) and had the least amount of noticeable native insect activity.

Red and Scots pine stand characteristics for each study site are summarized in Table 1. The average diameter of trees from the red pine study sites was in the range 20.1–30.9 cm. All red pine stands were overstocked, with basal area estimates in the range 37.7–52.3 m^2/ha. *Sirex noctilio* activity was relatively low in most stands, with half the sites having no signs of the invasive insect present. The other four sites had 16–81 trees per ha showing signs of *S. noctilio* attack. The average diameters of Scots pine stands were smaller than red pine, with diameters in the range 18.0–23.2 cm. Stand basal area of Scots pine stands were in the range 28.7–51.0 m^2/ha. Compared with red pine study sites, there were more *S. noctilio* attacked trees found in Scots pine study sites. All Scots pine stands had some *S. noctilio* activity, with a range of 33–163 trees attacked per hectare.

Table 2 Host attraction: mean ± SEM number of *Sirex noctilio* females captured in the different girdle age treatment groups

Host species	Control	April	June	July	*P*-value
Red pine	0.24 ± 0.16^{a}	0.33 ± 0.18^{a}	1.79 ± 0.61^{b}	$0.73 \pm 0.31^{a,b}$	0.002
Scots pine	2.83 ± 0.90^{a}	$5.90 \pm 1.71^{a,b}$	10.13 ± 2.80^{b}	7.25 ± 2.06^{b}	0.0032

Treatments with the same superscript letter are not significantly different.

Host attraction

A total of 38 *S. noctilio* were captured from 9 July to 21 September in traps hanging from red pine. An additional nine were captured in the period before 9 July from the treatments, although these were excluded from these analyses. There were significant differences in the number of *S. noctilio* captured at red pine trap trees girdled at different dates ($F = 6.43$; d.f. = 3, 27; $P = 0.002$). The June girdled trees were similar to July girdled trees but significantly different from the control and April girdled treatments (Table 2).

A total of 308 *S. noctilio* were captured in traps hanging from Scots pine trap trees. An additional 26 *S. noctilio* were captured before the dates used to compare treatment effects. Girdling date treatments significantly influenced the number of *S. noctilio* captured at Scots pine trap trees ($F = 5.87$; d.f. = 3, 27; $P = 0.0032$). Trees girdled in June and July were significantly more attractive to *S. noctilio* females than control trees. April girdled trees were not significantly different from control, June or July girdled trees (Table 2).

When samples from red pine and Scots pine stands were pooled by each species, overall mean ± SEM trap catch of *S. noctilio* for red pine (3.80 ± 1.28) and Scots pine (30.80 ± 6.02) were significantly different ($t = 4.38$; d.f. = 18; $P = 0.0004$).

The initial *S. noctilio* capture for 2007 occurred between 26 June and 9 July, with 60.3% of the overall catch occurring during a 2-week period in July 2007. Of all *S. noctilio* captured over the course of the study, 79.0% (77% on Scots pine and 81% on red pine) were caught by 8 August (Fig. 1). A second, smaller peak occurred between 8 and 20 August. The median catch occurred between 9 and 24 July. Several other species of siricids were also caught throughout the trapping study, including *Sirex nigricornis* Fabricius, *Sirex edwardsii* Brullé, *Urocerus albicornis* Fabricius, *Urocerus cressoni* Norton, *Tremex columba* Linnaeus and *Xiphydria* spp., although these were not included in any analysis.

Host suitability

There were a total of 2433 *S. noctilio* adults that emerged from the treatment material sampled from red pine (232 females, 457 males) and Scots pine (392 females, 1352 males). The

