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Incidence of *Ips grandicollis* (Coleoptera: Scolytinae) in trap trees prepared for biological control of *Sirex noctilio* (Hymenoptera: Siricidae) in Australia: Influence of environment and silviculture

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ABSTRACT

In Australia, the bark beetle *Ips grandicollis* (Eichhoff) (Coleoptera: Curculionidae) attacks trap trees prepared for *Sirex noctilio* Fabricius (Hymenoptera: Siricidae) biocontrol, potentially threatening biocontrol programs for this invasive pest. Trap trees are prepared in the summer to attract *S. noctilio* females to oviposit for later introduction of the nematode *Beddingia siricidicola* (Bedding), which is the biological control agent that has successfully managed populations of this exotic pest. In Australia, the bark beetle *I. grandicollis* has unprecedentedly been attacking these trap trees and the magnitude of the threat facing *S. noctilio* biocontrol as a result of attack by the bark beetle is unknown. Surveys for incidence of *I. grandicollis* in trap trees were conducted in four states of Australia – New South Wales, South Australia, Tasmania and Victoria – where *P. radiata* is grown commercially and *S. noctilio* biocontrol is important. Results showed that *I. grandicollis* attack of trap trees is widespread and prevalent in South Australia, southern New South Wales and Victoria and absent in Tasmania. The incidence of *I. grandicollis* in the trap trees was more severe in South Australia compared with New South Wales and Victoria. A more detailed analysis using New South Wales data examined the relative importance of biotic and abiotic factors in determining attack of trap trees by *I. grandicollis* in order to explain and allow prediction of the patterns of attack by the bark beetle and potential threat to *S. noctilio* biocontrol. The whole model accounted for 58.7% of the deviance; with the key predictors accounting for 46.3%. A linear regression model showed that maximum summer and winter temperatures, lower (0.5–1.9 m) soil moisture two years before the surveys, summer upper (0–0.7 m) soil moisture in the year of the surveys, autumn lower soil moisture in the year of survey, age of trap trees and damage to trees adjacent to trap tree plots are key predictors of *I. grandicollis* attack on trap trees. Some of these driving factors were expected; others were unexpected or contradictory to our expectations. These factors would be important considerations when identifying locations where trap tree plots are established to reduce the impact of *I. grandicollis* on the *S. noctilio* biocontrol program.

1. Introduction

The wood wasp *Sirex noctilio* Fabricius (Hymenoptera: Siricidae) is a major exotic pest of *Pinus* plantations in the Northern and Southern Hemisphere (Morgan, 1989; Dodds et al., 2010; Zylstra et al., 2010; Carnegie and Bashford, 2012). The wasp was first detected in Australia 60 years ago (Gilbert and Miller, 1952) and has now spread to all pine-growing states except Western Australia (Neumann and Minko, 1981; Neumann et al., 1987; Carnegie and Bashford, 2012). A severe outbreak of *S. noctilio* occurred in the Green Triangle region of Australia between 1986 and 1989 where five million trees were killed (Haugen and Underwood, 1990). Based on this outbreak, it was predicted that damage by *S. noctilio* could lead to losses of up to US$60 million per annum if no control measures were taken (Underdown, pers comm.). This outbreak, and potential future losses, provided impetus for the development of the *National Strategy for Control of S. noctilio in Australia* (Haugen and Underwood, 1990). An intensive, integrated control programme based on biological control has since been developed for the wood wasp and has been very successful (Bedding, 2009; Carnegie and Bashford, 2012). Recently,

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however, trap trees primed for the introduction of the biocontrol agents have been attacked by another exotic pest, *Ips grandicollis* (Eichhoff) (Coleoptera: Curculionidae) in parallel with a decrease in the effectiveness of the biological control program (Carnegie and Loch, 2010; Carnegie and Bashford, 2012). Interactions between the two exotic pests and their associated symbionts as well as the likely effects of global warming may be interfering with this novel biocontrol strategy for *S. noctilio*.

Spring and summer is the time that *S. noctilio* adults are expected to emerge and females fly searching for suitable trees in which to lay eggs (Morgan, 1968; Neumann and Minko, 1981). Every year in early summer, plots made of 8–12 trees are treated with herbicide to make them attractive for oviposition by *S. noctilio* (Neumann et al., 1987; Carnegie and Bashford, 2012). These trap tree plots allow the primary biological control agent, the nematode *Beddingia* (=*Deladenus*) *siricidicola* (Bedding) (Sphaerulariidae) to be introduced into locally concentrated areas of *S. noctilio*. The trap trees are felled in late autumn–early winter and inoculated with *B. siricidicola.* Infective female nematodes enter the wasp larvae and eventually invade the ovaries, making them sterile (Bedding, 1972; Bedding and Akhurst, 1974; Bedding and Iede, 2005). From late spring to early autumn, the nematode-infected wasps emerge from trees and the females deposit sterile eggs together with the nematodes into naturally stressed trees. When uninfected females also oviposit eggs into these trees, their larvae subsequently become infected with nematodes, thereby effectively spreading the biocontrol agent.

