Forestry Advance Access published October 22, 2015

Forestry An International Journal of Forest Research

Institute of Chartered Foresters

Forestry 2015; **0**, 1–6, doi:10.1093/forestry/cpv039

Sirex woodwasp range expansion in Australia: performance and parasitism on two commercial pine species

Helen F. Nahrung[1,2]*, Michael Ramsden[3] and Manon Griffiths[2]

[1]*Forest Industries Research Centre and Faculty of Science, Health, Education and Engineering,*
The University of the Sunshine Coast, Maroochydore DC, Queensland 4558, Australia
[2]*Queensland Department of Agriculture and Fisheries, Joe Baker Street, Dutton Park, Brisbane, Queensland 4012, Australia*
[3]*HQPlantations Pty Ltd, Science group, Fraser Road, Gympie, Queensland 4570, Australia*

*Corresponding author. E-mail: hnahrung@usc.edu.au

Received 5 May 2015

Sirex woodwasp was detected in Queensland in 2009 and rapidly established in softwood plantations (*Pinus radiata* and *P. taeda*) in southern border regions. Biocontrol inoculations of *Deladenus siricidicola* began soon after, and adults were monitored to assess the success of the programme. Wasp size, sex ratios, emergence phenology and nematode parasitism rates were recorded, along with the assessment of wild-caught females. Patterns varied within and among seasons, but overall, *P. taeda* appeared to be a less suitable host than *P. radiata*, producing smaller adults, lower fat body content and fewer females. Sirex emerging from *P. taeda* also showed lower levels of nematode parasitism, possibly due to interactions with the more abundant blue-stain fungus in this host. Sirex adults generally emerged between November and March, with distinct peaks in January and March, separated by a marked drop in emergence in early February. Temperature provided the best correlate of seasonal emergence, with fortnights with higher mean minimum temperatures having higher numbers of Sirex emerging. This has implications for the anticipated northward spread of Sirex into sub-tropical coastal plantation regions. Following four seasons of inundative release of nematodes in Queensland, parasitism rates remain low and have resulted in only partial sterilization of infected females.

Introduction

The native Eurasian woodwasp, *Sirex noctilio* (Hymenoptera: Siricidae) (Sirex) along with its symbiotic fungus, *Amylostereum areolatum*, was detected in Tasmania, Australia in 1952, after its first exotic establishment in New Zealand in 1900 (Carnegie and Bashford, 2012). By 1961, it was present on the Australian mainland, spreading slowly west to Mediterranean-climatic regions (1977), north to New South Wales (1980) and eventually to southern Queensland in 2009 (Carnegie *et al*., 2005; Carnegie and Bashford, 2012). The timing of Sirex reaching Queensland had been predicted remarkably accurately 20 years previously (Eldridge and Taylor, 1989; Carnegie *et al*., 2005). Despite successful biological control by the commercially produced nematode, *Deladenus siricidicola*, and the establishment of several species of parasitoids, Sirex continues to spread within Australia at a rate of 4–30 km/year (Eldridge and Simpson, 1987; Carnegie *et al*., 2005) and has not yet filled its predicted geographic range (Carnegie *et al*., 2006). Temperature is thought to explain variability in spread rates of *S. noctilio* (Lantschner *et al*., 2014), whereas outbreaks relate more to life-history's characteristics (Aparicio *et al*., 2013). The most serious outbreak in Australia occurred over 20 years ago, when over 5 million *Pinus radiata* trees were killed in the Green Triangle region of southern Australia (Haugen, 1990), although several minor outbreaks have occurred in New South Wales more recently (Carnegie and Bashford, 2012).

Unlike the majority of pine-growing regions of Australia where *P. radiata* is the main softwood species (Gavran, 2014), the temperate southern downs Queensland plantations within Passchendaele State Forest predominantly comprise a mixture of *P. radiata* and *P. taeda*. Establishment of Sirex in this region exposes both of these host taxa to attack: both species are considered equally susceptible to Sirex (Carnegie *et al*., 2005). If Sirex moves further northward in Queensland, large areas of previously unencountered host taxa (hybrids between *P. elliottii* var. *elliottii* and *P. caribaea* var. *hondurensis*) will also be threatened. Here, we compared the performance of Sirex in *P. taeda* and *P. radiata* by measuring adult size, sex ratios and fat bodies of adults collected both during management operations and as structured surveys. We also examined the efficacy of biological control nematodes between taxa when inundative nematode inoculation began at a commercial management scale in 2012.

The arrival of Sirex in Queensland also provided the opportunity to examine a newly establishing population at its range front and to look for ecological or behavioural change in the population over time. For example, because of haplo-diploidy, expanding populations of Sirex are expected to have a high male bias, with sex ratios becoming less male biased over time as mate availability increases post-colonization (Ryan and Hurley, 2012). We compared sex ratios over four seasons and also examined emergence patterns over time (within and among seasons) and relationships with biotic and abiotic factors.

