

The interaction of drought and the outbreak of *Phoracantha semipunctata* (Coleoptera: Cerambycidae) on tree collapse in the Northern Jarrah (*Eucalyptus marginata*) forest.



by
Stephen Seaton
(BSc Environmental Science)

This thesis is presented in partial fulfilment of the requirements for the degree of
Bachelor of Science (Honours)

School of Biological Sciences and Biotechnology,
Murdoch University, Perth, Western Australia
November 2012

COPYRIGHT ACKNOWLEDGEMENT

I acknowledge that a copy of this thesis will be held at the Murdoch University Library.

I understand that, under the provisions s51.2 of the Copyright Act 1968, all or part of this thesis may be copied without infringement of copyright where such a reproduction is for the purposes of study and research.

This statement does not signal any transfer of copyright away from the author.

Signed: Stephen Seaton

NAME OF DEGREE: Bachelor of Science with Honours in Biological Sciences

THESIS TITLE: The interaction of drought and the outbreak of *Phoracantha semipunctata* (Coleoptera: Cerambycidae) on tree collapse in the Northern Jarrah (*Eucalyptus marginata*) forest

AUTHOR: Stephen Ashley Hartley SEATON

YEAR: 2012

Declaration

I declare that that the work contained within this thesis is an account of my own research, except where work by others published or unpublished is noted, while I was enrolled in the Bachelor of Science with Honours degree at Murdoch University, Western Australia. This work has not been previously submitted for a degree at any institution.

Stephen Seaton

November 2012

Conference Presentations

Seaton, S.A.H., Matusick, G., Hardy, G. 2012. Drought induced tree collapse and the outbreak of *Phoracantha semipunctata* poses a risk for forest under climate change. Abstract presented at the Combined Biological Sciences Meeting (CBSM) 2012, 24th of August. University Club, University of Western Australia.

Seaton, S.A.H., Matusick, G., Hardy, G. 2012. Occurrence of Eucalyptus longicorn borer (*Phoracantha semipunctata*) in the Northern Jarrah Forest following severe drought. To be presented at The Australian Entomological Society - 43rd AGM & Scientific Conference and Australasian Arachnological Society - 2012 Conference. 25th – 28th November. The Old Woolstore, Hobart.

Acknowledgments

I greatly appreciate the guidance, enthusiasm and encouragement and tireless support from my supervisors Dr George Matusick and Prof Giles Hardy in the Centre of Excellence for Climate Change Forests and Woodland Health. I particularly appreciate the interaction and productive discussions regarding forest ecology and entomology and proof reading the manuscript.

I would like to acknowledge the financial support given from the National Climate Change Adaptation Research Facility (NCCARF) Terrestrial and Biodiversity Network. I would also like to thank the donors of the Myrtle AB Lamb Scholarship and the Men of the Trees/Shirley Fyfe Scholarship for their financial assistance during this Honours project.

Thank you to Dr Niels Brouwers of Murdoch University for advice on GIS analysis and Dr Bill Dunstan for his assistance. Thanks also to Prof Michael Calver for statistical advice.

Finally, grateful thanks to my parents for their ongoing support, advice and encouragement.

Abstract

The Eucalyptus longhorned borer *Phoracantha semipunctata* Fabricius is an endemic Cerambycid beetle to the Northern Jarrah Forest (NJF) of south-western Australia that attacks stressed trees. The population dynamics, distribution and biology of *P. semipunctata* in its native habitat are poorly understood. Following a recent drought event in 2010 patches of jarrah and marri trees throughout the NJF suffered high mortality with a noticeable increase in the borer populations. The aims of the present study were to determine the effect of this drought on *P. semipunctata* populations in jarrah (*Eucalyptus marginata* Donn ex Smith) and marri (*Corymbia calophylla* Hill) trees across the NJF and to determine if they would attack healthy adjacent trees, when their population levels were high. The association between the health of trees and *P. semipunctata* infestation was determined in standing dead, dying or healthy trees located in intact and collapsed areas of forest. Life cycle stages of *P. semipunctata* in terms of egg clutches, neonate feeding galleries, mature larvae and pupae in heartwood and adult emergence holes were determined by felling jarrah and marri trees. Distribution of *P. semipunctata* across the NJF was investigated by counting adult emergence holes in the bark of standing trees dead, dying or healthy trees at a number of collapsed sites.

The health of trees in collapsed areas had clearly deteriorated where 76 % of trees had lost all or part of their canopy and 18 % had recently died. In contrast, the health of the trees in the surrounding intact areas where 37 % had lost all or part of their canopy and less than 1 % of trees had recently died. There was a strong association between *P. semipunctata* infestation and the health of the trees, with the borers concentrated in trees in collapsed sites with an average of 4.5 emergence holes (m^{-2}) of *P. semipunctata* for the first 2 m of the tree in collapsed areas compared to an average of 0.1 emergence holes (m^{-2}) in the

healthy intact areas. *Phoracantha semipunctata* were attracted to trees that had lost all or part of their canopy or had died since the drought with 94 % of individuals in these trees and less than 1 % of *P. semipunctata* in healthy trees with an intact canopy. The low levels of *P. semipunctata* in the trees that had lost their canopy in the intact areas tends to indicate this may be the normal or 'background' level of infestation in the NJF. These background levels may increase with the occurrence of more collapsed areas under increased frequency of droughts, due to the predicted declines in rainfall in the south-west of Western Australia.

Destructive sampling in April showed that infestation levels within trees were very high with a maximum of 429 emergence holes per tree for jarrah and 345 emergence holes per tree for marri. Averaged across four collapsed sites, marri had higher levels of infestation with 15.42 emergence holes (m^{-2}) compared to jarrah with 10.55 emergence holes (m^{-2}) for the entire tree. In jarrah and marri an increase in clutch points (i.e. oviposition sites) and more neonate larvae (i.e. number of larval tracks) resulted in a higher number of emergence holes. Most of larvae in the heartwood had emerged at the time of sampling being low in number but were higher in jarrah compared to marri. The differences in the total *P. semipunctata* emergence holes (m^{-2}) between jarrah and marri was a result of a complex interaction of tree height and diameter over bark (DOB), where number of emergence holes (m^{-2}) decreased with height and tree species, giving a range of responses at different sites. These differences in *P. semipunctata* infestations between jarrah and marri varied with sites. The distribution of *P. semipunctata* infestations within trees were strongly associated with billet size as it varied with tree height with higher infestations of *P. semipunctata* occurring closer to the base of the tree where trees had a large diameter (15-22 cm). Bark thickness ranged from 10-14 mm and was found to be positively

correlated with billet diameter ($r^2 = 0.372$, $P < 0.001$). It was also thicker in marri (averaging 12 mm) than jarrah (averaging 10 mm). As jarrah stem diameter decreased less with height than marri, lower levels of infestation by *P. semipunctata* occurred for marri at the same height of tree as compared to jarrah. The damage (on a surface area basis) to the sapwood from larval feeding galleries was considerable with up to 100 % for jarrah and 76 % for marri with an average of 48.2 % and no difference between jarrah and marri across all sites. Sapwood damage decreased 30 to 50 % with tree height above 3 m where there were less emergence holes (m^{-2}).

Considerable variation in terms of site characteristics (rainfall, soils, stand density and proportion of jarrah to marri) occurred across the NJF and no one factor was critical in determining which sites had trees that were most affected by the drought. Sites where trees had suffered the most canopy loss had the highest (6 emergence holes (m^{-2})) or 20,000 borers/hectare. This relationship accounted for most of the variation of *P. semipunctata* populations differences between sites across the NJF. A consistent feature of *P. semipunctata* infestation in the NJF was the occurrence of collapsed patches of various sizes and different numbers of *P. semipunctata* across the NJF. Green height (G_H) (the proportion of the original tree height for which green foliage remained) and canopy remaining on the tree were found to be good estimates of tree health and canopy remaining was highly correlated with epicormic shoot occurrence. Trees that lost most of their canopy during the 2010 drought had recovered by producing a large number of epicormic shoots. However, some of these epicormic shoots died, indicating that recovery may be short term either from continued drought events in 2012, for example the low July rainfall and possibly the effects of damage from borers. Densities of jarrah and marri varied

between sites and had a large influence on the total number of *P. semipunctata* that occurred at a site.

The location, health of trees and stand characteristics determine the population levels of *P. semipunctata* in the NJF. The thesis demonstrates that (a) *P. semipunctata* infestation levels and sapwood damage was concentrated in drought affected trees in collapsed patches, (b) levels of infestation varied and depended on stem diameter, bark thickness and tree species (jarrah or marri), and (c) levels of infestation varied across the NJF and depended on the health of trees at individual sites and their stand characteristics. This study has increased our understanding of the ecology of *P. semipunctata* and its infestation dynamics in jarrah and marri. It will provide a basis for more detailed studies of the relationship between tree moisture deficits and the resistance to infestation by *P. semipunctata* in relation to tree characteristics and increased drought levels.

Table of Contents

Declaration	ii
Conferences	iii
Acknowledgments	iv
Abstract	v
Chapter 1: General Introduction and Review	1
1.1. Drought and insect infestation	1
1.2. Jarrah Forest	3
1.2.1. Extent of the Jarrah Forest	3
1.2.2. Northern Jarrah Forest	4
<i>Climate</i>	4
<i>Soils</i>	5
<i>Vegetation</i>	6
1.2.3. Climate change in Western Australia	6
1.3. Effects of drought on trees	7
1.3.1. Physiological response	7
1.3.2. Drought adaptation mechanisms of jarrah	9
1.4. Drought and predisposition to biotic agents	9
1.4.1. Manion decline spiral	9
1.4.2. Pathogen and insect biotic factors	10
1.5. Cerambycidae (Coleoptera).	12
1.5.1. Distinguishing characteristics Cerambycidae	12
1.5.2. Life cycles	12
1.5.3. Damage to trees	13
1.6. <i>Phoracantha semipunctata</i> (Fabricius)	14
1.6.1. Distinguishing characteristics	14
1.6.2. Life cycle	17
1.6.3. Occurrence of <i>Phoracantha semipunctata</i> throughout the world	19
1.6.4. Damage to trees	21
1.7. Cerambycids and <i>P. semipunctata</i> movement and predation	22
1.7.1. Pheromones, visual cues and flight	22
1.7.2. Native enemies that help control Cerambycid populations	22
<i>Native enemies of Cerambycids</i>	22
<i>Parasitoids of <i>P. semipunctata</i></i>	23
1.8. Defence mechanisms of trees against Cerambycids	24
1.8.1. Chemical defences against woodborers	24
1.8.2. Physical defences against woodborers	25
1.9. Thesis Aims	25