Pine plantations in Australia are surveyed annually by forest health survey units in each state (Carnegie et al., 2008). Surveys in some states have shown that the bark beetle *I. grandicollis* is also attracted to the weakened trap trees (Carnegie, 2008; Carnegie and Loch, 2010; Carnegie and Bashford, 2012). Bark beetle feeding and associated infection with the beetle associated fungus *Ophiostoma ips* (Rumbold) Nannfeldt is likely to hasten tree drying and death (Zhou et al., 2001) reducing the period over which trap trees are attractive to *S. noctilio*. Earlier work by Carnegie and Loch (2010) indicated that *S. noctilio* preferred to oviposit into trap trees that had not been attacked by *I. grandicollis* and that attack on the trees by the bark beetle appeared to reduce the "window of opportunity" for *S. noctilio* to oviposit. Consequently, this reduces the effectiveness of trees to act as traps for the introduction of nematodes. Furthermore, bark beetle associated fungi (*O. ips*) and nematodes (*Contortylenchus grandicollis* (Massey) Rühm) that *I. grandicollis* introduces into trap trees may interfere with the *S. noctilio* associates, *Amylostereum aereolatum* (Fr.) Boidin (Basidiomycotina: Corticiaceae) and *B. siricidicola* and thus, disrupt female parasitism. The actual role of *O. ips* in *I. grandicollis* biology is not yet known, but such blue-stain fungi are known to block the xylem thus interfering with water flow and physiology of trees (Kopper et al., 2004) and can cause tree death (Christiansen and Solheim, 1990; Yamaoka et al., 1995).

Adult *I. grandicollis* attack stressed, declining or dead trees, freshly cut wood and slash from harvesting or thinning operations (Neumann and Morey, 1984a). They can also attack healthy trees when present in large numbers (Neumann and Morey, 1984a; Neumann, 1987; Byers, 1989). Large numbers of beetles normally arise during drought in areas with plentiful slash due to recent logging operations or where silvicultural practices have been neglected over several years (Kausrud et al., 2012). Recent outbreaks of *I. grandicollis* in Australia have been associated with severe drought and sub-optimal thinning schedules that result in increased tree stress (Carnegie, 2008; Stone et al., 2012). Earlier outbreaks in South Australia, Western Australia and Victoria were associated with drought conditions, ample breeding material such as slash and trees damaged due to storms and fires, and overstocked stands (Neumann, 1987; Morgan, 1989; Wylie et al., 1999). Both *I. grandicollis* and *S. noctilio* have synchronised flight seasons. While *I. grandicollis* can go through multiple generations and has a longer flight season (Neumann and Morey, 1984a; Morgan, 1989; Erbilgin et al., 2002), *S. noctilio* has short flight season and goes through a single generation in the cooler southern states (South Australia, Tasmania and Victoria) and possibly two generations in sub-tropical Queensland (Neumann and Minko, 1981; Taylor, 1981; Wylie et al., 1999). Both pests can hence attack trap trees at the same time, introducing their respective fungus into the wood, but with *I. grandicollis* having the potential to attack trees over a longer period. Since *B. siricidicola* feeds on *A. aereolatum*, there are potential negative implications for *S. noctilio* biocontrol because the *I. grandicollis* associated fungus has potential to spread widely and further (Ghaioule et al., 2007) through the trap trees thus interfering with the nutrition of the wasps' biocontrol agents.

Australia's 1.02 million ha of pine plantations (Garvan and Parsons, 2011) provide ideal breeding material for *I. grandicollis,* but the severity and extent of infestations on trap trees by *I. grandicollis* in areas where *S. noctilio* biocontrol is important is not known. Both biotic and abiotic factors affect bark beetle population growth and spread (Jactel et al., 2009; Bassett et al., 2011; Kausrud et al., 2012). Biotic factors such as pests and damage of trees from diseases, tree age and health influence bark beetle population biology and hence infestations. Abiotic factors related to weather, such as extended periods of drought, fires and storms, stress trees making them susceptible to bark beetle attack (Logan et al., 2003; Bentz et al., 2010). Climate has been directly and indirectly implicated in decline of forest trees, predisposing trees to bark beetle attack and enabling population expansion (Marini et al., 2012). Recent studies have shown that warm winters and dry summers are ideal for build-up of bark beetle populations due to an increase in the number of summer generations (Kausrud et al., 2012). Drought is a leading cause of forest decline, either directly or through drought-induced stress that makes trees susceptible to attack by bark beetles (Allen et al., 2009; Stone et al., 2012). Soil moisture can be used as a measure of the amount of water available for plant growth regardless of site and soil characteristics within an area of homogeneous climate and can be used to assess drought risk in forest trees (Sheffield and Wood, 2008). Damage to trees as a result of fire, wind, pests and diseases can lead to accumulation and presence of litter and slash in forests (Wallin et al., 2004; Jactel et al., 2009). The damaged trees and debris that is left on the ground after thinning or harvesting operations can harbour bark beetle populations (McCullough et al., 1998; Logan et al., 2003; Jactel et al., 2009; Simard et al., 2012) that can migrate to trap trees established for *S. noctilio* biocontrol.

In this study, we surveyed trap trees in south-eastern Australia for the distribution and severity of attack by *I. grandicollis.* The relative importance of weather, soil types, tree health and silviculture within and adjacent to compartments where trap trees plots were established as well as landscape characteristics were factors modelled, in order to explain patterns of attack on trap trees by *I. grandicollis*. Understanding biotic and abiotic factors influencing attack of trap trees by *I. grandicollis* is not only vital in predicting and responding to outbreaks but also in identifying suitable locations for establishing trap tree plots for efficiency of *S. noctilio* biocontrol. Unlike many other studies that have looked at factors influencing bark beetle attack on "green" trees and in natural disturbances and within localised regions (Negro et al., 2008; Santos and Whitham, 2010; Millar et al., 2012), we studied attack by *I. grandicollis* in artificially stressed plantation trees in geographically diverse regions. Based on a literature search, factors that might influence bark beetle attack on trap trees were examined.