Materials and methods

Pinus radiata and *P. taeda* were sampled across four seasons (2011–2012, 2012–2013, 2013–2014 and 2014–2015) within the Passchendaele region of southern Queensland, an area comprising 1951 ha of plantations (Michael Ramsden personal communication). All samples were collected within ~13 km of each other, with the two taxa often co-planted within forest compartments, such that landscape effects were unlikely to influence our results. However, sampled *P. radiata* trees were older (mean = 19 ± 0.1 years) than *P. taeda* (11 ± 0.1 years; *t*-test, $t_{92} = 5.78$, $P < 0.001$), although their mean diameter at breast height (DBH) did not differ (17.5 ± 0.5 and 16.7 ± 0.5 cm, respectively; $t_{91} = 1.41$, $P = 0.26$). Within each season, the two taxa were poisoned, felled, inoculated, collected and housed under the same conditions as each other. Dicamba200 (1 mL/10 cm DBH) was used as the herbicide for TTP establishment in the first three seasons, and Glyphosate360 (1 mL/10 cm DBH) was used in the final season for operational reasons. Billets (~70 cm in length) cut from around the mid-bole of felled trees from trap tree plots established the preceding season following recommended guidelines (Neumann, 1987) were collected in October 2011, 2012, 2013 and 2014 and housed in emergence bins (44-gallon drums with the open end covered with gauze netting) within an emergence facility at Passchendaele. Generally, each bin contained two billets from one tree so that individual tree characteristics could be related to emerging adults (Table 1). Adults were collected alive from bins every 1–3 days, labelled and frozen for later assessment. Because the presence of bark beetles and blue-stain fungi has been implicated in reduced Sirex performance and nematode parasitism rates (Hurley *et al.*, 2012b; Yousuf *et al.*, 2014c), a visual assessment of blue-stain (proportion of cut end surface discoloured, scored as 0; 1–25 per cent; 26–50 per cent; 51–75 per cent; >75 per cent), and the severity of *Ips grandicollis* infestation (number of emergence holes scored as none 0; mild 1; moderate 2; severe 3), was made for each billet. Female Sirex were also collected from within plantations in each season either by trapping with intercept traps baited with kairomone lures (SIRNOC lures) or hand-picked live from trees. These were measured and dissected to compare with billet-emerging adults in each season.

All Sirex adults that emerged from billets ($n = 1517$, across all seasons) were assessed to compare size (head capsule width, measured with a digital vernier calliper (±0.01 mm)) and sex ratios. Commercial-scale nematode inoculations were not conducted for the first (2011–2012) season, but during the subsequent three seasons, parasitism rates were assessed by dissecting all adult Sirex collected from emergence bins. For these three seasons (2012–2015), ten individual eggs (five from proximal and five from distal end of ovarioles) from each parasitized female were examined to assess whether nematodes were present within them. In the 2013–2014 and 2014–2015 seasons, fat bodies were visually assessed during dissection for nematode parasitism and given a score on a 0 (no fat) to 5 (abdomen full of fat) scale. Emergence dates were used to ascertain emergence patterns each season, with climate data sourced from the nearest weather station (16 km from Passchendaele) from http://www.bom.gov.au/climate/data/.

Table 1 Number of bins (each typically containing two billets from one tree of either *Pinus radiata* or *P. taeda*) and the number of Sirex that emerged and were measured in each season

Season	*P. radiata*		*P. taeda*	
	Number of bins	Number of Sirex	Number of bins	Number of Sirex
2011–2012	2	39	2	85
2012–2013	12	396	2	141
2013–2014	8	226	8	235
2014–2015	13	276	10	119

Analyses

Overall differences in male and female adult size (unparasitized adults only, because parasitism status can influence body size – Ryan and Hurley, 2012) using average head capsule widths per bin were initially examined between sex and host taxon for each season using a split-plot design ANOVA, with bin.species as block factors and sex as sub-plots. Then, following Hurley et al. (2008), to examine the population as a whole, for each taxon in each season, head capsule width of males and females was compared using *t*-tests, and sex ratio was compared using a one-way chi-square test. Sex bias in parasitism by nematodes was examined using two-way chi-square test. Patterns were further explored using *t*-test and one-way ANOVA (with Fisher's LSD *post hoc* test when significant differences were detected) where appropriate, and when data did not fit their assumptions Mann–Whitney *U* and Kruskall–Wallis tests (with multiple pairwise comparisons when required) were used instead. One-way contingency tables were used to assess the deviation of sex ratios from normal, and two-way contingency tables were used to compare proportions. Standard errors for proportions were calculated using the equation $\mathrm{SE_p} = \sqrt{p(1-p)/n}$, where, *p* is the proportion and *n* is the sample size. Spearman's rank correlation was conducted using data averaged for each emergence bin from which >6 Sirex adults emerged ($n = 38$ bins over three seasons) to more closely examine factors that might correlate with variables including size, sex ratio, nematode parasitism and fat body, as well as to examine relationships with emergence and temperature. The statistics programme used was GenStat Version 16 (VSN International). Data are presented as mean ± standard error unless otherwise stated.