CHAPTER 2: The association between <i>Phoracantha semipunctata</i> (Coleoptera: Cerambycidae) and drought-induced tree damage in the Northern Jarrah (<i>Eucalyptus marginata</i>) Forest of Western Australia	27
2.1. Introduction	27
2.2. Methods	29
2.2.1. Site selection	29
2.2.2. Sample point selection	31
2.2.3. Sampling methods	31
2.2.4. Statistical analysis	35
2.3. Results	35
2.3.1. Effect of drought on the jarrah forest	35
2.3.2. Effect of drought on <i>P. semipunctata</i>	36
2.4. Discussion	38
CHAPTER 3: Within-tree population dynamics of <i>Phoracantha semipunctata</i> (Coleoptera, Cerambycidae) in drought stressed trees in the Northern Jarrah (<i>Eucalyptus marginata</i>) Forest.	42
3.1. Introduction	42
3.2. Methods	44
3.2.1. Sample tree selection	44
3.2.2. Harvesting and tree measurements	45
3.2.3. <i>P. semipunctata</i> population measurements	45
3.2.4. <i>P. semipunctata</i> feeding damage	47
3.2.5. Data Analysis	48
3.3. Results	49
3.3.1. Tree measurements	49
3.3.2. <i>P. semipunctata</i> population measurements	51
3.3.3. <i>P. semipunctata</i> damage of sapwood and heartwood	58
3.4. Discussion	63
CHAPTER 4: Site and tree characteristics influencing the distribution of <i>Phoracantha semipunctata</i> in the northern jarrah (<i>Eucalyptus marginata</i>) forest.	68
4.1. Introduction	68
4.2. Methods	70
4.2.1. Site selection	70
4.2.2. Site characteristics	71
4.2.3. Forest stand characteristics and canopy health measurements	72
4.2.4. Adult <i>P. semipunctata</i> measurements	72
4.2.5. Data analysis	73
4.3. Results	73
4.3.1. Site and stand characteristics	73

4.3.2.	P. semipunctata density and tree health	74
4.3.3.	Factors related to P. semipunctata emergence hole numbers	78
4.3.4.	Adult P. semipunctata emergence holes and tree health	80
4.3.5.	Adult P. semipunctata emergence holes and stand characteristics	82
4.3.6.	Adult emergence and site characteristics	83
4.4.	Discussion	84
Chapter 5: <i>Phoracantha semipunctata</i> (Coleoptera, Cerambycidae) colonisation patterns and larval success in water stressed marri trees induced by ringbarking at two sites impacted by drought in the Northern Jarrah (<i>Eucalyptus marginata</i>) Forest.		
5.1.	Introduction	90
5.2.	Methods	91
5.2.1.	Experimental sites, tree selection and harvest	91
5.2.2.	Tree moisture and beetle sampling	92
5.3	Results	93
5.3.1.	Harvest and tree measurements	93
5.3.2.	Insect visitation	95
5.4.	Discussion	95
CHAPTER 6:	General Discussion	98
6.1.	Response of <i>P. semipunctata</i> to drought	99
6.2.	Outbreak levels	100
6.3.	Modelling tree infestation levels	101
6.4.	Dispersal	103
6.5.	Distribution	104
6.6.	Future Research	104
6.7.	Management practices	106
References		109

List of Tables

Table 1.1. Worldwide localities of *Phoracantha semipunctata* and tree hosts.

Table 2.1. Tree health scores.

Table 2.2. Analysis of variance of adult *Phoracantha semipunctata* emergence holes (m^{-2}) comparing intact or collapsed areas for the collapsed sites N2, N3, N7 and N8,

Table 3.1. Height (mean \pm SE) and diameter (mean \pm SE) of jarrah and marri trees selected at collapsed sites.

Table 3.2. Analysis of variance of DOB comparing sites (N2, N3, N7 and N8), species (jarrah and marri) and height.

Table 3.3. Analysis of variance comparing *Phoracantha semipunctata* population characteristics of emergence holes (m^{-2}), clutch points (m^{-2}), larval galleries (m^{-2}) and mature larvae (m^{-2}) across sites N2, N3, N7 and N8 and between jarrah and marri. Larval galleries refer to galleries formed by larvae in the sapwood and mature larvae refer to galleries formed in the heartwood by mature larvae.

Table 3.4. Analysis of variance comparing *P. semipunctata* population characteristics as determined by emergence holes (m^{-2}), clutch points (m^{-2}), larval galleries (m^{-2}) and mature larvae (m^{-2}) for sites (a) N2, (b) N3, (c) N7 and (d) N8 for jarrah and marri. Larval galleries refer to galleries formed by larvae in the sapwood and mature larvae refer to galleries formed in the heartwood by mature larvae.

Table 3.5. Analysis of variance of adult emergence holes (m^{-2}) for different heights in jarrah and marri trees for sites (a) N2, (b) N3, (c) N7 and (d) N8.

Table 3.6. Analysis of variance comparing average damage to sapwood (%) across sites N2, N3, N7 and N8 and between species of jarrah and marri.

Table 3.7. Analysis of variance of *Phoracantha semipunctata* sapwood damage (%), comparing species (jarrah and marri) height for sites (a) N2, (b) N3, (c) N7 and (d) N8.

Table 4.1. Coordinates of collapsed sites sampled in the NJF.

Table 4.2. Site physical characteristics

Table 4.3. Correlation matrix showing pair-wise comparisons of tree health variables and emergence for 11 collapsed sites sampled in the NJF.

List of Figures

Figure 1.1. A collapsed site near North Dandalup in Northern Jarrah Forest impacted by the drought (Photo by George Matusick and Giles Hardy).

Figure 1.2. Extent of (a) the sclerophyllous forests of south-western Australia and location of the Northern Jarrah Forest (boxed) (from <http://>) and (b) isohyets (solid lines) and evaporation contours (dashed lines) (Gentili (1989)).

Figure 1.3. Trends in (a) temperature ($^{\circ}\text{C}/10\text{years}$) and (b) rainfall ($\text{mm}/10\text{years}$) in Australia for the last 40 years (Bureau of Meteorology 2012).

Figure 1.4. The Manion decline spiral (Manion 1981), showing abiotic (primary or inciting) factors and secondary (contributing) biotic factors.

Figure 1.5. Life cycle of the red oak borer (*Enaphalodes rufulus*) (sourced from Fierke et al., 2005).

Figure 1.6. Adults of (a) *Phoracantha semipunctata* (by Hoskovec 2010), (b) *Phoracantha recurva* (Paine et al., 2009), (c) *P. impavida* (CSIRO 2004) and (d) *P. acanthocera* (Farr 2010). Arrows indicate elytra pattern on *P. semipunctata*.

Figure 1.7. Schematic diagram of *Phoracantha semipunctata* life cycle in *Eucalyptus* plantations in USA, South Africa, Europe and Australia, showing 5 stages with estimates of the time for each stage (compiled from references quoted in text).

Figure 2.1. Location of the collapsed sites N2, N3, N7 and N8 (green pins) in the Northern Jarrah Forest. Inset shows location of study sites in relation to south-western Australia. The green pins are also the sites used in Chapter 3 and both the green and yellow pins indicate the collapsed sites measured in Chapter 4.

Figure 2.2. A collapsed area (light grey), with 10 m buffer zone (white) and a surrounding intact area (dark grey) in this case site N2. Also shown are the random points (dark grey for collapsed area and white for intact area) used for sampling.

Figure 2.3. Example of trees with (a) health score 1= >90 % green and healthy with full crown, (b) health score 2= 40 to 90 % green and healthy with part of crown missing, (c) health score 3= <40 % green and healthy with no crown present (not including coppice and epicormic shoots), (d) health score 4= tree recently dead (intact bark, fine branches present), and (e) health score 5= tree long dead with grey appearance (in foreground) (trunk lost bark, fine branches missing).

Figure 2.4. Emergence hole of (a) *Phoracantha semipunctata* in the bark of jarrah and (b) entry to the pupal cell of *P. acanthocera* in the sapwood of marri. Scale next to emergence hole is in mm.

Figure 2.5. Proportion (mean \pm SE) of trees in each health class (1 healthy to 5 long dead) (HS 1 to HS 5) as a percentage of the total number of trees measured for intact area and collapsed area averaged across all collapsed sites N2, N3, N7 and N8.

Figure 2.6. *Phoracantha semipunctata* emergence holes (m^{-2}) (mean \pm SE) (measured by counting the number of emergence holes made in the bark by adults measured from the first 2 m of tree height) in intact area and collapsed area averaged for the four collapsed sites N2, N3, N7 and N8. LSD ($P < 0.050$) for comparing intact area and collapsed area = 1.379, $n = 184$.

Figure 2.7. *Phoracantha semipunctata* emergence holes (m^{-2}) (mean \pm SE) (measured by counting the number of exit holes made in the bark by adults measured from the first 2 m of tree height) for each health class (1 healthy to 5 long dead (no trees were found)) (for HS 1 $n = 65$, HS 2 $n = 47$, HS 3 $n = 58$ to and H4 $n = 15$) for intact areas and collapsed areas averaged across all collapsed sites 2, 165, 166 and 214. For health score \times treatment area interaction LSD ($P < 0.05$) = 3.952, $n = 27$.

Figure 3.1. Clutch point and larval tracks as seen in sapwood of jarrah at site N2. The number of larvae that emerged from this clutch point was 39.

Figure 3.2. Felled jarrah tree showing billets and method of splitting billets for within tree sampling.

Figure 3.3. The larvae (left), pupae (middle) and adult (right) of *P. semipunctata* collected from sectioned billets of felled trees.

Figure 3.4. Transparent 10 cm \times 10 cm grid used to measure larval damage to the sapwood after outer bark removal. Black arrows indicate damage and red arrows indicates where the sapwood was undamaged.

Figure 3.5. Relationship (mean \pm SE) between billet diameter (cm) and surface area (cm^2) and tree height for jarrah (\bullet) and marri (\circ) averaged between the four sites jarrah, $y = -0.97x + 21.64$ $r^2 = 0.9615$, $P < 0.001$ marri, $y = -1.37x + 22.73$ $r^2 = 0.9575$, $P < 0.001$.

Figure 3.6. The effect of tree species (jarrah and marri) on *P. semipunctata* population characteristics (mean \pm SE) (a) emergence holes (m^{-2}), (b) clutch points (m^{-2}), (c) larval galleries (m^{-2}) and (d) mature larvae (m^{-2}) measured per m^2 at four different sites north (N1, N2) and south (N3, N4). Larval galleries refer to galleries formed by larvae in the sapwood and mature larvae refer to galleries formed in the heartwood by mature larvae. Means marked with different letters are significantly different, means separation test $P < 0.050$.