2. Materials and methods

2.1. Incidence of I. grandicollis in trap trees in all states

Surveys for *I. grandicollis* attack in trap trees were conducted in four states of Australia where *S. noctilio* biocontrol is important, namely, New South Wales, Victoria, South Australia and Tasmania (Fig. 1). 244 trap tree plots were visited in New South Wales, 69 in Victoria, 50 in South Australia and nine in Tasmania. In December of 2009 and 2010, 8–12 trees were treated with herbicide to make them attractive for oviposition by *S. noctilio* (Carnegie and Bashford, 2012). The trap trees were felled in winter of 2010 and 2011, respectively, and examined along the entire trunk length for entry or exit holes of *I. grandicollis*. For ease of access to the entire tree length, fallen trees were assessed and just the part that was exposed was examined. Presence of *I. grandicollis* was confirmed if holes were accompanied with red-brown or pale white frass at points of entry or exit. The presence of *I. grandicollis* was confirmed if adults, teneral adults, larvae or eggs were present in the galleries after peeling off the bark (Neumann, 1987). In total, 372 trap tree plots and 3,799 trap trees were examined for presence/absence of *I. grandicollis* in all states.

To assess the severity of attack by the beetles, 1913 of 3799 trap trees examined above were assessed by visually dividing the trees into bottom, middle and upper sections. Presence or absence of exit or entry holes in the bottom, middle and upper section was recorded. Attack on trap trees by *I. grandicollis* was later assigned 0 if no entry holes were observed on the tree, 1 if attack was confined to a single section, 2 if attack was observed on two sections or 3 if attack was recorded on all three sections. These data provided information on severity of attack (severity rating) by the bark beetle at the tree level, and was also used to determine the section of tree where *I. grandicollis* most frequently attacks trap trees. This assessment was conducted only on trap trees in Hume, Macquarie, Monaro-Bombala and Monaro-Moss Vale (New South Wales) and Bombala (Victoria) during 2010.

Fig. 1. Regions in New South Wales, Victoria, South Australia and Tasmania in south-eastern Australia where *S. noctilio* biocontrol is important and surveys for incidence of *I. grandicollis* in trap trees were conducted in 2010/2011. Symbols on the map indicate location of trap tree plots in the respective grower regions (Shaded areas indicate *National Forest Inventory regional classification*).

2.2. Explanatory factors for I. grandicollis attack on trap trees

Age of trees (in years), damage of trap trees in the trap tree plot and in the adjacent compartment, longitude-latitude, rotation, year of survey, slash in the compartment where trap trees were located, maximum and minimum temperatures during the year of survey and 1, 2, 3 years before the surveys, total rain during the year of survey and 1, 2, 3 years before the surveys, lower and upper soil moisture during the year of survey and 1, 2, 3 years before the surveys, slope, direction, soils were potential explanatory factors expected to influence *I. grandicollis* infestation on trap trees (Table 1). These factors were investigated for New South Wales as records on silviculture and forest health were readily available from project partners. The factors were recorded at the trap tree plot location, the compartment where trap tree plots were established and in compartments adjacent to trap tree plots (Table 1). Biotic and abiotic factors were recorded for 239 trap tree plots that were surveyed in Monaro-Moss Vale, Monaro-Bombala, Hume, Macquarie, Northern-Walcha (Fig. 1). Northern-Grafton region was omitted in the model since only two trees of the eight that were examined had been attacked by *I. grandicollis*. Location data were recorded as Geographic Positioning System (GPS) records which allowed retrieval of biotic and abiotic data from New South Wales Forestry Corporation geodatabase. The GPS recordings were recorded as Universal Transverse Mercator (UTM) values using the Geocentric Datum of Australia 1994 (GDA94) covering three UTM Zones (54, 55 and 56). For analysis, latitude and longitude were calculated from the UTM values. Slope was expressed as the angle in degrees between the ground and the horizontal base line. Age of trap trees was recorded from the New South Wales fire Atlas during the time of surveys.

Monthly maximum and minimum temperatures as well as monthly rainfall data for 2006–2011 were sourced from the Commonwealth Bureau of Meteorology (BOM) climatic datasets. The

Table 1
Variables included in the model to assess factors that influence *I. grandicollis* infestation of trap trees established for the biological control of *S. noctilio*. The variables were measured at trap tree plot location, compartment level and at compartments adjacent the trap tree plots.

Variable	Scale of assessment	Possible relationships	Source of data
Response variable			
Incidence of I. grandicollis	Trap tree plot	*I. grandicollis* attacks trap trees primed for *S. noctilio* biocontrol and reduces the window of opportunity for wasp females to oviposit	Current study
Explanatory variables			
Age class (in years)	Trap tree plot	Older stands may be more susceptible to *I. grandicollis* due to accumulated damage	Forestry Corporation of NSW geodatabase
Aspect	Trap tree plot	Trees growing on east–west-facing slopes may have a higher phloem temperature, which increases winter survival and development rate in the summer. Trees are also more water stressed on east–west-facing slopes	Commonwealth bureau of meteorology (BOM)
Slash evidenced by clearfall or thinning operations	Compartment of trap tree plot and adjacent compartment	Slash left on the ground after thinning and harvesting operations harbours populations of *I. grandicollis* which could migrate to attack weakened trap trees	Forestry Corporation of NSW geodatabase
Elevation (m)	Trap tree plot	Tree mortality is low at high elevation due to cooler temperatures and reduces development of bark beetles and increases winter mortality Trees growing in lower-elevation sites may be more water stressed and more susceptible to bark beetles.	Forestry Corporation of NSW geodatabase
Quarterly maximum temperatures (°C) in 2006–2011	Trap tree plot	High phloem temperature may increase *I. grandicollis* winter survival and development cycles and warm temperatures may trigger outbreaks. Warm winters would be ideal for build-up of *I. grandicollis*	Commonwealth bureau of meteorology (BOM)
Quarterly minimum temperatures (°C) in 2006–2011	Trap tree plot	Mild seasonal temperatures may increase *I. grandicollis* survival and development rate	Commonwealth bureau of meteorology (BOM)
Total and quarterly rainfall (mm) in 2006–2011	Trap tree plot	Less rainfall may lead to water stress on trees and dry summers would be ideal for build-up of *I. grandicollis* through increased reproduction and drought-induced stress on the trees	Commonwealth bureau of meteorology (BOM)
Regions	Trap tree plot	Bark beetle populations vary between locations due to infrequent climatic events which may synchronise population cycles across geographic areas.	Present study
Regolith	Compartment	Regolith influences soil erosion which can cause water stress on trap trees	Forestry Corporation of NSW geodatabase
1st and 2nd rotation	Trap tree plot	Prior non-forested sites produce logs with lower density and less able to withstand stress.	Forestry Corporation of NSW geodatabase
Slope (°)	Trap tree plot	Slope influences soil depth, soil slippage, direct disturbance from wind, water availability and root health	Commonwealth bureau of meteorology (BOM)
Soils	Trap tree plot	Trees growing on coarse-textured soils may be more water stressed Trees growing on acidic soils may have reduced growth rates because of lower nutrient availability	Atlas of Australian Soils Bureau of Rural Sciences (BRS)
Quarterly upper and lower soil moisture (upper layer = 0–0.7 m, lower layer = 0.5–1.9 m)	Trap tree plot	Relative soil moisture, the amount of water available for plant growth can be used to assess drought risk of forest trees	Australian Water Availability Project (AWAP) CSIRO, Canberra, Australia
Year of survey	Trap tree plot	Bark beetle populations vary between years as population dynamics are influenced by both density-dependent interactions with natural enemies and environmental effects on host trees	Present study
Damage events- Tree damage from wind, fire, drought, *Diplodia pinea*, *S. noctilio* outbreaks	Compartment of trap tree plot and adjacent compartment	Damage due to wind, fire or drought may result in tree stress or slash on the ground which triggers attacks or harbours *I. grandicollis* Diseases e.g., from the fungus *Diplodia* sp. and outbreak of other pests induce stress on trees	NSW DPI Forest Health geodatabase

