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# Bark beetle (*Ips grandicollis*) disruption of woodwasp (*Sirex noctilio*) biocontrol: direct and indirect mechanisms

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ABSTRACT

Interactions between invasive pest species, especially those mediated by microbial associates, are poorly understood. In this study, we examined the consequences for the woodwasp, *Sirex noctilio*, biocontrol program of the bark beetle *Ips grandicollis*, and its fungal associate, *Ophiostoma ips*. Pine trees treated with herbicide are used internationally to attract ovipositing *S. noctilio* and to introduce the biocontrol agent nematode, *Beddingia siricidicola*. This study measured the rate of drying in such trees with and without *I. grandicollis*, and studied the effect on emerging insects and fungal occupancy in wood. *Ips grandicollis* attack led to accelerated wood drying, reduced the percentage of nematode-parasitised *S. noctilio* of both sexes, and reduced the size of emerging females. There was a negative correlation between wood moisture content and *O. ips* occupancy in billets (bolts) whilst *I. grandicollis* infested trap trees had lower occupancy of the *S. noctilio*-associated fungus *Amylostereum areolatum* on which larval *S. noctilio* and *B. siricidicola* feed. The observed effects of *I. grandicollis* on *S. noctilio* are detrimental to the inoculative biocontrol program which requires high emergence of large, parasitised female *S. noctilio* to disperse the nematode agent in the wild population. *Ophiostoma ips* is known to competitively exclude *A. areolatum* so the association of *O. ips* with dry wood may be an indirect mechanism by which *I. grandicollis* adversely affects *S. noctilio* biocontrol. This new knowledge will guide changes to forestry practice to protect the efficacy of biocontrol of this serious pine pest.



## 1. Introduction

*Sirex noctilio* F. is a major forestry pest of introduced *Pinus* plantations in the Southern Hemisphere (Hurley et al., 2007) and has more recently been detected in endemic *Pinus* spp. in North America (de Groot et al., 2006). It is native to Eurasia and North Africa (Spradbery and Kirk, 1978; Eichhorn, 1982), primarily attacking trees that have been stressed due to overcrowding and drought (Dodds et al., 2010; Smith and Schiff, 2002). The wasp can attack healthy trees if its population density is high. *Sirex noctilio* damages trees by depositing a phytotoxic mucus and an obligate symbiotic fungus, *Amylostereum areolatum* (Chaillet) Boiden, in the trees during oviposition. The fungus, together with the mucus, causes extensive dry white rot of the wood and kills the trees (Coutts and Dolezal, 1969). The developing *S. noctilio* larvae feed on the fungus and white-rotted wood (Kukor and Martin, 1983; Madden and Coutts, 1979).

Sirex noctilio has caused severe damage to pine plantations in many Southern Hemisphere countries (e.g. Hurley et al., 2007; Iede et al., 1998). In Australia in the late 1980s, an outbreak killed more than 5 million trees with a royalty value of AU$10–12 million (Haugen et al., 1990). To manage this pest, several parasitic wasps have been introduced in Australia including species of *Ibalia* (Ibaliidae), Rhyssa and Megarhyssa (Ichneumonidae) and *Schlettererius cinctipes* (Cresson) (Stephanidae) (Taylor, 1976). *Ibalia leucospoides* (Hochenwarth) is by far the most successful

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parasitoid (Carnegie et al., 2005; Collett and Elms, 2009), but provides insufficient control.

The parasitic nematode *Beddingia* (=*Deladenus*) *siricidicola* (Nematoda: Beddingidae) has been found to effectively control *S. noctilio* (Bedding, 1984) when used inundatively. The adult female nematode is extraordinary, having two distinct morphological forms: a free-living (mycophagous) form that feeds and reproduces on *A. areolatum* and a parasitic (entomophagous) form that parasitises *S. noctilio* larvae (Bedding, 1972). The biocontrol program for *S. noctilio* exploits this nematode by annually setting up 'trap tree plots' consisting of ten trees in the most susceptible age-class areas in a forest where the *S. noctilio* population is likely to be prevalent (Carnegie and Bashford, 2012; Neumann et al., 1987). Nematodes are inoculated into infested trap trees where they feed and reproduce on *A. areolatum*, and parasitise *S. noctilio* larvae. The parasitised larvae complete their metamorphosis normally within the infested trees and adults emerge. Parasitised female adults, however, are sterile, with eggs filled with juvenile nematodes which are laid in other trees so dispersing the biocontrol agent (Bedding, 1972; Bedding and Iede, 2005). Male adults also carry the nematodes within their testis but cannot disperse them (Bedding, 2009). Therefore, female *S. noctilio* are important for an effective biocontrol nematode dispersal and thus for maintaining low *S. noctilio* densities.