Figure 3.7. Relationship between mean adult *P. semipunctata* emergence holes (m^{-2}) for jarrah and marri and height at collapsed sites (a) N2, (b) N3, (c) N7 and (d) N8. LSD for site N2=13.92 ($P < 0.05$), site N3=13.92 ($P < 0.05$) site N7=13.92 ($P < 0.05$) and site N8=13.92 ($P < 0.05$).

Figure 3.8. Relationship between emergence and billet diameter (DOB) for jarrah (\bullet) and marri (\circ) trees averaged across all sites. Best fit regression equation: $y = -9.07 \times 10^{-2}x^2 + 3.29x - 15.747$ $r^2 = 0.8598$, $P < 0.001$.

Figure 3.9. Relationship between total adult borers/tree (measured as the number of exit holes made in the bark by adults of each billet summed for each tree) and adult borer numbers at DBH for trees at collapsed sites N8. Best fit regression equation $Y = 5.0763X + 13.033$ ($R^2 = 0.782$, $P < 0.001$). This regression could be used to provide a quick estimation of total borer emergence of a tree from numbers at DBHOB.

Figure 3.10. The effect of tree species (jarrah and marri) on *P. semipunctata* damage (%) to sapwood (mean \pm SE) at different sites N2, N3, N7 and N8. Means marked with different letters are significantly different, means separation test $P < 0.05$.

Figure 3.11. Sapwood galleries of *Phoracantha semipunctata* in jarrah.

Figure 3.12. Relationship between *Phoracantha semipunctata* sapwood damage (%) for jarrah (\bullet) and marri (\circ) and height at collapsed sites (a) N2, (b) N3, (c) N7 and (d) N8. LSD for site N2=13.92 ($P < 0.05$), site N3=13.92 ($P < 0.05$) site N7=13.92 ($P < 0.05$) and site N8=13.92 ($P < 0.05$) comparing, species at different heights.

Figure 3.13. Heartwood galleries of *Phoracantha semipunctata* in jarrah. Arrow indicates the position of the pupal chamber.

Figure 3.14. Relationship between average *Phoracantha semipunctata* damage (%) and average emergence holes (m^{-2}) for 80 trees (jarrah (\bullet) and marri (\circ)) sampled from sites N2, N3, N7 and N8. Best fit regression equation was $y = -0.0496x^2 + 3.9731x$ ($R^2 = 0.2009$).

Figure 3.15. Pupal chambers in the heartwood of four different trees (a) filled with kino and a live larvae present, (b) stained and partially filled by kino, (c) containing an adult *Phoracantha semipunctata* which has been consumed by a fungus and (d) with parasitic larvae (arrowed) emerging from a pupae of *P. semipunctata*.

Figure 4.1. The location of the 11 collapsed sites with major jarrah forest townships.

Figure 4.2. The (a) mean \pm SE of emergence holes (m^{-2}) (measured by counting the number of emergence holes made in the bark by adults measured from the first 2 m of tree height), (b), mean \pm SE green height G_H (where increases in percentage G_H indicated green foliage occupied more of the trees height), (c) proportion (%) of trees in each health class (1 healthy to 5 long dead) (HS 1 to HS 5) as a percentage of the total number of trees and (d) density (trees/ha) of jarrah and marri trees in all collapsed sites (N1-N8, S1-S3).

Figure 4.3. Collapsed sites (circled red) are indicated where the highest numbers of *Phoracantha semipunctata* densities/ha occurred and sites (circled orange) with lowest numbers of *P. semipunctata* in the NJF.

Figure 4.4. The relationship between DBHOB and density for trees at 11 collapsed sites (N1-N8, S1-S3) in the NJF (n=11). Best fit regression equation $Y = -0.0321x + 37.661$ ($R^2 = 0.3712$).

Figure 4.5. The relationship between epicormic shoots (%) and green height (G_H %) (for 11 collapsed sites, (N1-N8, S1-S3) sampled in the NJF (n=55). Best fit regression equation $Y = -0.0092x^2 + 0.2944x + 97.858$ $R^2 = 0.5703$.

Figure 4.6. Adult *P. semipunctata* emergence holes (m^{-2}) (mean \pm SE) (measured by counting the number of emergence holes made in the bark by adults measured from the first 2 m of tree height) for healthy trees with a health a score of 1 (HS 1) and trees that had lost part or all of their canopy or had died (HS 2 -5) (n=55). Columns with asterisks are different at $P < 0.050$, resulting from t-test.

Figure 4.7. Relationship between *Phoracantha semipunctata* emergence holes (m^{-2}) and green height (G_H %), Best fit regression equation $Y = -3.301\ln(x) + 15.606$ ($R^2 = 0.5218$), for the 11 collapsed sites in the NJF (n=55). Where percentage G_H is the height of the tree to which foliage was present as a percentage of the total tree height.

Figure 4.8. Number of adult *P. semipunctata* density/ha (measured by counting the number of emergence holes made in the bark by adults measured from the first 2 m of tree height) (mean \pm SE) at the 11 collapsed sites (N1 to N8 and S1 to S3) sampled in the NJF.

Figure. 5.1. A marri tree showing the ringbarked section of the collar.

Figure. 5.2. Canopy of ringbarked marri tree showing some yellow leaves.

Figure 5.3. Bark moisture (\pm SE) in ringbarked and control marri trees.

Figure 5.4. *Phoracantha* spp. found on the sticky trap of a ringbarked tree and *P. semipunctata* from split billets (on the right). Not to scale.

Figure 6.1. Schematic diagram of the way in which drought, stem diameter at breast height (DBHOB) and species type control *P. semipunctata* infestation. The level of infestation is represented by the shaded surface where increasing density of shade indicates higher infestation.

CHAPTER 1:

General Introduction and Review

1.1 Drought and insect infestation

Forest ecosystems have evolved under a range of natural disturbance agents including fire, drought, high temperature, storms, insect pest outbreaks and pathogen attack, salinity and low nutrients (Hobbs 1999; Battisti 2006, Martini et al., 2007; Chmura et al., 2011). These disturbances allow forest ecosystems to develop an ability to cope with change and influence their composition, structure, and functional processes (Dale et al., 2001). The level of resilience to a particular disturbance depends on the type of natural disturbance regime experienced by the forest in the past (Hobbs 1999). For example, a gap created in a forest by fallen trees allows trees to regenerate and maintain forest heterogeneity (Lundquist and Beatty 2002) rather than cause a change in species composition (Brokaw and Scheiner 1989). Infrequent rainfall causing drought as a disturbance agent increases tree water stress and may cause a shift in ecosystem state (Asbjornsen et al., 2011). High temperatures can lead to stress and a breakdown of proteins which may decrease the function of the tree causing some trees to die (Coder 1999). Forest ecology can be altered depending on the frequency and intensity of drought, fire and high temperatures.

Insect infestations are also primary disturbance agents in natural ecosystems. Insects exist to defoliate, consume, breakdown plant material and act as vectors distributing pollen and spores for fertilization and pathogen establishment within the tree (Weisser and Siemann 2004). They can also be secondary disturbance agents with infestations being triggered by other disturbances such as drought (Allen et al., 2010; Anderegg et al., 2012). In these situations where trees suffer water stress episodes they may alter the physiology and

biochemistry of the tree sufficiently to cause a decline in host tree resistance (Rouault et al., 2006) reducing the tree's ability to defend against insects. Prolonged attack by insects causing excessive damage may prevent tree recovery (Hooper et al., 2010) and eventually kill the tree.

There has been past evidence of global forest die offs (Allen et al., 2010) including; ponderosa pine between 1953 and 1958 in New Mexico, (Mueller et al., 2005), 1993 and 1994 failure of hydraulic architecture of Pine in Spain (Martínez-Vilalta and Piñol 2002a,b) and southwestern North American woodlands in 2002-2003 in North America (Breshears et al., 2005). Future projections by climate change models predict a decrease in rainfall and a 2-5°C increase in global temperatures by 2070 (IPCC 2007). As a result of drought and heat stress large-scale forest decline is likely to increase (Anderegg et al., 2012). This has occurred in Wandoo (*Eucalyptus wandoo* Blakely) and powderbark wandoo (*E. accedens* W. Fitzg.) woodland where trees have experienced a succession of drought events and has declined (Smith 2003). Of interest in the present study is the effect of the 2010 drought on Northern Jarrah (*Eucalyptus marginata* Donn Ex Smith) Forest (NJF). Perth, Western Australia experienced the driest year for 107 years and the hottest summer on record, which was 1.7 °C above the long term average (Bureau of Meteorology 2010). As a result of this drought the NJF suffered sudden forest collapse (Figure 1.1) in areas defined by a reddening or appearance of anthocyanins of foliage where the primary crown had died. The area affected was approximately 19,000 hectares or 1.7 % of the NJF (Matusick et al., accepted). As a result of this drought it is expected that a number of secondary disturbance agents such as frequent outbreaks of insect populations and pathogens will occur. One agent of particular interest is the Eucalyptus longhorned borer *Phoracantha semipunctata* (Cerambycidae: Coleoptera) Fabricius that occurs in the NJF (Wang 1995).



Figure. 1.1. A collapsed site near North Dandalup in Northern Jarrah Forest impacted by the drought (Photo by George Matusick and Giles Hardy).

1.2. Jarrah Forest

1.2.1. Extent of the Jarrah Forest

The jarrah forest extends from Moora in the North to Albany in the south and consists of an open eucalypt forest. On the coast *E. marginata* grows as short trees within tuart (*E. gomphocephala* DC.) woodland (Specht et al., 1974) and on the eastern edge grows as a multiple stemmed mallee interspersed with *E. wandoo* and *E. accedens* (powderbark wandoo) (Beard 1981). The middle region of the jarrah forest is dominated by large jarrah trees interspersed with Marri (*Corymbia calophylla* Hill) (Bell and Heddle 1989). To the south the jarrah forest becomes dominated by *E. diversicolor* F. Muell. The Northern Jarrah Forest (NJF) is located in south-western Australia in the Darling Range, extending 200 km north to south from Moora to Collie 50 km west to east from the Darling scarp to Boddington (Figure 1.2a).

1.2.2. Northern Jarrah Forest

Climate

The NJF experiences a Mediterranean climate (Gentili 1989) with prolonged hot dry summers and cool wet winters, with rainfall ranging from 1000 mm in the North to 1100 mm in the south (Maher et al., 2010) (Figure 1.2b). Rainfall decreases towards the east of the Darling Range to 635 mm (Gentili 1989; Williams and Mitchell 2001) with evaporation increasing from 550 mm in the southwest to 750 mm in the northeast (Gentili 1989) of the Darling Range. In recent years rainfall has decreased throughout southwestern Australia by approximately 14 % (Bates et al., 2008), including a record dry year in 2010 with rainfall 40-50 % below the long term average. For example, Mundaring, Western Australia (located in the northern section of the NJF) recorded 599.6 mm of rain in 2010 compared to the long term average of 1100 mm (Bureau of Meteorology 2010).