BOM datasets for minimum and maximum temperature and rainfall were based on Australia Gridded monthly temperature and Gridded monthly rainfall (resolution of approximately $0.05 \times 0.05°$). Data on upper soil layer (0–0.7 m) and lower soil layer (0.5–1.9 m) moisture (hereafter referred to as upper soil moisture and lower soil moisture) were expressed as percentile ranks (pcr) (Raupach et al., 2009; Raupach et al., 2012) and were obtained from the Australian Water Availability Project (AWAP) CSIRO, Canberra, Australia (Raupach et al., 2012). The data from March 2006 to May 2011 were used to create a surrogate drought index that investigated whether soil moisture was a source of stress on trees and hence influenced the impact of attack on trees by *I. grandicollis*. The corresponding rainfall (mm d^{-1}), and pcr for the maximum daily temperatures were calculated at 5 km grid cells.

Average quarterly rainfall, maximum and minimum temperatures, lower and upper soil moisture were calculated for the four seasons in the year of survey: winter (June, July, August), spring (September, October, November), summer (December, January, February) and autumn (March, April, May). Total rainfall, lower and upper soil moisture in the preceding three years from the year of surveys (survey year-1, survey year-2, survey year-3) from June to May of each year were used to assess drought indices and how this influenced occurrence of *I. grandicollis* in trap trees. Information on rotation (first rotation sites were previously pastureland; second rotation sites were previously pine plantations), regolith (a 1–4 classification of soil erodability, Murphy et al. (1998)), and recent harvesting operations (either final harvest or thinning) that would result in slash and litter left on the ground were sourced from the New South Wales Forestry Corporation geodatabase. Data on tree damage as a result of wind, fire, drought, *S. noctilio* outbreaks or trees infected with *Diplodia pinea* (=*Sphaeropsis sapinea*), were sourced from the NSW DPI Forest Health geodatabase, and are based on annual surveys over the entire pine plantation estate (Carnegie et al., 2008). Data from 2006 to 2011 were used, and the damage events were combined as the values were too few to analyse each individual factor for the different regions. Rotation, regolith, slash, and damage data were recorded at the compartment level where trap tree plots were located and also from the immediate adjacent compartments.

2.3. Statistical analysis

The proportion of trap trees that was attacked by *I. grandicollis* in a trap tree plot was used as the response variable and modelled against tree age, state and region using a Generalised Linear Model (GLM) assuming a binomial distribution and a logit link. Northern-Walcha region in New South Wales and all regions in Tasmania were omitted from this analysis as *I. grandicollis* was not observed in trap trees. To determine the section of tree most attacked by *I. grandicollis*, data was analysed using a Generalised Linear Mixed Model (GLMM) assuming a binomial distribution and repeated measures within trees.

To examine the influence of environment and silviculture on the incidence of *I. grandicollis* on trap trees, the proportion of trees attacked by *I. grandicollis* in a trap tree plot was modelled against the biotic and abiotic factors. The analysis used a GLM assuming a binomial distribution and a logit link as follows.

$$E(Y) = \mu = g^{-1}(X\beta),$$

where $E(Y)$ is the expected proportion of trees attacked by *I. grandicollis*; μ the Binomial distribution; g the logit link function; X the environment and silviculture factors (Table 1).

Stepwise regression methods, starting with all terms were used to create a model in which all terms were significant ($P < 0.05$). The terms were; tree age, elevation, regolith, rotation, aspect, year of survey, slope (in degrees), slash presence, latitude, longitude, damage in 2006, 2007 and 2008 for trees in the compartment where trap tree plots were located and sourced from the forest health survey database, damage of trees in the adjacent compartment in 2006, 2007 and 2008, damage of trees in the compartment of trap trees assessed during the surveys (sourced from the forest health survey database), maximum and minimum temperature in 2006–2011 (in autumn, spring, summer and winter), total rain (1, 2, 3 years before survey), total rain (in autumn, spring, summer, winter) in the year of survey, upper and lower soil moisture (in autumn, spring, summer, winter) during the year of survey and upper and lower soil moisture 1, 2 and 3 years before the surveys (sourced from BOM).