Results

At the tree level, split-plot ANOVA showed size differences between (unparasitized) males and females only in the second season, and a significant effect of host species in the two latter seasons, with a consistent trend towards smaller adults from *P. taeda* in each season (Figure 1). For individual wasp data (as in Hurley et al., 2008), across all season, females were significantly larger than males, and for both sexes, adults were significantly larger from *P. radiata* (M: 3.34 ± 0.03 mm; F: 3.75 ± 0.05 mm) than from *P. taeda* (M: 2.67 ± 0.03 mm; F: 3.08 ± 0.07 mm) (two-way ANOVA, sex: $F_{1,1483} = 145.1$, $P < 0.001$; taxon $F_{1,1483} = 338.7$, $P < 0.001$). There was no significant interaction between sex and host taxon (sex × taxon $F_{1,1483} = 0$, $P = 0.97$). Adult size varied considerably, with adults of the same sex emerging from the same tree varying up to 1.9-fold.

Nematode parasitism (proportion of adults infected) for adults emerging from inoculated billets was similar between sexes for each taxon (*P. taeda*: M – 0.35 ± 0.02, F – 0.29 ± 0.02, $\chi^2_1 = 0.91$, $P = 0.34$; *P. radiata*: M – 0.49 ± 0.02, F – 0.52 ± 0.02, $\chi^2_1 = 0.57$, $P = 0.45$), but parasitism rates were significantly lower for adults emerging from *P. taeda* than from *P. radiata*, for all individuals (0.34 ± 0.02, 0.50 ± 0.02, respectively). Across all trees, the average proportion of adults parasitized by nematodes was twice as high in *P. radiata* than that in *P. taeda*: 0.51 ± 0.05 (range 0–0.93) *vs* 0.23 ± 0.08 (range 0–0.76) (Mann–Whitney *U*-test, $U = 61$, $P = 0.007$)bin.

Overall, mean adult size was unaffected by parasitism status in either taxon for either sex (*P. radiata*: F – $t_{267} = 1.84$, $P = 0.07$; M – $t_{599} = 1.82$, $P = 0.07$; *P. taeda*: F – $t_{66} = 0.8$, $P = 0.43$; M – $t_{413} = 1.01$, $P = 0.32$), although in 2012–2013 parasitized females were significantly larger than unparasitized females (ANOVA; taxon: $F_{1,11} = 5.11$, $P = 0.045$; nematode: $F_{1,6} = 12$, $P = 0.013$; interaction: $F_{1,6} = 19.3$, $P = 0.005$).

Sex ratios differed between host taxa in the 2012–2013 ($\chi^2_1 = 33.2$, $P < 0.001$) and 2013–2014 ($\chi^2_1 = 21.5$, $P < 0.001$) seasons, with a significantly higher proportion of males emerging from *P. taeda* (0.92 ± 0.02 and 0.89 ± 0.02, respectively) than *P. radiata* (0.67 ± 0.02 and 0.73 ± 0.03). Overall, sex ratios were significantly male biased each season, and the extent of bias differed significantly among seasons for *P. taeda* but not for *P. radiata* (Table 2). Similarly, nematode parasitism rate differed among seasons, with 2012–2013 having higher parasitism rates than the subsequent seasons (Table 2).

The proportion of eggs that contained nematodes was lower than expected and did not differ between taxa (Mann–Whitney *U*-test, $U = 493$, $P = 0.34$) but did differ among seasons (Kruskall–Wallis test, $H = 29$, $P < 0.001$), with 0.53 ± 0.05^{a}, 0.37 ± 0.04^{b} and 0.73 ± 0.04^{a} in 2013, 2014 and 2015, respectively. The presence of nematodes in eggs was related to the position of eggs within ovarioles: in each season significantly more eggs from the proximal (lower) ovary contained nematodes than eggs from the distal (upper) ovary (2013: upper 0.8, lower 0.42; 2014: upper 0.6, lower 0.13; 2015: upper 0.9, lower 0.6. $\chi^2_1 = 15.2$, 125, 55; all $P < 0.001$, respectively).