The nematode biocontrol program has been used in every Southern Hemisphere continent in which *S. noctilio* is a known pest: Australasia, South America and southern Africa. It has been the most successful biocontrol strategy of *S. noctilio*, attaining parasitism levels of almost 100% (Bedding, 2009) in emerging *S. noctilio* from trap trees. However, in recent years, the percentage of nematode parasitism for *S. noctilio* has declined in several regions in Australia and it has been speculated that interference by another exotic pest, the bark beetle, *Ips grandicollis* Eichhoff (Coleoptera: Scolytidea) is involved (Carnegie and Bashford, 2012; Carnegie and Loch, 2010). This beetle is native to North and Central America and was inadvertently introduced to Australia in the 1940s (Swan, 1950) where it has spread to all pine-growing states except Tasmania (Bashford, 2008; Gitau et al., 2013b). Like *S. noctilio, I. grandicollis* is attracted to recently damaged, stressed, weakened or unhealthy trees (Erbilgin et al., 2002) and observations of it attacking trap trees have been reported over the last decade (Carnegie and Bashford, 2012; Carnegie and Loch, 2010; Phillips, 2002). Trap trees that have been attacked by *I. grandicollis* have variable and inconsistent percentages of *S. noctilio* parasitism (7–44%) (Carnegie and Loch, 2010). The mechanism behind such inconsistencies is unknown but could involve both direct and indirect factors.

During *I. grandicollis* attack, beetles tunnel through the bark to the cambium, carrying spores of its associated fungus, *Ophiostoma ips* (Rumbold) Nannfeldt. The trees then undergo rapid physiological changes which could be due to blockage of water transport as the fungus invades the wood (e.g. Ballard et al., 1984; Långström et al., 1993) or the result of phloem feeding, tunneling and construction of galleries by adult beetles and their larvae that disrupts photosynthate transfer (Hubbard et al., 2013). Such changes can contribute to changes in tree moisture content (Hubbard et al., 2013) and have the potential to cause tree mortality.

These direct effects of the beetle on tree moisture content may influence the growth of *A. areolatum* (Hurley et al., 2012) that in turn can affect *S. noctilio* survival, growth and development. Negative effects are also possible on parasitism of *S. noctilio* by *B. siricidicola* because a moisture content of at least 50% is essential for successful inoculation (Bedding and Akhurst, 1974) and subsequent reproduction in wood of *B. siricidicola* (Hurley et al., 2008; Hurley et al., 2007).

Thus, the initial aim of our study was to monitor in the field, the moisture content of trap trees with and without *I. grandicollis* and to determine whether *I. grandicollis* infestation affects *S. noctilio* development and nematode parasitism. To achieve this *S. noctilio* infested trap trees, with and without *I. grandicollis* infestation, were monitored every 2 weeks for 10 months for changes in moisture content. Later, rates of *S. noctilio* emergence, size and parasitism were monitored in billets cut from the trap trees. Finally, the extent of *O. ips* and *A. areolatum* growth in wood was determined and correlated against the moisture content of trap trees.

## 2. Methods

### 2.1. Study site and trap tree plot selection

A total of 25 trap tree plots (=250 trees) were established between December 2011 and January 2012 in nine commercial plantation forests (814–1246 m elevation) (see supplementary Table S1) in the Central Tablelands region of New South Wales, Australia. Trees were treated with herbicide in a manner to mimic standard forestry practice for the establishment of trap tree plots (see Carnegie and Bashford, 2012). Briefly, an axe cut was made at the base of each tree approximately 100 cm from the ground and 5 ml of glyophosate (N-(phosphonomethyl) glycine), a broad-spectrum systemic herbicide injected into the wound. The herbicide caused the trees to die slowly, making them attractive oviposition sites for gravid *S. noctilio*.

### 2.2. Moisture measurements of trap trees

Moisture level of trap trees was assessed using wood cores collected 1.3 m from ground level using a 5 mm diameter increment borer (Suunto, Queensland, Australia). Wood cores (2 cm in length) were randomly taken from three positions around each tree 15–20 days after herbicide treatment, and immediately placed in a pre-weighed, labeled aluminium container and sealed in a labeled zipper bag so that any moisture lost from the wood cores during transit to the laboratory was collected. The bags were placed in a cooler filled with ice for transportation and immediate processing. Fresh weights of wood cores were obtained, and the cores were placed in a dehydrator in the same aluminium container at 105 °C, and then re-weighed after 48 h and percentage moisture content of the wood cores was determined. This process was repeated at every 2 weeks intervals for all 250 trap trees between January and May 2012 to monitor changes in moisture content. At the end of this period (early winter), all trees were felled and inoculated with *B. siricidicola* according to standard procedures (Bedding and Iede, 2005). Thereafter, moisture readings were continued in the wood of felled trees, but now cores were taken randomly throughout the length (bottom to top) of the tree until October 2012, but restricted only to selected (Ips infested and Ips uninfested) trees as described below. Moisture loss data are presented for these selected trees only.

### 2.3. Monitoring for Ips grandicollis infestation

All 250 trees in trap tree plots were monitored every 2 weeks for signs of insect infestation. Trees with brown/rusty colored frass at the site of small entry holes on the bark were considered to be attacked by *I. grandicollis*. Trees with distinct, white/cream beading of tree exudate characteristic of *S. noctilio* oviposition were considered to be attacked by *S. noctilio* (Dodds et al., 2007). This allowed individual trees that were known to be attacked by *S. noctilio* to be categorised into Ips infested (trees that were attacked by *S. noctilio* and *I. grandicollis*) and Ips uninfested (trees that were attacked by *S. noctilio* with no *I. grandicollis*). The first symptoms of attack by *I. grandicollis* were seen after 20–25 days after herbicide treatment