A model was also created starting with no terms and adding terms from the above list which gave key variables that significantly were identified as key predictors of f *I. grandicollis* in trap trees. The predicted means were obtained from the model weighted for other factors according to their marginal distribution. Analysis was conducted in GENSTAT v 15 (VSN International, 2012) at $p < 0.05$ level of significance. Distribution of *I. grandicollis* maps and all mapping components were conducted using ESRI's ArcGIS 10.0, with an ArcInfo licence and Spatial Analyst extension.

3. Results

3.1. Incidence of I. grandicollis in trap trees in all states

Results showed a significant difference in *I. grandicollis* attack in trap trees amongst the regions surveyed (df = 2; $F = 25$; $P < .001$: Table 2, Fig. 1). Incidence of *I. grandicollis* was particularly high on trap trees in one or more of the sampled sites in every region where attack was recorded. Estimated mean proportion of trap trees attacked by *I. grandicollis* in South Australia was highest, followed by New South Wales and Victoria which had the least incidence of attack (Table 2). Bark beetle incidence was especially high in trap trees in all regions in South Australia (77–99%) and in Hume in the Murray Valley in New South Wales (58%). In Victoria, the highest incidence of trap trees attacked by *I. grandicollis* was in Ballarat in Central Victoria (38%) (Table 2).

Position of tree that was attacked by *I. grandicollis* differed significantly between states (df = 2; $F = 89$; $P < .001$). Trap trees in South Australia were frequently attacked by the bark beetle over two-thirds of tree length compared to a third of tree length in New South Wales. Estimated mean proportions for Ranges in South Australia was highest with a mean predicted proportion of 59% trees attacked along the entire length, followed by Hume (53%), Macquarie (14%), Monaro-Bombala (12%), Monaro-MossVale (8%) and Bombala (0%) which had the least proportion of trees attacked. There were also significant differences in position of attack between regions ($P < .001$: Table 3). In South Australia, attack by *I. grandicollis* was concentrated in the upper and middle sections of trees while there was no preference of attack on attacked trees in Victoria and New South Wales (Table 3).

3.2. Explanatory factors for I. grandicollis attack on trap trees

Starting with the full model with all the terms included and dropping non-significant terms, the following factors were fitted as the key predictors of *I. grandicollis* in trap trees: age of trees (in years), number of damage events in 2006, number of damage events in trees adjacent the trap tree plot, longitude-latitude, rotation, year of survey, presence of slash in the compartment where trap trees were located, maximum spring, summer and winter temperatures during the year of survey, minimum autumn and winter temperatures during the year of survey, total rain one year

Table 2
Infestation by *I. grandicollis* in trap trees in *P. radiata* production regions of Australia.

State	Grower Region	Numbers of trees examined	Percent *I. grandicollis* attack (mean (±SE)
New South Wales	Hume	868	58 ± 4
New South Wales	Macquarie	1064	22 ± 3
New South Wales	Monaro–Bombala	291	16 ± 5[b]
New South Wales	Monaro–Moss Vale	60	17 ± 11
New South Wales	Northern–Grafton	28	25 ± 36
New South Wales	Northern–Walcha	180	–[a]
South Australia	Limestone Coast	10	99 ± 1
South Australia	Mt. Gambier	220	77 ± 7
South Australia	Ranges	250	79 ± 7
South Australia	Upper South East	20	99 ± 1
Tasmania	Pittwater	30	–[a]
Tasmania	Retreat	30	–[a]
Tasmania	Virginstone	30	–[a]
Victoria	Ballarat	470	38 ± 5
Victoria	Bombala	140	2 ± 3[c]
Victoria	Gippsland	130	18 ± 8

[a] Trees not infested with *I. grandicollis*.
[b] Trap trees were in the privately owned Willmott Forests Pty Ltd plantations at the border of New South Wales and Victoria.
[c] Some trap tree plots were state forest plantations and others were in the privately owned Willmott Forests Pty Ltd. plantations.

Table 3
Mean proportion (± std err) of trees infested with *I. grandicollis* in the lower, middle and upper sections in New South Wales, South Australia and Victoria.

State	Growers region	Trees attacked in lower section	Trees attacked in middle section	Trees attacked in upper section
New South Wales	Hume	0.73 ± 0.02	0.68 ± 0.02	0.56 ± 0.03
New South Wales	Macquarie	0.22 ± 0.02	0.28 ± 0.02	0.22 ± 0.02
New South Wales	Monaro/Bombala	0.19 ± 0.03	0.23 ± 0.03	0.21 ± 0.03
New South Wales	Monaro/Moss Vale	0.10 ± 0.05	0.15 ± 0.06	0.20 ± 0.06
South Australia	Ranges	0.10 ± 0.05	0.61 ± 0.03	0.60 ± 0.03
Victoria	Bombala	0.01 ± 0.01	0.01 ± 0.01	0.02 ± 0.01

before the surveys, rainfall in autumn, spring and summer in the year of survey, lower soil moisture in spring and summer in the year of survey, upper soil moisture two and three years before the surveys and lower soil moisture one and two years before the survey. This model accounted for 58.7% of the deviance.