The amount of fat body did not differ among seasons (Mann–Whitney *U*-test, $U = 83\,023$, $P = 0.7$), nematode parasitism status ($U = 72\,358$, $P = 0.26$) or sex ($U = 55\,154$, $P = 0.06$) but differed significantly between taxa ($U = 66\,755$, $P < 0.001$), with *P. radiata* adults having significantly more fat body (2.38 ± 0.06) than adults emerging from *P. taeda* (1.96 ± 0.06).

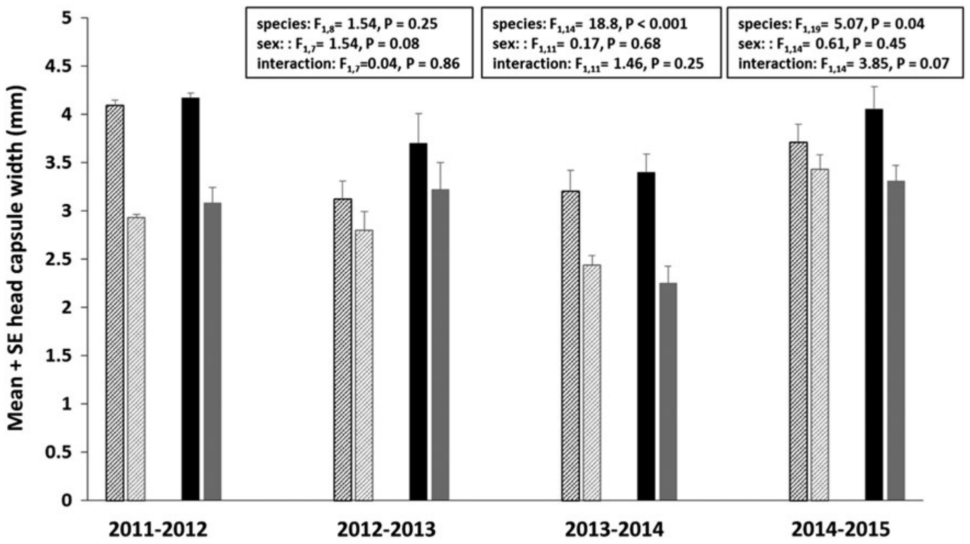

Figure 1 Mean + SE head capsule width (mm) of unparasitized *Sirex noctilio* males (stippled) and females (solid) emerging from individual *Pinus radiata* (black) and *P. taeda* (grey) trees over three seasons. Results of split-plot ANOVA for each season are inset (replication in the first season was insufficient to allow analysis).

Table 2 Proportion of adult *Sirex noctilio* emerged from *P. radiata* and *P. taeda* billets that were (a) female, and (b) parasitized with *Deladenus siricidicola* following inoculation. Different letters within columns designate significant differences between seasons

Season	*P. radiata*		*P. taeda*	
	Proportion of all adults that were:		Proportion of all adults that were:	
	Females	Parasitized by nematodes	Females	Parasitized by nematodes
2011–2012	0.38 ± 0.07	NA	0.36 ± 0.06* (a)	NA
2012–2013	0.33 ± 0.02*	0.54 ± 0.02 (a)	0.08 ± 0.02* (b)	0.54 ± 0.04 a
2013–2014	0.27 ± 0.03*	0.46 ± 0.03 (b)	0.10 ± 0.02* (b)	0.24 ± 0.03 b
2014–2015	0.34 ± 0.02*	0.43 ± 0.03 (b)	0.34 ± 0.04* (a)	0.29 ± 0.04 b
Pairwise chi-square tests	$\chi^2 = 0.03–5.4$	$\chi^2 = 2.13–8.2$	$\chi^2 = 0.29–24.5$	$\chi^2 = 0.901–33.9$
	$P = 0.06–0.85$	$P = 0.15$ to <0.001	$P = 0.59$ to <0.001	$P = 0.34$ to <0.001

Asterisks denote significant within-season deviation from normal (1:1) sex ratio.

Table 3 Spearman rank correlation matrix for characteristics associated with *S. noctilio* performance and parasitism

	%nem	%F	DBH	blue-stain	Ips	F_{size}	M_{size}	F_{fat}	M_{fat}
%nem	*	0.293	**0.386**	−0.017	**−0.532**	**0.393**	0.137	**0.541**	**0.496**
%F	0.059	*	0.008	−0.165	−0.187	**0.536**	**0.691**	0.141	0.294
DBH	**0.028**	0.243	*	−0.271	−0.086	0.292	0.138	0.099	**0.507**
Blue-stain	0.237	0.127	0.068	*	**−0.365**	−0.106	−0.198	0.263	0.199
Ips	**0.006**	0.113	0.182	**0.034**	*	0.053	0.171	**−0.581**	−0.242
F_{size}	**0.026**	**0.006**	0.059	0.167	0.208	*	**0.812**	**0.331**	**0.661**
M_{size}	0.147	**0**	0.145	0.107	0.123	**0**	*	0.08	**0.538**
F_{fat}	**0.005**	0.144	0.173	0.073	**0.003**	**0.044**	0.187	*	**0.51**
M_{fat}	**0.009**	0.058	**0.008**	0.105	0.083	**0.001**	**0.006**	**0.008**	*

Numbers above the diagonal are the Rho-values and below the diagonal are the *P*-values. Significant relationships are highlighted in bold.