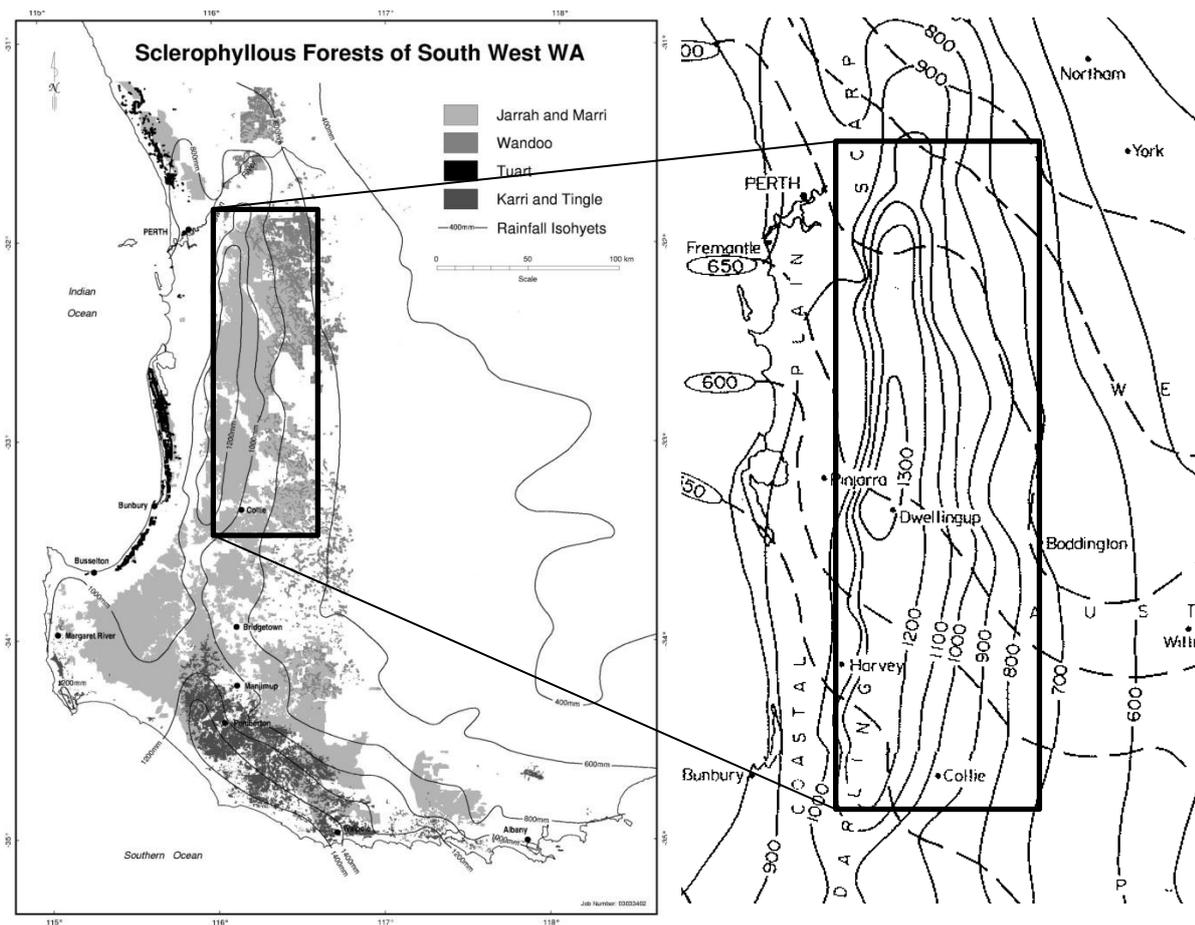


Figure 1.2. Extent of (a) the sclerophyllous forests of south-western Australia and location of the Northern Jarrah Forest (boxed) (from <http://>) and (b) isohyets (solid lines) and evaporation contours (dashed lines) (Gentili (1989)).

Soils

The underlying soils of the NJF are composed of the Archaean crystalline rocks associated with the south-western margin of the Yilgarn craton (McArthur et al., 1977). The soils along the western margin of the forest are gravelly and characterised by deep extensive laterites which may be dissected from drainage with shallow soils associated with granite outcrops (McArthur et al., 1977; Weaving 1999). The uplands, which have an average elevation of 300 m, are gently undulating with hills and valleys with gravelly soils. In the eastern region of the NJF the laterite becomes deeply dissected (CSIRO 1980, 2012).

Vegetation

The NJF is dominated by jarrah (*E. marginata*) with some marri (*C. calophylla*) overstorey which can reach between 30-40 metres particularly towards the western edge of the plateau and ranges from 15 to 24 metres towards the east (Abbott et al., 1989). The midstorey of the NJF is mainly composed of *Acacia*, *Banksia*, *Hakea*, *Leptospermum*, *Melaleuca*, *Persoonia* and which range from 4-7 metres (Abbott et al., 1989), with ground cover typically dominated by *Anigothanthus*, *Euphorbia*, *Grevillea*, *Hibbertia*, *Verticordia*, *Macrozamia* and *Xanthorrhoea* and can be invaded by exotic grasses (Barrett and Tay 2005). The uplands are dominated by jarrah and marri, where *E. megarcarpa* F. Muell., *E. patens* Benth., *C. calophylla*, *E. rudis* Endl., *Banksia* spp., and *Melaleuca* spp. dominate the lower slopes and drainages (Powell 1991; Havel 1975). The eastern, drier region is composed mainly of shorter, more open jarrah stands with mixed wandoo-marri woodland (Williams and Mitchel 2001). This is distinguished from the southern jarrah forest where jarrah mixes with karri (*E. diversicolor*) extending towards Manjimup (Maher et al., 2010).

1.2.3 Climate Change in Western Australia

Over the last 40 years there has been a decrease in synoptic events with the circumpolar westerly winds which have strengthened and the frontal low pressure systems, which bring the winter rainfall, have both moved further south (Bates et al., 2008; Pittock 2009). This has led to increase in temperatures by 1.2 °C, and a rapid decrease in rainfall in southwestern Australia by 60 mm (Bureau of Meteorology 2011) (Figure 1.3a and b). Australia is predicted to warm by between + 0.5 to + 2.1 °C by 2030, and between +1 to +6 °C by 2070 (Bates et al., 2008) and Perth, Western Australia is expected to experience a doubling in the number of days over 35 °C (Cleugh et al., 2011). Based on modelling for

the period 2010-2040 south-western Australia is likely to experience an increased frequency of very dry conditions (Cleugh et al., 2011). Rainfall in the southwest is predicted to decrease by between 2 and 20 % by 2030 and 5 and 60 % by 2070 (Bates et al., 2008). Also potential evaporation is predicted to increase by 10 % or more by 2030 and 30 % or more by 2070 (Bates et al., 2008).

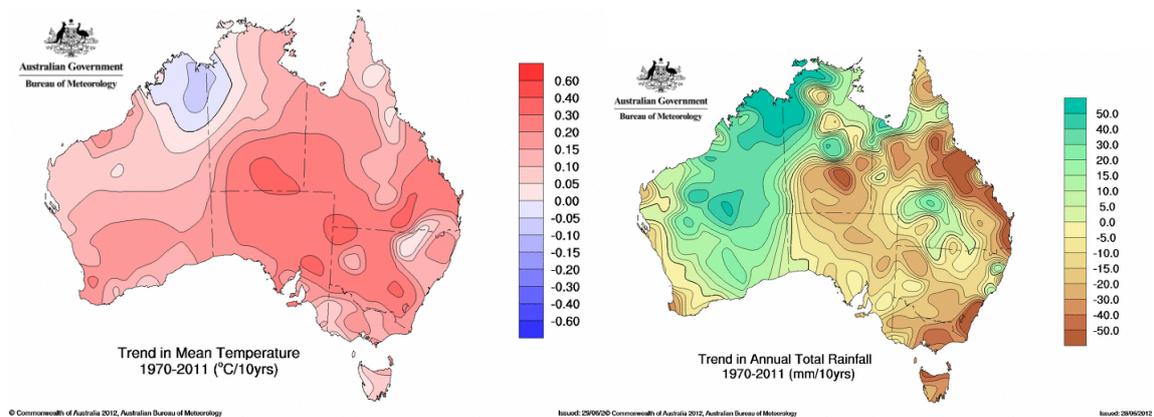


Figure 1.3. Trends in (a) temperature ($^{\circ}\text{C}/10\text{years}$) and (b) rainfall ($\text{mm}/10\text{years}$) in Australia for the last 40 years (Bureau of Meteorology 2011).

With the lack of rainfall and higher temperatures there will be reduced soil moisture storage in forest catchments causing soil water deficits within the root zone of the forest. As a result of drought it is predicted there will be a 5.1 % reduction in area of the jarrah forest by 2030 (Maher et al., 2010).

1.3 Effects of drought on trees

1.3.1. *Physiological response*

The physiological effects of drought on trees include a reduction in photosynthesis, respiration, transpiration, nitrogen metabolism and hydrolysis of proteins, turgor, cell division, cell enlargement and growth (Slatyer 1967; Kramer 1969). Reduction in net photosynthesis and transpiration can occur through reductions in leaf area (Kramer 1969),

reductions in stomatal conductance (Leuzinger et al., 2005), and stomatal closure (Vaz et al., 2010) all of which may occur in response to soil drying (Loewenstein and Pallardy 1998). Also photosynthesis is limited by down regulation of leaf nitrogen and chlorophyll concentration (Vaz et al., 2010). Drought can also lead to reductions in cell sugars and depletion of carbohydrate reserves, which has been observed in the lignotubers of Mediterranean holm oak, causing further crown deterioration (Galiano et al., 2012). Biochemical effects may also include accumulation of indole-3-acetic acid and abscisic acid as second signals following a reduction in cytokinin levels, as observed in needles of *Pinus radiata* D. trees in Spain during simulated drought conditions (De Diego et al., 2012).