Starting with a null model and building a model with all the significant terms from the full model, four weather and two silvicultural factors were found to be key predictors of *I. grandicollis* in trap trees accounting for 46.3% of the deviance (Fig. 2). Maximum summer temperature in the year of survey accounted for the highest percent deviance of all the variables that were found to influence the incidence of *I. grandicollis* in trap trees accounting for 21.1% of the variance. This was followed by maximum winter temperature in the year of survey, lower soil moisture two years before the surveys, upper soil moisture in summer in the year of survey, age of trees, damage of trees within the trap tree plot and lower soil moisture in Autumn in the year of survey (Fig. 2). *Ips grandicollis* incidence increased as maximum summer temperature increased (Fig. 3a) and decreased as maximum winter temperatures increased (Fig. 3b). The estimated probability of trap trees attacked by *I. grandicollis* increased with lower soil moisture two years before the surveys increased (Fig. 3c) which contrasts with a decrease in bark beetle incidence when upper soil moisture in summer increases (Fig. 3d). The model showed that younger trees were more vulnerable to attack by *I. grandicollis* compared to older trees (Fig. 3e). As lower soil moisture in autumn increases, the incidence of *I. grandicollis* attacking trap trees also increases (Fig. 3f). Trap tree plots situated in compartments that had trees damaged by fire, drought, *Diplodia*, wind or outbreaks by *S. noctilio* had a higher probability of being attacked by *I. grandicollis* (0.46 ± 0.04) compared to plots located in compartments that sustained no damage (0.35 ± 0.06) (df = 1; $F = 11.92$; $P < .001$). Damage in compartment where trap trees were located in 2006, longitude, rotation, year of survey, slash (evidenced by thinning and

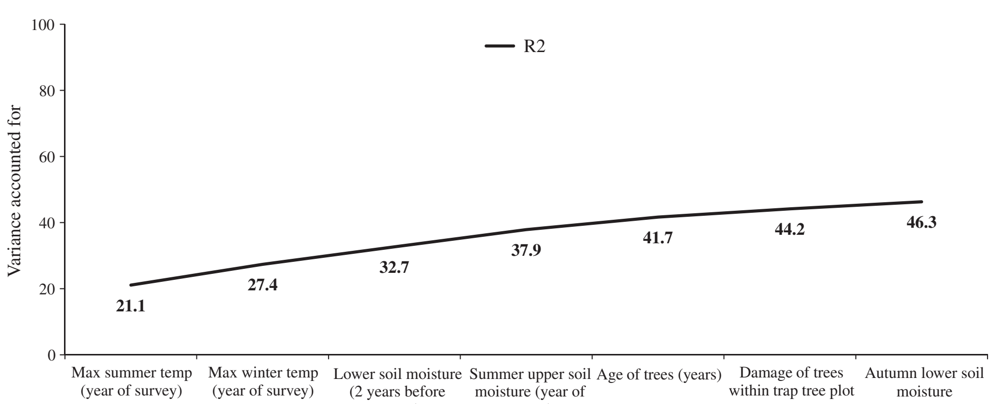

Fig. 2. Cumulative deviance in trap tree infestation by *I. grandicollis* accounted for by environmental, site and silvicultural factors. (max = maximum and temp = temperature).