Wild-caught females were significantly larger than those from billets in each season (two-way ANOVA, wild *vs* billet $F_{1,446} = 65.9$, $P < 0.001$; season: $F_{3,446} = 7.24$, $P < 0.001$), with no significant interaction between season and origin ($F_{3,446} = 0.62$, $P = 0.61$), although size of wild-caught and billet females were correlated across seasons (Spearman rank correlation, Rho = 0.8, $P = 0.02$). Nematode parasitism of wild-caught females was <5 per cent in 2011–2012 ($n = 16$) and 2012–2013 ($n = 74$), and nil in 2013–2014 ($n = 11$) and 2014–2015 ($n = 16$).

Nematode parasitism was positively correlated with male and female fat body size, tree DBH and female size (Table 3) and negatively correlated with ips bark beetle severity. Sex ratio was positively correlated with male and female size (trees with larger adults also had higher proportion of females), and larger trees produced males with larger fat bodies. There was a very strong relationship (Rho = 0.81) between the size of males and females emerging from the same tree (Table 3).

The severity of blue-stain fungi was significantly higher in *P. taeda* (2.7 ± 0.3) than that in *P. radiata* (1.3 ± 0.4) (Mann–Whitney *U*-test, $U = 74$, $P = 0.004$), but the severity of *I. grandicollis* attack did not differ significantly between taxa ($U = 117$, $P = 0.168$).

Fortnightly emergence patterns followed similar trends in each season, the most significant being two distinct emergence peaks, and a drop in emergence in early February each season (Figures 1 and 2).

Males began to emerge before females from both taxa and in each season. Considering maximum, minimum and mean temperature; and total and average rainfall in the two-week period of emergence, the factor best correlated with Sirex emergence was mean minimum temperature (2011–2012: rho = 0.6, $P = 0.014$; 2012–2013: rho = 0.81, $P = 0.001$; 2013–2014: rho = 0.71, $P = 0.004$; 2014–2015: rho = 0.64, $P = 0.009$).

Discussion

The newly established population of *S. noctilio* in Queensland was consistently protandrous and male-biased, with actual sex ratios differing among seasons and taxa. Overall, the sex ratio remained around 3:1 males:females in *P. radiata* but dropped to ~10:1 for *P. taeda* in two of the four seasons. These ratios are well within recorded male bias of populations worldwide, where up to 32:1 has been recorded (Ryan and Hurley, 2012). Although generally considered an artefact of mate availability in expanding populations (Ryan and Hurley, 2012), the disparity in male bias we found between taxa might indicate that host quality may play a role in sex allocation. Wooding (2014) found that moisture content (as a proxy of host quality) did not influence sex ratios, but other host quality traits may. The proportion of females emerging per tree was significantly positively correlated with adult size, further suggesting an interaction with host suitability. Hurley *et al.* (2008) likewise recorded more females, and larger adults, emerging from the lower bole than the mid- or upper bole of *P. patula* trees, suggesting that host attributes may influence these factors. Taylor (1981) also thought sex ratio could relate to susceptibility of host trees but did not propose a mechanism. Higher female ratios within and among trees could arise through differential performance of males and females, or by female allocation during oviposition. Female investment in daughters may have more influence on sex ratios than mating frequency or success (Wooding, 2014); it is possible that ovipositing females assess host ‘quality’ during oviposition (Madden, 1974; Hayes *et al.*, 2015) and lay fertilized or unfertilized eggs accordingly.

Despite large variation in adult size within trees (up to 1.9-fold) and nematode parasitism among trees (0–93 per cent), several patterns were apparent. There was a very strong correlation between the average size of males and females emerging from the same trees, providing further evidence that host attributes influence Sirex success. Overall, *P. taeda* appeared to be a poorer host than *P. radiata*, producing smaller adults of both sexes, lower fat body content and fewer females. Large *S. noctilio* lay more eggs, live longer and fly further than smaller adults (Bedding, 2009), so the overall reproductive potential of adults emerging from *P. taeda* is lower than from *P. radiata*. However, *P. taeda* also exhibited lower nematode parasitism success of adults.