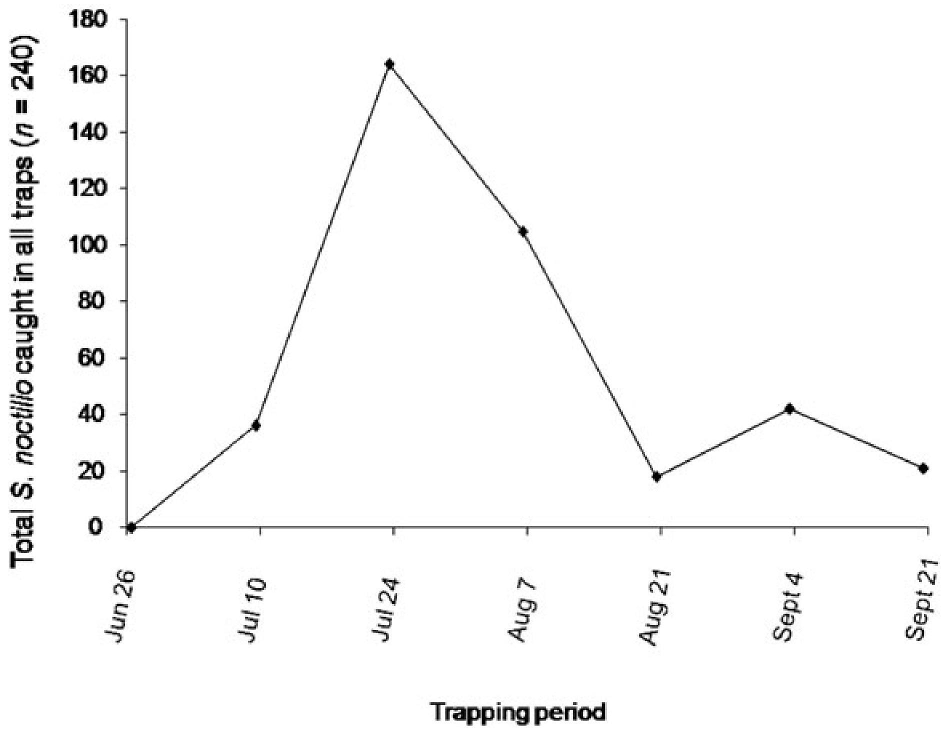

Figure 1 Total number of *S. noctilio* caught in all traps ($n = 240$) in 2007. Dates represent the final day of each 2-week trapping period.

Table 3 Host suitability: mean ± SEM number of *Sirex noctilio* females reared from the different girdle age treatment groups

Host species	Control	April	June	July	*P*-value
Red pine	1.80 ± 0.70^{a}	0.10 ± 0.10^{a}	8.30 ± 2.74^{b}	12.4 ± 4.03^{b}	0.0001
Scots pine	1.06 ± 0.74^{a}	0.49 ± 0.38^{a}	$5.98 \pm 3.78^{a,b}$	18.06 ± 11.23^{b}	0.0014

Treatments with the same superscript letter are not significantly different.

date when trees were girdled had a significant effect on the abundance of *S. noctilio* adults from sampled red pine and Scots pine. Red pine trees girdled at 1 month before (June) or at flight (July) produced significantly more *S. noctilio* females than the control or April treatment date ($F = 10.23$; d.f. = 3, 27; $P = 0.0001$; Table 3). Likewise, Scots pine trees girdled at flight (July) also produced significantly more *S. noctilio* females than the control and April treatment but not the June girdle treatment ($F = 6.85$; d.f. = 3, 27; $P = 0.0014$; Table 3).

When samples from red pine and Scots pine stands were pooled by each species, the overall mean ± SEM emergence of female *S. noctilio* for red pine (8.56 ± 2.74) and Scots pine (11.23 ± 2.74) were not significantly different ($t = 0.69$; d.f. = 18; $P = 0.5006$). The mean number of males and females emerged in red pine was 13.4 and 8.1, respectively (ratio 1.7 : 1). The mean number of males and females emerged in Scots pine was 35.6 and 14.0, respectively (ratio 2.5 : 1).

Discussion

In the southern hemisphere, trap (or lure) trees are critical tools for managing *S. noctilio*, acting both as a means of detection and inoculation points for *B. siricidicola*. To date, no effective semiochemical lure has been developed that has been as attractive as a stem-injected trap tree (K. Böröczky & D. Crook, unpublished data) in the northeastern U.S. Optimal trap tree methods for the northeastern U.S.A. may differ from those used in the southern hemisphere as a result of variation in such factors as climate, host tree species, stand conditions, natural enemy complexes, and populations of pine-inhabiting insects and microorganisms. Determining effective trap tree methodology for *S. noctilio* in North America is important to the development of effective integrated pest management plans that include population monitoring/detection and potential biological control programmes.