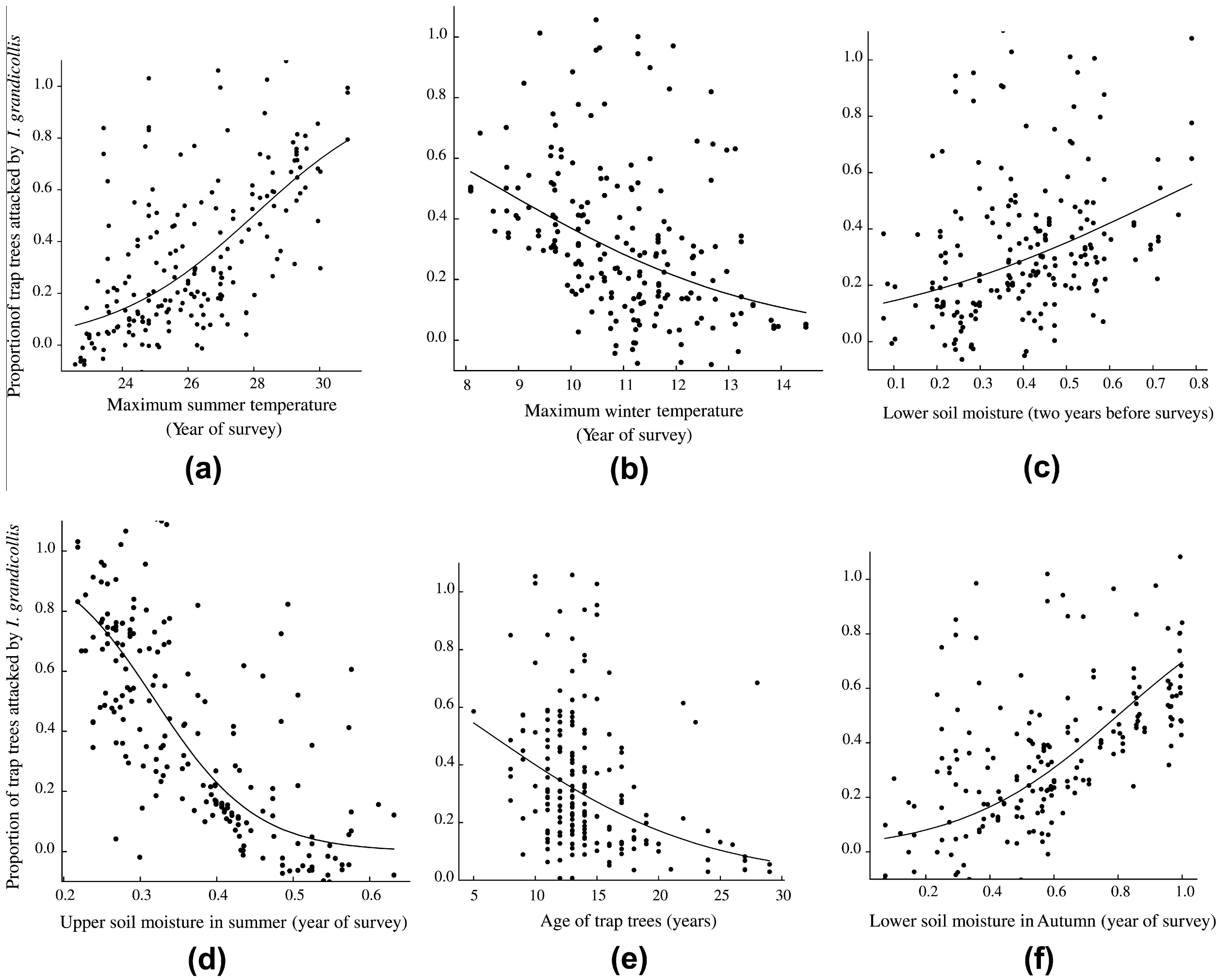

Fig. 3. Correlation between estimated mean proportion of numbers of trap trees attacked by the bark beetle, *I. grandicollis*, and tree and environmental factors (a) maximum summer temperatures (°C) (b) maximum winter temperatures (°C) (c) lower soil moisture two years before the surveys (d) upper soil moisture in the year of survey (e) age of trap trees (in years) and (f) upper soil moisture in autumn in the year of survey.

harvesting operations), maximum spring temperature in the year of survey, maximum and minimum autumn temperature in the year of survey, minimum winter temperature in the year of survey and total rain one year before the surveys were less important but significant predictors of *I. grandicollis* in trap trees accounting for 12.4% of the variance.

4. Discussion

This is the first comprehensive study on *I. grandicollis* attack of trap trees established for *S. noctilio* biological control, covering all major pine plantation areas in south-eastern Australia. The surveys identified the main areas where *I. grandicollis* may be disrupting *S. noctilio* biological control. *Ips grandicollis* was observed attacking trap tree in plots in all mainland states where surveys were conducted (South Australia, Victoria and New South Wales), but not the island state of Tasmania, where the bark beetle is known not to be established (Elliott et al., 1998, Bashford, 2012, unpublished data). Within the mainland states, *I. grandicollis* was present in all regions, with significant differences between incidences of attack on trap trees amongst regions. Attack was most severe in South Australia, with 77–99% of trap trees attacked by *I. grandicollis* in the four regions surveyed. In some respects this was not expected, as specific management operations such as chopper-rolling of slash post-harvest are conducted to reduce levels of *I. grandicollis* in plantations in the Green Triangle (Phillips, 2011, pers. comm.). There has, however, been a history of tree damage by *I. grandicollis* in certain regions in South Australia, including attack on live trees during drought (Morgan, 1968) and more recently on *S. noctilio* trap trees (Phillips, unpublished).

There was a lot of variability in attack amongst regions in New South Wales, with Hume having the most severe attack (58% of trap trees) and low levels of between 16% and 25% of attack in most of the other regions other than Northern-Walcha where no beetle attack was recorded on trees. In Victoria, incidence of *I. grandicollis* in trap trees was generally low, with Ballarat having the highest incidence of trees attacked (38%) moderate attack in Gippsland (18%) and negligible attack in Bombala which is adjacent to the New South Wales border region of Monaro-Bombala. Drought and fire incidences in the Hume region over the years (Carnegie 2008; Stone et al., 2012) are possible factors that may have induced stress on trees and this had a carry- over of beetle populations leading to subsequent attacks on the herbicide treated trees. In Northern regions of New South Wales (Grafton and Walcha), *I. grandicollis* is known to be present in plantations and can be found in high numbers in slash following harvesting operations (Carnegie, 2011, unpublished, Stone, 1993; Stone et al., 2012). Previous surveys in Northern-Grafton have shown that high numbers of trap trees (50–100%, mean 90%) are attacked by *I. grandicollis* (Kent, 2005, unpublished data). As a consequence of this high attack, static traps (Bashford, 2008; Bashford and Madden, 2012) are now used in this region in place of trap trees for early detection of *S. noctilio* and for decision making on whether trap tree plots are needed. In Northern-Walcha, though, during the period of this study there were no thinning or harvesting operations in areas where trap trees were established and therefore there would not have been significant migration of beetles to trap trees from litter in the neighbouring compartments.

Previous studies have been conducted on an endemic pest and forest ecosystem, whereas our study was performed on an exotic pest in an artificial plantation system of exotic hosts. Drought was the major driver for *I. grandicollis* incidence in trap trees. Drought-induced damage on trees in compartments where trap trees are located or in adjacent compartments could have led to accumulated damage and hence availability of potential breeding sites for *I. grandicollis* facilitating easy migration into the artificially stressed trap trees. Recent studies (Stone et al. 2012) showed that some plantations of *P. radiata* within southern New South Wales experienced significant mortality in the stand when exposed to prolonged and severe drought that prevailed for 10 years. Maximum summer temperature was the next key predictor of *I. grandicollis* attack on trap trees, with high summer temperature corresponding with high attack by *I. grandicollis* on trap trees. Warm summers are likely to influence bark beetle attack by providing favourable temperature conditions for breeding (Aukema et al., 2008; Raffa et al., 2008) and also by causing further stress on trees, thus providing susceptible host trees for beetle attack (Aukema et al., 2008; Friedenberg et al., 2008). Low maximum winter temperatures were also a predictor of *I. grandicollis* attack on trap trees. The decline in overwinter survival with increasing temperature maybe an outcome of the proportion of insects entering diapause, a quiescent phase used by many species to survive periods of adverse environmental conditions. The only study of overwintering of *I. grandicollis* (Lawson, 1993) found high rates of mortality in a South Australian population but did not identify the existence of diapause. Other bark beetles, however, are known to enter winter diapause; *I. typographus* (Berec et al., 2012) and *Dendroctonus ponderosae* Hopkins (Lester and Irwin, 2012), so future investigations are likely to establish the same capacity in *I. grandicollis*. Low temperature is an important cue for the onset and maintenance of diapause in many insects so are likely to favour overwinter survival in bark beetles. Cold winters are expected to reduce bark beetle numbers through mortality of the over-wintering generation (Neumann and Morey, 1984b; Neumann, 1987; Friedenberg et al., 2008) and as such warm winter temperatures are expected to increase beetle survival as well as potentially add another generation (Friedenberg et al., 2008; Kausrud et al., 2012). Winters in the New South Wales region where data in this study was modelled, however, are less severe compared to other studies in North America where there would be many days of sub-zero temperatures (Aukema et al., 2008; Friedenberg et al., 2008; Bentz et al., 2010). In New South Wales, the reason could be that the days in which *I. grandicollis* are exposed to the low winter temperatures are less than five days thus a large number of larvae survive the winter and are available to attack trees in spring.