Pinus taeda had higher severity of blue-stain fungus than *P. radiata*. The presence of blue-stain fungus can significantly impact Sirex development through competitive interaction between Sirex’ fungal symbiont, *A. areolatum*, and the blue-stain fungus (King, 1966; Hurley *et al.*, 2012a;b; Yousuf *et al.*, 2014a) and can interfere with nematode parasitism success (Yousuf *et al.*, 2014b). The difference in severity of blue-stain fungus between the two host taxa here provides a probable explanation for the poorer performance and lower parasitism of Sirex in *P. taeda*. The amount of blue-stain was unrelated to the severity of *I. grandicollis*, and in contrast to Yousuf *et al.* (2014b), we

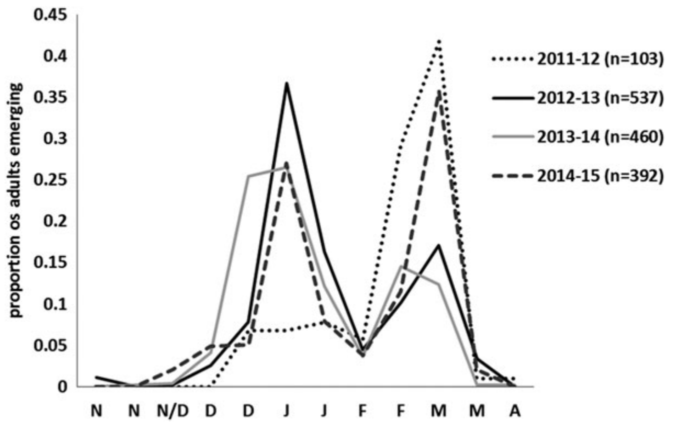

Figure 2 Emergence patterns (proportion of adults emerged in 2-week intervals) of *S. noctilio* between 2011 and 2015.

found no clear relationships between Ips severity and Sirex performance or nematode parasitism. The blue-stain fungus in our billets was isolated and identified as *Diplodia (Sphaeropsis) sapinea* (MR, personal communication), rather than *Ophiostoma ips*. *Diploida sapinea* is ubiquitous among *Pinus* throughout South Africa and in low wood moisture conditions in summer rainfall areas is strongly competitive against both *O. ips* and *A. areolatum* (Hurley *et al*., 2012a;b) and may explain the poorer performance of Sirex and *D. siricidicola* found here.

There are varying reports of parasitized adults being both smaller (Bedding, 2009) and larger (Hurley *et al*., 2008) than unparasitized adults (Kroll *et al*., 2013). We found occasional size differences in parasitized and unparasitized adults between host taxon across seasons. Inoculated trees should yield >90 per cent parasitism of emerging adults (Carnegie and Bashford, 2012), but we recorded this level of success in <10 per cent of inoculated trees, whereas ~15 per cent produced no parasitized adults. Across both taxa, on average, inoculated trees yielded less than half of emerging adults parasitized with nematodes. Variable and low nematode efficacy has characterized control programmes worldwide (Hurley *et al*., 2007; Slippers *et al*., 2012), with no clear mechanisms to explain this variation (Hurley *et al*., 2008). The success of the biological control of Sirex by nematodes is influenced by interactions between wasp, nematodes and fungal strains (Morris *et al*., 2012; Slippers *et al*., 2015), other insects and fungi (Yousuf *et al*., 2014b), climatic conditions (Hurley *et al*., 2007) and host tree characteristics (Bedding, 2009).

In addition to low adult parasitism rates, we also found that only about half of the eggs sampled from parasitized females had nematodes within them, and some parasitized females had no eggs with nematodes. This has been reported for other, non-sterilizing strains of *D. siricidicola* (Bedding, 2009), and although nematodes can still be transmitted during oviposition, partial or incomplete sterilization can impact Sirex population dynamics (Kroll *et al*., 2013). Non-sterilizing strains are often associated with solitary siricid species where they can persist through vertical transmission (Kroll *et al*., 2013). However, *D. siricidicola* used in biological control in Australia is considered a fully sterilizing strain (Bedding, 2009), so our findings of partial sterilization warrant further investigation. Yousuf *et al*. (2014c) found decreasing egg parasitism success with increasing temperature but in their study all eggs at similar temperature to ours contained nematodes, suggesting temperature is not the mechanism to explain our results.