The water use of a forest depends on the density of trees and site soil characteristics (Cornish and Vertessy 2001) and stomatal control during periods of high evaporative demand (Kallarackal and Somen 1997; Sala and Tenhunen 1993). Reduced tree density by thinning reduced transpiration in *Pinus ponderosa* Dougl. Ex Laws (Simonin et al., 2007). Under conditions of drought and depletion of soil moisture, the limited water available is more tightly bound by small soil pores (Marshall 1959) making extraction of water and soil nutrients by roots increasingly difficult (Charlesworth 2000). Trees will continue to become water stressed initiating stomatal control to restrict transpiration (Slatyer 1967). Ultimately the trees run out of water, lose complete turgor and permanently wilt and die. Eucalypts vary in their control of water loss, jarrah freely uses water with little stomatal control (Ridge et al., 1984) whilst marri restricts water loss before deep water resources are exhausted (Grieve 1960; Grieve and Helmuth 1968). However, *E. accedens*, *E. wandoo* showed a greater ability to withstand summer drought than *E. marginata* and *C. calophylla* (Poot and Veneklas 2012). Jarrah trees have adapted

to cope with a dry Mediterranean climate in terms of their phenology and growth (Abbott et al., 1989).

1.3.2 *Drought adaptation mechanisms of jarrah*

Jarrah has developed a number of drought adaptation mechanisms. One prominent adaptation is the development of a three tiered root system comprising of dense horizontal roots, riser roots and deep sinker roots, which allows for utilization of both surface and deep soil water sources (Abbott et al., 1989). Jarrah roots have a unique ability to penetrate the hard lateritic duricrust and extend down 40 metres in soil profiles over granite (Crombie et al., 1988; Abbott et al., 1989) and are known to reach 14 m depth to maximise soil water access in deep sands (Farrington et al., 1996). Another adaptation is the ability to resprout (or produce epicormic shoots) after a drought episode and resprouts from lignotubers. In south-western Australia forests, water limited jarrah and marri trees may limit stress by decreasing leaf area, to limit transpirational demand (Pekin et al., 2009). However, reduced leaf area may reduce carbohydrate reserves and limit the ability of jarrah to resprout (Pekin et al., 2009). Jarrah also contains a lignotuber which stores carbohydrates containing dormant buds and allows the tree to initiate new shoots in response to the effects of drought (Abbott et al., 1989).

1.4 Drought and predisposition to biotic agents

1.4.1 *Manion decline spiral*

When certain trees experience excessive water stress, they become more vulnerable to secondary effects, such as insect and pathogen attack (Gaylord et al., 2009; Anderegg et al., 2012). In the Manion spiral (Figure 1.4) lack of rainfall causing drought (a inciting factor) increases stress in the forest which can be magnified by poor soil water holding

capacity (Breshears et al., 2005; Maher et al., 2010). The droughted forest then becomes more vulnerable to secondary disturbances including pathogen infection (Anselmi and Giorcelli 2007) and insect infestation (Hanks et al., 1991a; Lieutier 2004) accelerating the decline of the forest.

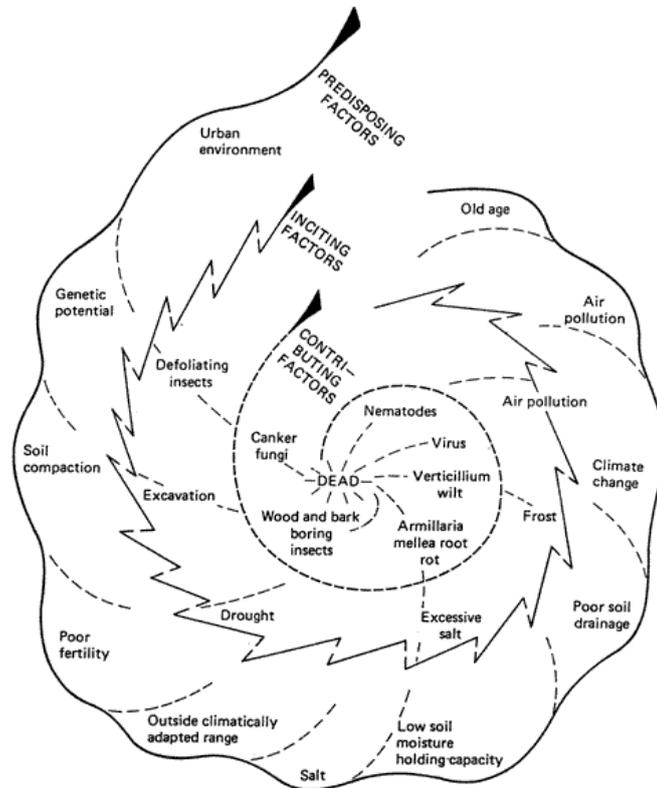


Figure 1.4. The Manion decline spiral (Manion 1981), showing abiotic (primary or inciting) factors and secondary (contributing) biotic factors.

1.4.2. Pathogen and insect biotic factors

The pathogenic soil borne oomycete *Phytophthora cinnamomi* Rands infects the roots of *E. marginata* and other susceptible understorey jarrah forest species (Shearer and Tippett 1989) and starves jarrah trees of water and nutrients resulting in chlorosis of foliage and dieback of tree crowns, eventually causing tree mortality (Podger 1972; Tippett et al., 1985; Dell and Malajczuk 1989). This oomycete has affected large areas of the Northern Jarrah Forest (Wills and Keighery 1994), and another oomycete *P. multivora* sp. nov. is likely to be the cause of a similar level of damage in the forest (Scott et al., 2009). Other pathogens that infect forest trees include basidiomycetes and the ascomycetes (Blanchard

and Tattar 1997). Fungal infection can increase following woodborer activity (Lawson 2003) and are commonly present in larval galleries breaking down bark and xylem tissue (Jacobs et al., 2002; Jankowiak and Rossa 2007; Jankowiak et al., 2007). In other examples, bark beetles have been responsible for transferring the Dutch elm disease, a blue-stain fungus (*Ophiostoma ulmi* Buism.) to trees and these have had devastating consequences in North American forests (Långström et al., 2001).

A wide range of phytophagous insects play important roles in forest tree mortality, contributing to forest die-offs in North America, Europe and Australia (Allen et al., 2010). Insects that commonly invade stressed trees, include bark beetles (Coleoptera: Scolytidae) (Evans et al., 2004), long-horned beetles (Coleoptera: Cerambycidae), jewel beetles (Coleoptera: Buprestidae) (Carne et al., 1987, CSIRO 1991), woodwasps (Hymenoptera: Ciricidae) (Thomsen and Harding 2010) and woodboring moths (Lepidoptera: Cossidae) (Leite et al., 2011). Bark beetles and woodwasps damage the outer cambial tissues while Cerambycids also damage the inner xylem (Hanks et al., 1993). Woodborers are also known to be vectors of harmful nematodes (Luzzi et al., 1984) and pathogenic fungi (van Wyk et al., 2007), which in turn can further exacerbate forest mortality.

The Cerambycids comprise one of the largest groups in the Coleoptera and have become a serious pest damaging felled timber which has had considerable economic impact (Evans et al., 2004). The family contains approximately 40, 000 described species worldwide (Cocquempot and Lindelöw 2010) with about 1250 identified Cerambycid beetles in Australia. One genus *Phoracantha* Newman (sub family Cerambycinae) consisting of 40 species have been found to occur in *Eucalyptus* trees (Wang 1995).

1.5. Cerambycidae (Coleoptera).

1.5.1. Distinguishing characteristics Cerambycidae

Cerambycids are distinguished from others in the Chrysomelloidea superfamily by having an elongated body shape, distinctive and attractive elytral colouration and kidney shaped eyes. Adult antennae typically have 11-segments and are at least two-thirds or longer than the body length, hence the name longhorned or longicorn beetles (Crowson 1967; Imms 1967; Hangay and Zborowski 2010). Other distinguishing features are that the antennae are usually inserted on prominent tubercles on margins of the eyes. They have prominent mandibles that are often enlarged. The pronotum covering the prothorax is convex in shape. The legs are long with two spurs and the tarsus have 5 segments with the 4th tarsal hidden and only being present as a flap (Comstock and Comstock 1901; Hangay and Zborowski 2010). The larvae are white to yellowish in colour with a soft body, a small head, strong jaws, an enlarged thoracic segment and a body that tapers towards the tail with legs small or absent (Comstock and Comstock 1901; Hangay and Zborowski 2010).

1.5.2. Life cycles

One of the well-studied Cerambycids the red oak borer *Enaphalodes rufulus* Haldeman. has a synchronous life cycle lasting 2 years (Fierke et al., 2005) (Figure 1.5). The eggs are laid under the bark, hatch in less than 2 weeks and larvae develop by consuming phloem tissue for 4 months forming small feeding galleries under the bark where they over winter until spring. They then form new second year galleries in the phloem and heartwood plugging them with frass where they overwinter from November to June. They then pupate and emerge as adults from June to July when they mate and oviposit eggs (Fierke et al., 2005) (Figure 1.5).

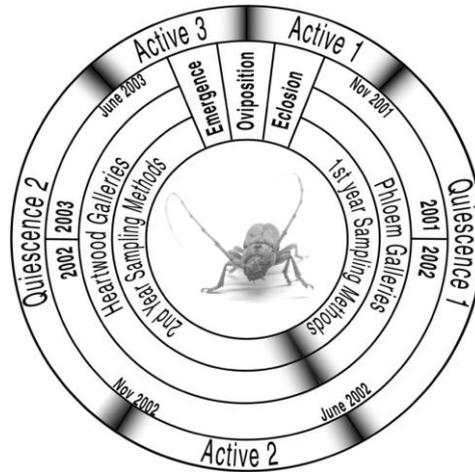


Figure 1.5. Life cycle of the red oak borer (*Enaphalodes rufulus*) (sourced from Fierke et al., 2005).

The Asian longhorned borer *Anoplophora glabripennis* (Coleoptera: Cerambycidae) completes its life cycle in 1 to 2 years depending on seasonal conditions (Hu et al., 2009). Eggs are laid under the bark and hatch out in 8-12 days. First instar larvae consume decayed phloem and move away from the egg niche where second instar larvae feed primarily on the healthy phloem/cambium as they tunnel under the bark. Third and fourth instar larvae tunnel into the xylem creating horizontal galleries plugged with frass, where they may remain during winter. After winter larvae take 20 days to pupate and then metamorphose into adults before emerging from the tree by creating exit holes 6-18 mm in diameter (Hu et al., 2009).

1.5.3. Damage to trees

Most species of Cerambycids are secondary pests attacking moderately or severely stressed, dying, wounded, felled trees (Seybol et al., 2008; Thomsen and Harding 2010) or trees with decayed wood (Cocquempot and Lindelöw 2010). For example, the red-shouldered pine borer *Stictoleptura canadensis* LeConte infest dying or dead ponderosa pine (*Pinus ponderosa*) (Costello et al., 2011). The decline of red oak *Quercus rubra* L. in the Ozark-Ouchita Highlands of Arkansas has been attributed to an unprecedented

outbreak of the red oak borer *E. rufulus* (Fierke et al., 2005). There are a few Cerambycids that attack healthy trees (Cocquempot and Lindelöw 2010). For example, the Asian longhorned beetle *A. glabripennis* attacks healthy poplar (*Populus* spp.) in Asia and Korea and have become established in eastern US (Hu et al., 2009) and Europe (MacLeod et al., 2003). While the Cerambycid *Crioprosopus magnificus* LeConte feeds on branches of healthy oak species (*Quercus potosina* Trel. and *Q. grisea* Liemb.) causing significant damage (Sanchez-Martinez et al., 2010).