Coupled with high summer temperatures, drought may have a direct impact on soil moisture by increasing the rate of evapotranspiration from trees. Upper (0–0.7 m) soil moisture was a good predictor of *I. grandicollis* incidence, with low soil moisture raising the incidence of the bark beetle attack. Low soil moisture is likely to result in water stress to trees, thus reducing oleoresin production and increased tree susceptibility to *I. grandicollis.* Successful attack by bark beetles in living trees is associated with lower oleoresin pressure, which can be triggered by damage, drought and in our case, herbicide treatment. Tree resistance factors include increased production of phenolics at attack sites, increased resin flow and oleoresin pressure, increased bark thickness and levels of Calcium oxalate crystals in the phloem (Hudgins et al., 2003) which are negatively affected by water availability within the tree. Combined with high mean annual temperatures, drought is likely to result in reduced available soil water in many parts of pine plantations in Australia. This leads to likely build-up of bark beetles in trees in the adjacent compartments within a plantation which would lead to migration of the pests to trap trees.

Tree damage from fire, wind and disease influences bark beetle outbreaks by providing large numbers of susceptible trees (McCullough et al., 1998; Wylie et al., 1999; Logan et al., 2003; Jenkins et al., 2008; Simard et al., 2012). In this study, damage to trees (associated with fire, wind-throw, disease from *Diplodia pinea* and *S. noctilio* outbreaks) four years before the surveys was an important predictor of *I. grandicollis* attack in trap trees. These damage events may have caused tree death and increased litter on the ground over time which may have harboured populations of *I. grandicollis*. Tree age was the other key predictor for presence of *I. grandicollis* in trap trees. Tree age influences bark beetle attack by increased food availability in larger trees (Negro et al., 2008; Santos and Whitham, 2010). Neumann and Morey (1984a,b), who studied attack of green trees by *I. grandicollis* in Victoria, also showed that attack occurred to younger (7–19 years), smaller trees. In our study, one explanation for the observed attack on smaller trees could be that younger trees are usually selected as trap trees. In New South Wales, for example, *S. noctilio* attack in plantations is concentrated in 8–16 year-old trees (Carnegie, unpublished).

4.1. Implications for S. noctilio biological control

Incidences of *I. grandicollis* in trap trees primed for nematode inoculation could have far reaching implications for the biological control of *S. noctilio*. Results from this study highlight areas where potential management strategies in order to reduce attack of trap trees by *I. grandicollis* could be deployed. Establishing the incidence and variability of attack by *I. grandicollis* on trap trees in different regions may lead to understanding the causes of attack. This knowledge will be useful to forest managers for selecting areas for setting up trap trees for *S. noctilio* biocontrol.

Studies by Carnegie and Loch (2010) and Gitau et al. (unpublished data) showed that trap trees attacked first by *I. grandicollis* are unattractive for oviposition by *S. noctilio* females. Secondly, *I. grandicollis* introduces the *O. ips* fungus which grows rapidly, spreading into the sap wood and competing for resources with the *S. noctilio* fungus, *A. aereolatum*. Thus, *O. ips* may impede development and survival of *S. noctilio* larvae which depend on *A. aereolatum* for nutrition, resulting in emergence of small sized progeny (Villacide and Corley, 2008). Assessing factors that impact on trap trees is an approach that gathers information which forest managers could consider in the management and re-evaluation of standard operating strategies when establishing trap trees. Weather components, especially temperature and rainfall, and damage within trap tree plots, were the significant drivers for the incidence of *I. grandicollis* attack on trap trees. Drought increases susceptibility of trees to insect attack and may harbour populations of the bark beetle which could migrate to attack dying trap trees setup for *S. noctilio* biocontrol. Removing or treating damaged trees, e.g. from wind-throw, drought, lightning, fire and storm, would reduce breeding and feeding habitat thus minimising bark beetle numbers. Thinning under optimum prescriptions (Stone et al. 2012) may help in maintaining proper stand densities, thus reducing tree stress, and hence reducing the likelihood of bark beetle attack in trap trees. Unfortunately, silvicultural practices are not always economically or operationally feasible, and environmental changes are often unavoidable. As forest managers have no control over weather factors, silvicultural and landscape factors may be taken into account when selecting compartments in which to establish trap tree plots in areas where *S. noctilio* is prevalent. Forest managers should avoid establishing trap tree plots in areas of high drought risk or sites known to have poor water holding capacity or low site quality. As mentioned above, the trees assessed in this study had been treated with a herbicide, in an exotic plantation estate, while previous studies have investigated bark beetle outbreaks and damage under natural disturbances. Our study identified factors that may influence attack by bark beetles under these artificial settings, highlighting the need for such investigations to ellucidate factors that may be utilised in improving pest management programs. This study also demonstrates the need to consider other predictors on possible interference to pest management programs other than those that have been documented as key in natural mortality conditions.

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