Host attraction

We found that the best time to stem-inject (using Dicamba) a host tree with the aim of capturing the greatest numbers of *S. noctilio* for detection purposes in New York was 1 month before flight (i.e. June) for red pine and either 1 month before (June) or at flight (July) for Scots pine. These are similar to the findings reported in Australia regarding timing when a mechanical girdle was used (Madden, 1971). Mechanical girdling removes the cambium and phloem layers of the tree (thus preventing the transport of carbohydrates and water), whereas the mode of action of Dicamba destroys plant tissue through uncontrolled cell division and growth (mimicking auxins). However, basal stem injections are more effective and replaced mechanical girdling early on in the southern hemisphere for monitoring and management.

Higher numbers of *S. noctilio* were captured on Scots pine compared with red pine in the present study. In addition, the forest stand surveys showed that *S. noctilio* was more common and killed more trees in Scots pine stands compared with red pine sites. Scots pine is a native host for *S. noctilio* and an exotic pine in the U.S.A. that originates from Europe. Scots pine was once a popular Christmas tree in North America and planted in tree farms throughout the currently infested area. Many of these Scots pine Christmas tree farms are now abandoned, in poor condition, and have never received intermediate silvicultural treatments to improve growing conditions. As a result, these stands may be a more attractive and exploitable resource for pine-infesting insects, such as *S. noctilio*. Interestingly, there was no statistical difference in the mean number of *S. noctilio* that emerged from the two host species in the present study. The fact that we found no difference in the number of females emerging from the two host species used in the present study suggests that both hosts can be successfully utilized by the woodwasp as a developmental substrate.

A beneficial characteristic of trap trees in the southern hemisphere is the length of time they are suitable for *S. noctilio* oviposition (Minko, 1981). A tree dying slowly over a long period of time is ideal but, unfortunately, in the northeastern U.S.A., trees showed signs of death much quicker (within 3–4 weeks) than described in the southern hemisphere: 3–11 months (Minko, 1981); 4 months (Neumann *et al*., 1982). It is unknown why tree death was quicker in Scots and red pine compared with that described elsewhere, but it could be the result of variation in tree species physiology, the effects of colonizing insects and microorganisms, or the slightly higher levels of herbicide used in the present study. At least 50 species of insects were captured in the traps hanging from the trap trees, suggesting a large community of insects was visiting this ephemeral resource. The fungal communities of the trap trees are unknown, but bluestain fungi were common in trees that were removed from the field and used for rearing *S. noctilio*. The activity of these organisms probably quickened tree death in North America compared with the southern hemisphere where insect and fungal competitors for trap tree resources are limited.

Peak flight of *S. noctilio* occurred earlier than the peak flights of native siricid species, with very little overlap in flight season between *S. noctilio* and the native, pine-boring, siricids (data not shown). Of the species of pine-boring siricids common in the northeast, there was a bias towards *S. noctilio* emerging from billets removed from experimental trees. It is possible that a higher number of native species would have emerged from experimental billets if given more time but, because of space constraints, billets were discarded after 3 months in the laboratory. It is also possible that the removal of trees from the field in November negatively affected native siricids that were only in the early stages of development within the tree. Most native, pine-inhabiting siricids are active in the autumn (data not shown) so it is likely oviposition would have only recently occurred when trees were felled.

Host suitability

The emergence data showed that chemically girdling a tree 1 month before (red pine) or at flight (red and Scots pine) was optimal for producing more adult *S. noctilio* compared with other girdling dates. There was a trend for more trap captures of females in the June treatments, although there was no statistical difference between the June and July girdle treatments. Despite no statistical difference being found, it is interesting that we caught fewer females in traps in the July treatment group yet had more female progeny produced from that treatment. Several mechanisms could be responsible, including wood moisture content, competing insects and microorganisms, or greater *S. noctilio* oviposition on these trees. It is not possible to estimate the number of *S. noctilio* eggs laid into trap trees to assess survivability. It is uncertain whether females were attracted to the June girdled treatments but, upon probing, found the oviposition substrate unsuitable or whether larvae were less likely to develop to adulthood in this treatment group because of the timing or effects of the girdle. Female *S. noctilio* could have preferentially oviposited on July girdled trees or survivability may have been higher compared with the other treatments.