1.6. Phoracantha semipunctata (Fabricius)

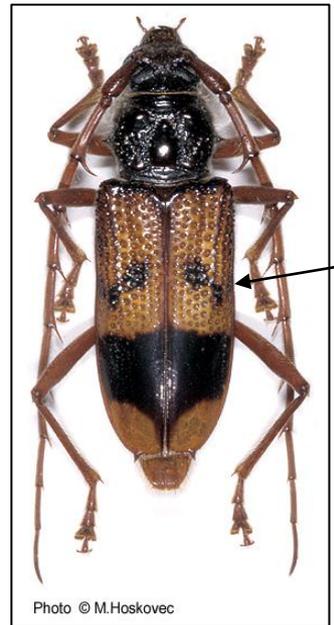
1.6.1. Distinguishing characteristics

The adult Eucalyptus longhorn borer *Phoracantha semipunctata* (Coleoptera: Cerambycidae) are distinguished from other species of *Phoracantha* by the following colour and markings of the elytra. The elytra are dark reddish brown to black with a broad yellow band, through which is a complete brown zigzag pattern on the subfascia and a yellow mark on the apex of each elytra (Wang 1995; Matthews 1997) (Figure 1.6). The antennae are 1.1 x longer than the body and may be equal or longer than their body length (Wingfield and Hurley 2003; Hanks, et al., 1999), being between one and a half to two times longer in the male compared to only slightly longer than the body length of the female (Morelli and Sanchez 2002; French 1911). The colour of the larvae are off-white with an enlarged pronotum. The larvae are segmented and cylindrical, with length varying in size of 14 mm (Hanks et al., 1993), 20 mm (Wang 1995), 26 mm (Morelli and Sanchez 2002) to 32 mm length (Wingfield and Hurley 2003) depending on location. Preliminary measurements of total larvae length dissected from jarrah and marri trees in the NJF were at the higher end of this range being 30 ± 0.39 mm, with peristomal (mouthparts) width 4.00 ± 0.13 mm and abdomen had 10 segments. The adults were 25.84 mm long and

antennae were 1.5 times its body length. Other features which define collected adult borers as *P. semipunctata* such as the absence of long hairs, the absence of spines on the front dorsal side of hind femur and the presence of barbs on the backs of lower leg segments with a complete zigzag pattern on subfascia of its elytra agree with those described by Wang (1995) which define these specimens in the NJF as *Phoracantha semipunctata* and visually distinguished *P. semipunctata* from other *Phoracantha* spp (Figure 1.6a-d).



(a) *P. semipunctata* Fabricius



(b) *P. recurva* Newman



(c) *P. impavida* Newman



(d) *P. acanthocera* Macleay

Figure 1.6. Adults of (a) *Phoracantha semipunctata* (by Hoskovec 2010), (b) *Phoracantha recurva* (Paine et al., 2009), (c) *P. impavida* (CSIRO 2004) and (d) *P. acanthocera* (Farr 2010). Arrows indicate elytra pattern on *P. semipunctata*.

Phoracantha semipunctata is mostly closely related to *P. recurva* which has been recorded in the NJF (Wang 1995). The two species are distinguished by the elytra of *P. semipunctata* being dark reddish brown or blackish brown with the following yellowish brown markings: 1 narrow zigzag fascia at sub-base, 1 wide, more or less straight fascia

just before middle, and 1 oval or irregular spot on disc before apex (Wang 1995) (Figure 1.6a). In comparison, the elytra of *P. recurva* are pale yellow to yellowish brown with a narrow incomplete zigzag band which is reduced to a small spot before the middle of each elytra (Figure 1.6b). For *P. semipunctata* there is an absence of long hairs and sensilla filiformia on each antennal segment (Faucheux 2011), an absence of spines on the front dorsal side of hind femur, and the presence of barbs on the backs of lower leg segments (Wang 1995). In contrast, *P. recurva* has very dense and long golden hairs arising from the underside of each antennal segment and the hind femora with strong dense spines on the front-dorsal side.

1.6.2. Life cycle

The biology and life cycle of *P. semipunctata* has been described in detail in the northern hemisphere where it is an introduced species (Tooke 1935; Duffy 1963; Hanks et al., 1993, 1995, 1999; Wingfield and Hurley 2003). However, very little is known about the detailed life cycle and feeding habits of *P. semipunctata* in south-western Australia where it is endemic (Clark 1925; Curry 1981). In California, the borers' life cycle only takes about 3 to 4 months to complete during spring and summer or up to 9 months in autumn and winter (Paine et al., 2009). This is in contrast to the 2 year life cycles of *P. acanthocera* in south-western Australia (Farr et al., 2000) and the red oak borer in Arkansas (Fierke et al., 2005). The life cycle starts with females laying eggs in clutches of between 3 and 110 (Duffy 1963; Wingfield and Hurley 2003; Hanks et al., 2003; Paine et al., 2009) under loose bark or in bark crevices and cracks by probing the bark with its ovipositor, extended to 20 mm length (Hanks et al., 1993). Egg laying occurs between September and April in South Africa (Tooke 1935; Marshal et al., 2010) or throughout March to November in Palestine (Duffy 1963) (Figure 1.7). After an incubation period of

10 to 14 days (Duffy 1963) neonate larvae mine small trails (larval feeding tracks) on the inner bark and outer sapwood in all directions from the place of oviposition (Wang 1995). The larvae then pass through at least five instars taking about 2 to 4 months (Hanks et al., 1993; Wingfield and Hurley 2003) to complete development. During this time they destroy the cambium, outer xylem and sapwood tissues (Duffy 1963; Curry 1981) and create either longitudinal galleries for several feet or twist and turn in all directions (Duffy 1963). This feeding disrupts water transport and nutrient supply within the tree (Chen et al., 2012). Laboratory studies have shown a strong positive correlation between larval development and temperature with an optimum temperature of 25°C (Hanks et al., 1991). Mature larvae bore obliquely into the sapwood forming galleries, blocking the passage at one end with wood chips (the frass plug) (Duffy 1963; Hanks et al., 1993). After making the heartwood galleries, several inches from the surface, they create a pupal chamber. Here larvae remain for about 10 days (Wingfield and Hurley 2003) or enter a quiescent prepupal stage, then pupate for a period lasting about 10 days to 2 weeks (Hanks et al., 1999; Paine et al., 2009) (Figure 1.7). The adult then exits the tree by eating out the frass plugged hole (Wingfield and Hurley 2003; Paine et al., 2009). Adults usually emerge during late twilight from April through to October in California (Paine et al., 2009), fly up into the tree canopy and disperse through the forest (French 1911) flying all night (Barata and Araujo 2001). Mating occurs where males use antennal contact to locate females, which accounts for the long length of antennae, and do not rely on long-range pheromones attractants (Hanks et al., 1996a, 1999). *Phoracantha semipunctata* has a relatively short copulation time of about 1 minute compared to other species of Cerambycids of about 87 seconds (Hanks 1999). Adults live for between two weeks to a few months in South Africa (FAO 2009; Wingfield and Hurley 2003). Limited data have been collected on the timing of the complete life cycle of *P. semipunctata* in WA. Studies using artificial insertion of neonate larvae showed adult emergence took 60 days in fallen logs of

plantation *E. trabutii* (natural hybrid of *E. camaldulensis* Dehnhardt and *E. botryoides* Sm.) in California (Hanks et al., 2005).

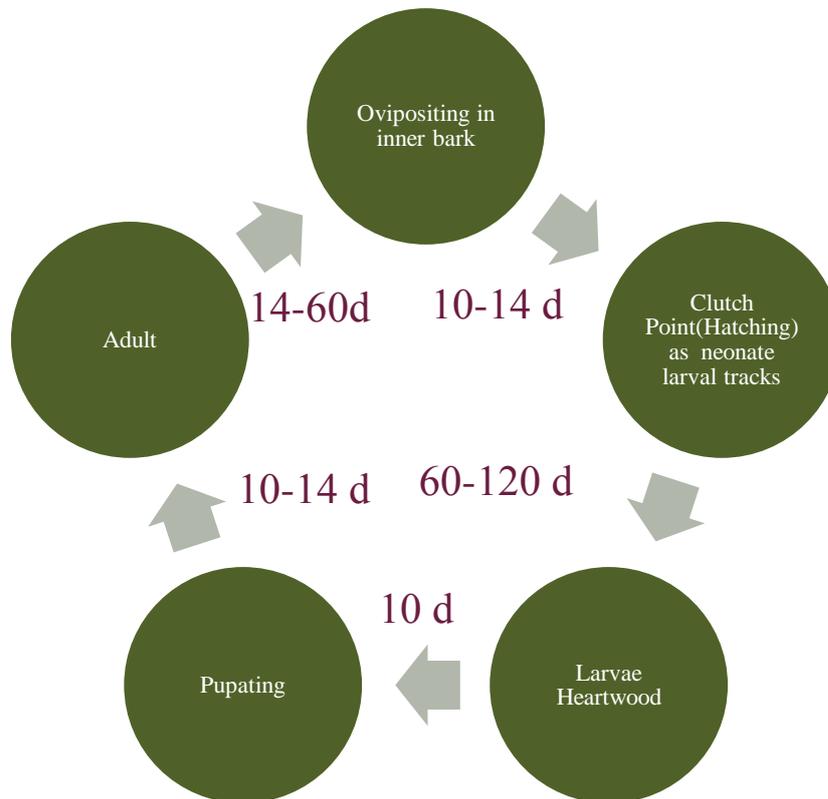


Figure 1.7. Schematic diagram of *Phoracantha semipunctata* life cycle in *Eucalyptus* plantations in USA, South Africa, Europe and Australia, showing 5 stages with estimates of the time for each stage (compiled from references quoted in text).

1.6.3. Occurrence of *Phoracantha semipunctata* throughout the world

Phoracantha semipunctata is endemic to Australia and parts of New Guinea since it's only hosts include *Eucalyptus* species and a few other tree species of closely related genera *Syncarpia laurifolia* SB. and *Angophora intermedia* D.C. in the Myrtaceae family (Duffy 1963; Wang 1995; Kliejunas et al., 2003; Lawson 2003). The borer has been found in the Darling Range (32°30'S, 116°00'E) near Nth Dandalup Dam (Wang 1995). It also became a major economic pest in *Eucalyptus* plantations in many temperate and tropical locations around the world (Amman and Ryan 1991; FAO 2009) including Tunisia (Chararas 1969), South Africa (Drinkwater 1975), Zambia (Ivory 1977), Uruguay (Morelli

and Sanchez 2002), southern Europe and California (Scriven et al., 1986) (Table 1.1). *Phoracantha semipunctata*'s primary means of establishment is from the importation of *Eucalyptus* wood and contaminated sea containers from Australia that harbour infestations (Stanaway et al., 2001).