Temperature provided the best correlate of seasonal emergence, however, with fortnights with higher mean minimum temperatures having higher numbers of Sirex emerging. Adults generally emerged between November and March, with two distinct emergence peaks around January and March. In each season, there was a marked drop in emergence in early February. The consistent two-peak pattern of emergence is similar to that reported in Tasmania, possibly resulting from a cessation of feeding between and within trees (Taylor, 1981). However, Neumann *et al*. (1987) considered that a second peak is the result of short-cycle individuals emerging (Ryan and Hurley, 2012). Our data do not favour this explanation, as females would have had to lay into the billets, and further, there are insufficient day-degrees (Madden, 1981) to complete another cycle within the emergence facility. Adults that emerged in the second peak were generally larger than those emerging in the first peak. Unlike Kroll *et al*. (2013), we did not find any patterns with nematode infection and emergence time.

Our main findings from this study of a newly invading population of *S. noctilio* include the differential performance (measured by sex ratio, size, fat body size and nematode parasitism) between *P. radiata* and *P. taeda*, which are considered equivalent hosts (Iede *et al*., 1998 in Carnegie *et al*., 2005), and the unexpected partial sterilization of female wasps by nematodes. This latter finding, in combination with low overall nematode parasitism, requires further investigation to ensure that it is not a harbinger of evolution of nematode resistance or strain incompatibilities (Slippers *et al*., 2015) that might lead to compromised biocontrol success.

Acknowledgements

We sincerely thank Jade Hetherington, Carl Sutherland and Ian Last (HQPlantations) for site access and preparation and provision of specimens, Ahmed Saad for assistance with dissections, Robin Bedding for helpful discussions on nematodes and Bob Mayer (Queensland Department of Agriculture and Fisheries) for his valued statistical advice and assistance. We also sincerely thank Matt Ayres, Ecki Brockerhoff and an anonymous reviewer for their helpful comments that improved the manuscript.

Funding

This work was funded with a grant from the National Sirex Coordination Committee, and in-kind support from the University of the Sunshine Coast, Queensland Department of Agriculture and Fisheries and HQPlantations Pty Ltd.

Conflict of interest statement

None declared.

References

Aparicio, J.P., Corley, J.C. and Rabinovich, J.E. 2013 Life history traits of *Sirex noctilio* F.(Hymenoptera: Siricidae) can explain outbreaks independently of environmental factors. *Math. Biosci. Eng.* **10**, 1265–1279.

Bedding, R.A. 2009 Controlling the pine-killing woodwasp, *Sirex noctilio*, with nematodes. In *Use of Microbes for Control and Eradication of Invasive Arthropods*. Hajek, A.E., Glare, T.R. and O'Callaghan, M. (eds). Springer, pp. 213–235.

Carnegie, A.J. and Bashford, R. 2012 Sirex woodwasp in Australia: current management strategies, research and emerging issues. In *The Sirex Woodwasp and its Fungal Symbiont*. Slippers, B., deGroot, P. and Wingfield, M.J. (eds). Springer, pp. 175–201.

Carnegie, A.J., Eldridge, R.H. and Waterson, D.G. 2005 History and management of Sirex wood wasp in pine plantations in New South Wales, Australia. *New Zealand J. Forestry Sci.* **35**, 3.

Carnegie, A.J., Matsuki, M., Haugen, D.A., Hurley, B.P., Ahumada, R., Klasmer, P. *et al*. 2006 Predicting the potential distribution of *Sirex noctilio* (Hymenoptera: Siricidae), a significant exotic pest of Pinus plantations. *Annals Forest Sci.,* **63**, 119–128.

Eldridge, R.H. and Simpson, J.A. 1987 Development of contingency plans for use against exotic pests and diseases of trees and timber: 3. Histories of control measures against some introduced pests and diseases of forests and forest products in Australia. *Austr. Forestry,* **50**, 24–36.

Eldridge, R.H. and Taylor, E.E. 1989 *Sirex Woodwasp: A Pest of Pine in NSW*. Wood Technology and Forest Research Division, Forestry Commission of New South Wales.

Gavran, M. 2014 Australian plantation statistics 2014 update. Technical report No. 42. Australian Bureau of Agricultural and Resource Economics and Sciences, p. 20.

Haugen, D.A. 1990 Control procedures for *Sirex noctilio* in the Green Triangle: review from detection to severe outbreak (1977–1987). *Austr. Forestry,* **53**, 24–32.

Hayes, R.A., Griffiths, M.W. and Nahrung, H.F. 2015 Electrophysiological activity of the *Sirex noctilio* ovipositor: you know the drill? *J. Asia-Pacific Entomol.* **18**, 165–168.

Hurley, B.P., Croft, P., Verleur, M., Wingfield, M.J. and Slippers, B. 2012a The control of the Sirex woodwasp in diverse environments: the South African experience. In *The Sirex Woodwasp and its Fungal Symbiont*. Slippers, B., deGroot, P. and Wingfield, M.J. (eds). Springer, pp. 247–264.