Previous research has shown that the sex ratio of *S. noctilio* always favours the males, with male/female ratios varying from 7 : 1 (Morgan & Stewart, 1966), 10 : 1 (Morgan, 1968) and 12 : 1 (Hurley *et al*., 2008). Collett and Elms (2009) summarized the emergence data from 1998 to 2006 for sites across Victoria and found that two-thirds of the *Sirex* were males and one-third were females. Our findings suggest a much lower male/female ratio than previously reported in the literature, with an average ratio of 1.7 : 1 in red pine and an average ratio of 2.5 : 1 in Scots pine. *Sirex noctilio* is haplodiploid and if a female does not mate then only males are produced (Neumann *et al*., 1987). If mating occurs, females can produce both male and female offspring. It is possible that overall landscape differences between the northeastern U.S.A. and the large plantation pine stands of the southern hemisphere play a role in the observed differences. Pine stands in the northeast are small, scattered among urban and pastoral land, and are often mixed with hardwoods. Pine stands in the southern hemisphere where *S. noctilio* has invaded tend to be large, monotypic plantations. Perhaps females are able to find males to mate with more readily in the northeastern system because of the nature and size of the pine stands. Host substrate limitations, as a result of habitat fragmentation, may actually increase male and female interactions. Additionally, the forest conditions might be considered ‘favourable’ to *Sirex noctilio* populations, as was alluded to by Morgan and Stewart (1966), where sex ratios closer to one were described when populations were increasing, or possibly owing to how well established *S. noctilio* is in the stand. Thus, populations of *S. noctilio* within these pockets of pine may be well established because we observed ratios closer to one. A ratio closer to one is more preferable and more effective for management using the biological control agent because nematodes are only spread by females (Collett & Elms, 2009).

Management recommendations

Unfortunately, it will not be possible to eradicate *S. noctilio* from North America. It is currently unknown what kind of impact *S. noctilio* has (or will have) as populations spread in the northeast or into other North American pine ecosystems. Consequently, it is imperative to develop effective, reliable detection tools to monitor *S. noctilio* populations as it spreads from the currently known infested area.

Trap trees offer a more effective, sensitive survey tool than currently available semiochemical-baited traps. Artificially baited traps may be more easily deployed and maintained but, until lures are improved, there is still a high likelihood of false negatives occurring during surveys. Although this concern is not completely removed with trap trees, it is probably reduced because of the concurrent survey opportunities (trap catches, symptoms of *S. noctilio* attack on trees, and rearing from trees) and the stronger cues that each trap tree provides to natural resource managers.

Timing has important implications for *S. noctilio* trap trees. To optimize trapping efforts, *S. noctilio* trap trees should be girdled 1 month before and/or up until the beginning of *S. noctilio* flight. To produce the most brood, trap trees should be girdled 1 month before (red pine) or at the beginning of flight (red and Scots pine). The time chosen to girdle trees is dependent on what the objectives are for trap trees and the host species. If detection is the focus, then earlier girdle times should be used (June) because trap trees caught higher numbers of *S. noctilio* during this period and also showed the most obvious signs of attack on tree boles. If progeny production is important, as it is for a biological control programme, then later girdling dates (July) should be implemented. It was generally apparent from the data that early (April) girdling times are not optimal and should be avoided if possible.

Data on *S. noctilio* flight phenology are important not only for increasing our understanding of the basic biology and behaviour of the woodwasp in the northeastern U.S.A, but also because they have important implications for survey and detection efforts. Although there will undoubtedly be some latitudinal variation, it appears to be critical that survey efforts using trap trees are in place by June to capture the initial *S. noctilio* flight. If natural resource professionals cannot deploy trap trees as a survey tool, traps baited with an artificial lure should be set by late June or early July (at least in the northeastern U.S.A.) to optimize trap catches and save resources in survey efforts.

So that we are best equipped to manage *S. noctilio* and protect North American pine, both for economic and ecological purposes, it is clear that there needs to be continued research (e.g. host preference, dispersal, community interactions, etc.), both with respect to the current distribution of *S. noctilio* and the regions to which it may spread. North American pine ecosystems vary considerably and it is likely that the methodology developed in the present study will need to be modified as *S. noctilio* enters new areas and attacks new host species to allow provision of the most effective management programme.

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