Table 1.1 Worldwide localities of *Phoracantha semipunctata* and tree hosts.

Location	Host	Reference
Australia	<i>E. oleosa</i> F. Muell. ex Miq., <i>E. gracilis</i> F. Muell. <i>E. nitens</i> H. Deane & Maiden, <i>E. cladocalyx</i> F. Muell., <i>E. botryoides</i> Sm.	Duffy 1963. Wang 1995
Africa, (Eastern)	<i>E. diversicolor</i> F. Muell., <i>E. saligna</i> Sm., <i>E. terticornis</i> Sm. and <i>E. cereba</i> L.	Austin and Dangerfield 1997; Tooke 1935; Wingfield and Hurley 2003
France, Turkey, Jordan,	<i>Eucalyptus</i> spp.	Austin and Dangerfield 1997
USA (California)	<i>E. rudis</i> Endl., <i>E. cladocalyx</i> F., <i>E. camaldulensis</i> Dehn., <i>E. trabutii</i> (hybrid), <i>E. tereticornis</i> Small., <i>E. grandis</i> Hill x Maiden.	Muzika et al., 2000; Paine et al., 2009; Hanks et al., 1993; Hanks et al., 1999
Tunisia	<i>E. camaldulensis</i>	Jaâma et al., 2009
South America (Argentina)	<i>E. amplifolia</i> Blakely, <i>E. cinerea</i> F. Muell. ex Benth, <i>E. dalrympleana</i> Maiden	Di-Iorio 2004
Morocco	<i>E. camaldulensis</i> and <i>E. gomphocephala</i> D C.	Faucheux 2011
Italy	<i>Eucalyptus</i> spp.	
Israel	<i>Eucalyptus</i> spp.	Sama et al., 2010
Uruguay	<i>E. globulus</i> Labill.	Morelli and Sanchez 2002
	<i>E. bicostata</i> (Maiden et al.) J. B. Kirkp. <i>E. gigantea</i> Hook. f., <i>E. globulus</i> Labill. <i>E. saligna</i> , <i>E. viminalis</i> Labill.	
Portugal	<i>E. ovata</i> Labill., and <i>E. viminalis</i>	Barata et al., 2000

Eucalyptus authorities from USDA Germplasm Resources Information Network, (<http://www.ars-grin.gov/cgi-bin/npgs/html/splist.pl?4477>).

1.6.4. Damage to trees

Phoracantha semipunctata a secondary pest, is attracted to and readily attacks stressed, dying and dead trees in *Eucalyptus* forests of Australia (Clark 1925; Curry 1981; Wang 1995) and healthy plantation trees in California (Kliejunas et al., 2003). In 2002 when rainfall was less than 600 mm in Western Australia *P. semipunctata* populations were recognised as a potential problem by Floyd, R.B of CSIRO, ACT (Kliejunas et al., 2003). In California, at low larval numbers (5 larvae/1 m log), damage doubled in *E. rudis* trees destroying the cambium at leaf water potentials at -1.2 MPa to below -2.8 MPa and bark moisture content from 70 to 50 %. In contrast at high larval numbers (50 larvae/ 1 m log) damaged increased with water potentials above -1.2 MPa (Hanks et al., 1999). *Phoracantha semipunctata* can also attack freshly cut logs with bark remaining (Duffy 1963). The larvae can destroy virtually the entire cambium layer of young trees resulting in rapid death of the trees and in older trees may not destroy the complete cambium but can weaken the tree and expose it to further attack by later generations of *P. semipunctata* (Duffy 1963; Chararas 1969; Drinkwater 1975). Also *P. semipunctata* was found in Italian eucalypt plantations impacted by several drought periods, fires and defoliation (EPPO 2007). In situations where species such as *E. globulus* originating from high rainfall areas in Victoria and Tasmania are planted in drought prone areas overseas such as California they are vulnerable to *P. semipunctata* infestation (Paine 2006). Whereas when planted in Brazil and Hawaii where there is a short dry summer season, these plantation trees were less attractive to the borer (Paine 2006).

1.7. Cerambycids and *P. semipunctata* movement and predation

1.7.1. Pheromones, visual cues and flight

Cerambycids are attracted to the release of pheromones, odours, semiochemicals and volatiles from the stressed trees (Barata and Araujo 2001). These chemicals include ethanol and monoterpenes, components of resin (i.e. α -pinene and 3-carene) and their combination (Costello et al., 2011). For example, *A. glabripennis* was attracted to drought stressed trees from the release of volatiles (Hu et al., 2009). In addition, sight recognition appears to influence the behaviour of Cerambycids, including *P. semipunctata*, which only landed on logs of *E. globulus* releasing an acetic acid odour and never landed on a PVC pipe releasing the same odour (Barata and Araujo 2001). Also its flight behaviour was more direct towards the log if it kept in contact with the odour and an erratic zigzag flight pattern was observed if its contact with the odour plume was lost, but it eventually landed on the log (Barata and Araujo 2001). In addition, logs not emitting an odour were ignored by the borer (Barata and Araujo 2001). This suggests that *P. semipunctata* mainly finds its host by utilising the odours being emitted by the tree and the borer's sight recognition of the tree. *Phoracantha semipunctata* has developed the ability to identify odours from healthy trees to feed as adults on pollen and nectar to match their dietary requirements (Hanks 1999) and also identify stressed trees to mate and oviposit eggs (Barata and Araujo 2001).

1.7.2. Native enemies that help control Cerambycid populations

Native enemies of Cerambycids

There are many enemies (predators) that help control Cerambycid populations (prey) involving vertebrates including birds, ants, wasps and predaceous beetles. For example, Black-backed woodpeckers primarily consume Buprestid and Cerambycid beetles in the

bark and xylem of standing dead trees (Powell 2000) and woodpeckers are natural enemies of *Enaphalodes rufulus* (Haavik 2006). Many other groups of birds including creepers, flycatchers, nighthawks, vireos, nuthatches, and warblers feed on adult Cerambycids (Linsley 1959). Birds are likely to locate Cerambycid larvae in trees by listening to their sound whilst feeding (Linsley 1959). Carpenter ants, *Camponotus pennsylvanicus* De Geer are important in controlling *E. rufulus* numbers (Haavik 2006). Parasitoid wasps (Hymenoptera) control Cerambycids mainly by ovipositing eggs into woodborer larvae (prey) which eventually become consumed by the wasp larvae (predator). For example, the following parasitoids *Nealiolus* n. sp. (Braconidae: Hymenoptera), *Agonocryptus* sp. (Ichneumonidae: Hymenoptera), and *Bracon* sp. (Braconidae: Hymenoptera) parasitised larvae of *Apagomerella versicolor* Boheman (Cerambycidae: Coleoptera) (Logarzo et al., 2002). There are also many predaceous beetles of Cerambycid larvae and adults including the clerids *Cymatodera*, *Thanasimus*, and *Chariessa*, ostomids *Tenebroides* and *Temnochila*, the elaterids *Alaus* and *Hemirhipis* and net-winged insects (Rhaphidiidae: Neuroptera) (Linsley 1959).

Parasitoids of P. semipunctata

There are a number of parasitic wasps native to Australia associated with *P. semipunctata*. These include the braconids *Jarra phoracantha* Marsh and Austin, *J. maculipenni*, *Callibracon lirnbatu* Brulle', *S. Lepidus*, *J. painei* sp.n, Marsh and Austin and *J. bicolor* Marsh and Austin, the megalyrid *Megalyra fasciipennis* Westwood (Austin and Dangerfield 1997), the pteromalid *Cleonymus* sp. and the ichneumonids *Xorides australiensis* Szepliget and *X. crudelis* Turner (Austin and Dangerfield 1997). The encyrtid wasp *Avetianella longoi* Siscaro (Hymenoptera) which oviposits in the eggs of *P. semipunctata* (Austin and Dangerfield 1997; Lahbib et al., 2009) has been utilised as a successful biological control agent in California (Hanks et al., 1995, 1996b). However, in

other parts of the world the use of parasitoid wasps as biological control agents of *P. semipunctata* have not been as successful (Paine 2006).

1.8. Defence mechanisms of trees against Cerambycids

Trees have developed a number of defence mechanisms to withstand and modify insect infestation including chemicals (resin and gums) within the tree and physical defences such as bark barriers and wood moisture (Martin et al., 2003; Franceschi et al., 1998).

1.8.1. Chemical defences against woodborers

Chemical defences of woodborers include, allelochemicals, sap flow and the production of kino (an aqueous solution of polyphenolic compounds) (Evans et al., 2004). Allelochemicals become synthesised once phloem vessels have become wounded (Lieutier 2004). Formations of kino veins are common in many *Eucalyptus* spp. (Eyles and Mohammed 2002) and are historically thought to be produced for defence. Drought stress changes physical structures (e.g. causes xylem cavitation and desiccation of tissues) and chemicals (slower resin flow and changes in chemicals released) of the tree (Evans et al., 2004). Drought stressed trees had reduced sap flow and kino production and resulted in decreased resistance to woodborer attack (Chararas 1969). Also changes in glycoside and phenolic acid content released from the bark of different poplar (*Populus*) trees caused changes in their level of resistance against *A. glabripennis* (Evans et al., 2004). In *E. rudis* plantations, a decrease in leaf water potential caused cambial damage from *P. semipunctata* larvae to double (Hanks et al., 1999). In addition, drought stressed *E. rudis* trees with reduced kino production in the bark (Hanks et al., 1999), did not prevent attack by *P. semipunctata*.

1.8.2. Physical defences against woodborers

There are many physical barriers in trees which limit woodborer attack including callus growth, bark thickness and moisture. High callus growth of experimentally wounded oak trees reduced attacks or successful colonisations by the twolined chestnut borer, *Agrilus bilineatus* Weber (Coleoptera: Buprestidae) (Dunn et al., 1990). Also galleries from woodborers were grown over by callus tissue (Paine and Millar 2002) and prevented further attack. In oak trees galleries of oak borer (*E. rufulus*) were compartmentalised by development of lesions extending in both directions from the gallery (Shigo and Marks 1977; Haavik and Frederick 2011). Bark thickness was an important defence mechanism in ash trees (*Fraxinus* spp.) where thin bark (less than 1.5 mm) and thick bark (greater than 5 mm) had the lowest gallery densities of the emerald ash borer *Agrilus planipennis* Fairmaire (Timms et al., 2006). High bark moisture content appears to be an important defence mechanism in healthy *E. rudis* trees was associated with a decline in larval survival (Hanks et al., 1999). Also no first instar larvae survived when inserted into the bark of healthy *E. grandis* trees (Hanks et al., 1990). These findings suggest *Eucalyptus* trees that maintain high bark moisture will resist successful colonisation and attack by *P. semipunctata*.