Hurley, B.P., Hatting, H.J., Wingfield, M.J., Klepzig, K.D. and Slippers, B. 2012b The influence of *Amylostereum areolatum* diversity and competitive interactions on the fitness of the Sirex parasitic nematode *Deladenus siricidicola*. *Biol. Control,* **61**, 207–214.

Hurley, B.P., Slippers, B. and Wingfield, M.J. 2007 A comparison of control results for the alien invasive woodwasp, Sirex noctilio, in the southern hemisphere. *Agri. Forest Entomol.,* **9**, 159–171.

Hurley, B.P., Slippers, B., Croft, P.K., Hatting, H.J., van der Linde, M., Morris, A.R. *et al*. 2008 Factors influencing parasitism of *Sirex noctilio* (Hymenoptera: Siricidae) by the nematode *Deladenus siricidicola* (Nematoda: Neotylenchidae) in summer rainfall areas of South Africa. *Biol. Control,* **45**, 450–459.

King, J.M. 1966 Some aspects of the biology of the fungal symbiont of *Sirex noctilio*. *Austr. J. Botany,* **14**, 25–30.

Kroll, S.A., Hajek, A.E., Morris, E.E. and Long, S.J. 2013 Parasitism of *Sirex noctilio* by non-sterilizing *Deladenus siricidicola* in northeastern North America. *Biol. Control,* **67**, 203–211.

Lantschner, M.V., Villacide, J.M., Garnas, J.R., Croft, P., Carnegie, A.J., Liebhold, A.M. and Corley, J.C. 2014 Temperature explains variable spread rates of the invasive woodwasp *Sirex noctilio* in the Southern Hemisphere. *Biol. Invasions,* **16**, 329–339.

Madden, J.L. 1974 Oviposition behaviour of the woodwasp, *Sirex noctilio* F. *Austr. J. Zoology,* **22**, 341–351.

Madden, J.L. 1981 Egg and larval development in the woodwasp, *Sirex noctilio* F. *Austr. J. Zoology* **29**, 493–506.

Morris, E.E., Jimenez, A., Long, S.J., Williams, D.W. and Hajek, A.E. 2012 Variability in growth of *Deladenus siricidicola* on strains of the white rot fungus *Amylostereum areolatum*. *BioControl,* **57**, 677–686.

Neumann, F.G. 1987 Introduced bark beetles on exotic trees in Australia with special reference to infestations of Ips grandicollis in pine plantations. *Austr. Forestry* **50**, 166–178.

Ryan, K. and Hurley, B.P. 2012 Life history and biology of *Sirex noctilio*. In *The Sirex Woodwasp and its Fungal Symbiont*. Slippers, B., deGroot, P. and Wingfield, M.J. (eds). Springer, pp. 15–30.

Slippers, B., Hurley, B.P., Mlonyeni, X.O., de Groot, P. and Wingfield, M.J. 2012 Factors affecting the efficacy of *Deladenus siricidicola* in biological control systems. In *The Sirex Woodwasp and its Fungal Symbiont*. Slippers, B., deGroot, P. and Wingfield, M.J. (eds). Springer, pp. 119–133.

Slippers, B., Hurley, B.P. and Wingfield, M.J. 2015 Sirex Woodwasp: A Model for Evolving Management Paradigms of Invasive Forest Pests. *Ann. Rev. Entomol.,* **60**, 601–619.

Taylor, K.L. 1981 The Sirex woodwasp: ecology and control of an introduced forest insect. In *The Ecology of Pests: Some Australian Case Histories*. Kitching, R.L. and Jones, R.E. (eds). CSIRO, pp. 231–248.

Wooding, A.L. 2014 Sex determination and symbiont transmission in the *Sirex-Amylostereum* mutualism. MSc Thesis, University of Pretoria, p. 136.

Yousuf, F., Carnegie, A.J., Bashford, R., Bedding, R.A., Nicol, H.I. and Gurr, G.M. 2014a Bark beetle (*Ips grandicollis*) disruption of woodwasp (*Sirex noctilio*) biocontrol: direct and indirect mechanisms. *Forest Ecol. Manag.,* **323**, 98–104.

Yousuf, F., Carnegie, A.J., Bedding, R.A., Bashford, R., Nicol, H.I. and Gurr, G.M. 2014b Effect of temperature on woodwasp (*Sirex noctilio* F.) development and parasitism by the entomopathogenic nematode, *Deladenus siricidicola*. *Biol. Control,* **79**, 67–74.

Yousuf, F., Gurr, G.M., Carnegie, A.J., Bedding, R.A., Bashford, R., Gitau, C.W. and Nicol, H.I. 2014c The bark beetle, *Ips grandicollis*, disrupts biological control of the woodwasp*, Sirex noctilio*, via fungal symbiont interactions. *FEMS Microbiol. Ecol.,* **88**, 38–47.