1.9 Thesis Aims

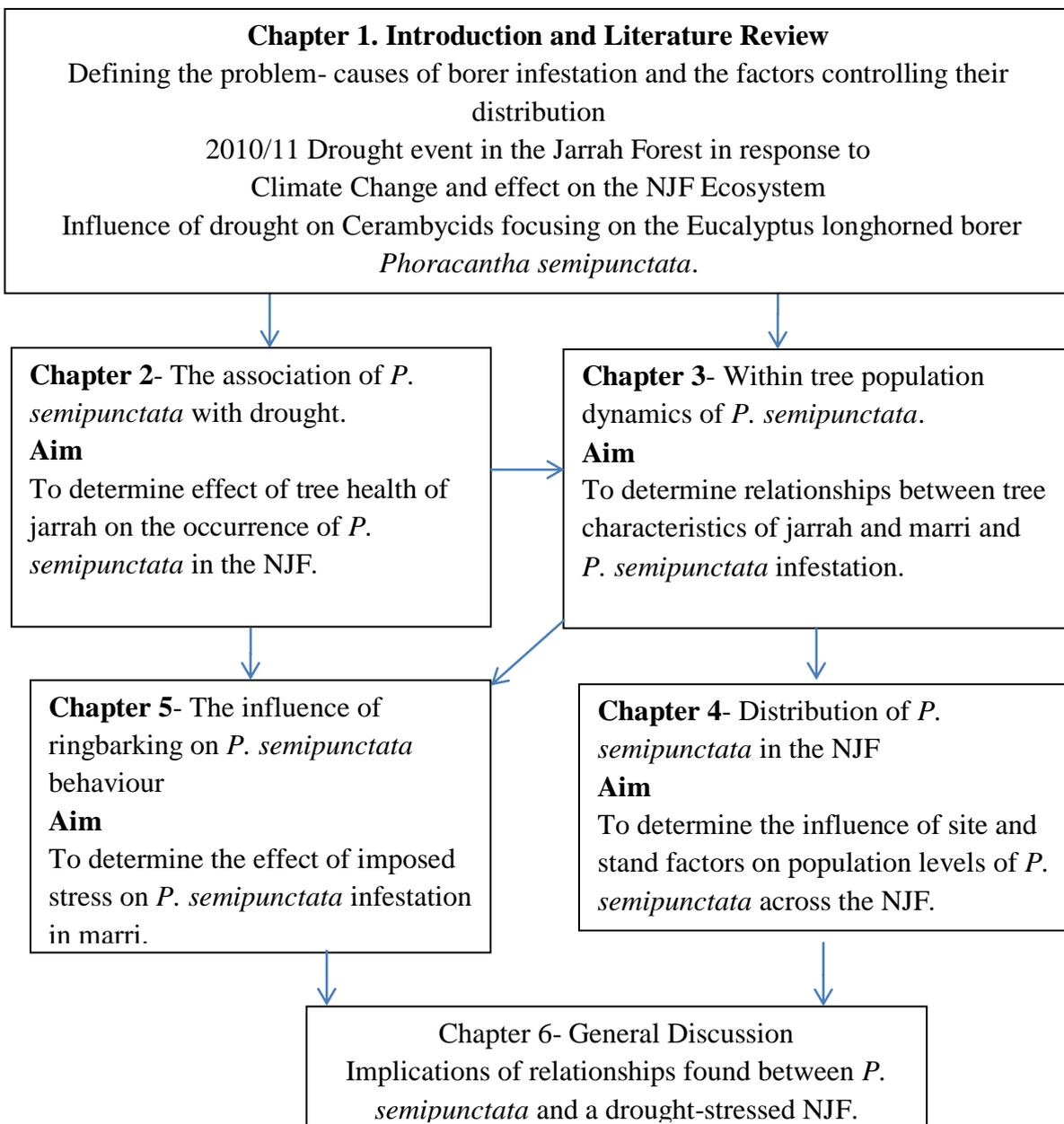
Little research has investigated the interaction between *P. semipunctata* and drought in the drought-prone jarrah forest of south-western Australia. By studying the incidence of *P. semipunctata* at collapsed sites in the NJF and borer infestation will enable better control measures to be developed. The aim of this thesis was to survey and determine if there is a relationship between *P. semipunctata* infestation and drought affected jarrah and marri trees following the 2010 drought in the NJF. Secondly to study the within-tree population

dynamics of *P. semipunctata* for jarrah and marri, thirdly to determine site and tree factors associated with the distribution of *P. semipunctata* across the NJF and fourthly the effect of ringbarking on *P. semipunctata* visitation.

The following hypotheses were examined:

1. H0= *Phoracantha semipunctata* equally infest stressed and healthy trees.
2. H0= *Phoracantha semipunctata* are distributed evenly within infested trees.
3. H0= *Phoracantha semipunctata* population levels are equally distributed throughout collapsed sites within the Northern Jarrah Forest.
4. H0= *Phoracantha semipunctata* equally visit healthy and ringbarked (stressed) trees.

In order to test these hypotheses the thesis was structured as follows;



CHAPTER 2

The association between *P. semipunctata* (Coleoptera: Cerambycidae) and drought-induced tree damage in the Northern Jarrah (*Eucalyptus marginata*) Forest of Western Australia.

2.1 Introduction

The Northern Jarrah Forest (NJF) in the south-west of Australia, which is dominated by jarrah (*Eucalyptus marginata* Donn Ex Smith) and marri (*Corymbia calophylla* Hill), have developed sinker roots and lignotubers to cope with drought (Abbott et al., 1989). However, during the summer of 2010/2011 and in the midst of extreme drought conditions, patches of jarrah and marri scattered throughout the NJF, suffered sudden canopy mortality leading to significant stem mortality, with approximately 16,800 ha (1.7 %) of the forest affected (Matusick et al., accepted). Observations made shortly following the onset of symptoms suggested woodboring Coleoptera were associated with dying stems. The lack of information regarding woodboring Coleoptera in the NJF made it impossible to predict the ultimate impact of the unprecedented drought on woodboring coleopteran populations and tree mortality. Drought events in other forest types have been shown to trigger woodboring beetle outbreaks leading to extensive beetle-induced tree mortality following drought (Lawson 2003; Coulson and Stephen 2006; Fierke et al., 2007; Hebertson and Jenkins 2008).

Many native coleopteran woodborers are secondary disturbance agents infesting trees stressed from other disturbances, such as pathogenic fungi (Jacobs et al., 2002; Jankowiak and Rossa 2007; Jankowiak et al., 2007), high winds (hurricanes and tornados) (Hobbs 1999; Dickens and Johnson 2007), fire (Costello et al., 2011), and drought (Muilenburg et

al., 2008). In certain woodboring coleoptera, a strong relationship between infestation and drought occurs (Evans et al., 2004; Dunn and Crutchfield 2009). During a multi-year drought in Europe in the 2000's woodboring bark beetle populations of *Ips typographus* L. increased substantially in many important forest types (Rouault et al., 2006). In the south-eastern United States, bark beetles *Ips lecontei* Swaine respond strongly to drought by readily invading water-stressed ponderosa pine (*Pinus ponderosa* Dougl. ex Laws) trees (McMillin and DeGomez 2008). Many woodboring beetles are thought to be among the primary opportunistic pests, which act in removing weakened trees from populations (Lawson 2003; Duerr and Mistretta 2011). However, in situations where woodborers are introduced to new areas or endemic populations reach outbreak levels, extensive damage can occur (Coulson and Stephen 2006; Hanks et al., 1999).

Phoracantha semipunctata Fabricius (Coleoptera: Cerambycidae; Cerambycinae: Phoracanthini), an Australian native woodborer and pest of eucalypts has been introduced to many areas of the world, causing extensive damage in plantation-grown trees (Duffy 1963). For example, the borer can destroy the entire cambium layer, causing rapid death of the tree (Hanks et al., 1993). *Phoracantha semipunctata* favours drought stressed trees (Clark 1925; Curry 1981; Hanks et al., 1999; Paine 2006). Research suggests inner bark moisture is a primary predictor of infestation, where low moisture levels facilitate invasion (Hanks et al., 1999). These facts suggest a strong relationship between drought stress and *Phoracantha semipunctata* populations. Although this relationship has been shown in plantations overseas where both the pest and its hosts have been introduced, it has not been established in Australian forests where both are native.

In the NJF, preliminary data suggests the primary woodborer infesting drought-impacted dying trees is *P. semipunctata*. The 2010/2011 extreme drought event in the NJF,

provides a good opportunity to better understand the relationship between drought, tree water stress, and *P. semipunctata*. The aim of the present study was to determine if there is an association between drought-affected *Eucalyptus marginata* (jarrah) and *Corymbia calophylla* (marri) overstorey trees and *P. semipunctata* in the NJF. The study compared *P. semipunctata* populations, estimated from tree-level infestation sampling (Fierke et al., 2005), within collapsed and adjacent intact areas of forest and tested the hypothesis that *P. semipunctata* equally infest healthy and stressed trees.

2.2. Methods

2.2.1. Site selection

Four drought-affected sites used in the study were chosen from a population of drought-affected sites identified during an aerial survey conducted in May 2011, during the peak of the drought (Matusick et al., accepted). The aerial survey identified 240 distinct areas greater than 0.3 ha, characterized by a red and brown forest canopy, which were different from the green foliage of the surrounding healthy forest. A random subset of 34 drought-affected sites were delineated accurately using a differential GPS (Pathfinder Pro XRS receiver, Trimble Navigation Ltd., Sunnyvale, CA) using ArcGIS to form a shapefile (Matusick et al., accepted). Out of these 34 sites, four collapsed sites, including two in the northern and two in the southern section of the aerial survey, were chosen for sampling of the *P. semipunctata* populations. The northern sites were located in the Chandler forest block; and site N2 (32°13'36.96"S: 116° 8'1.24"E) site N3 (32°14'32.70"S: 116° 7'55.49"E) and the two southern sites located approximately 50 km south of the northern sites; site N7 (32°33'58.41"S: 116° 0'17.67"E) and site N8 (32°33'45.76"S: 116° 0'32.41"E) (Figure 2.1). The sites in the north and the south were chosen close (within 1

km) to each other to sample sites with similar climatic conditions but having different site conditions.

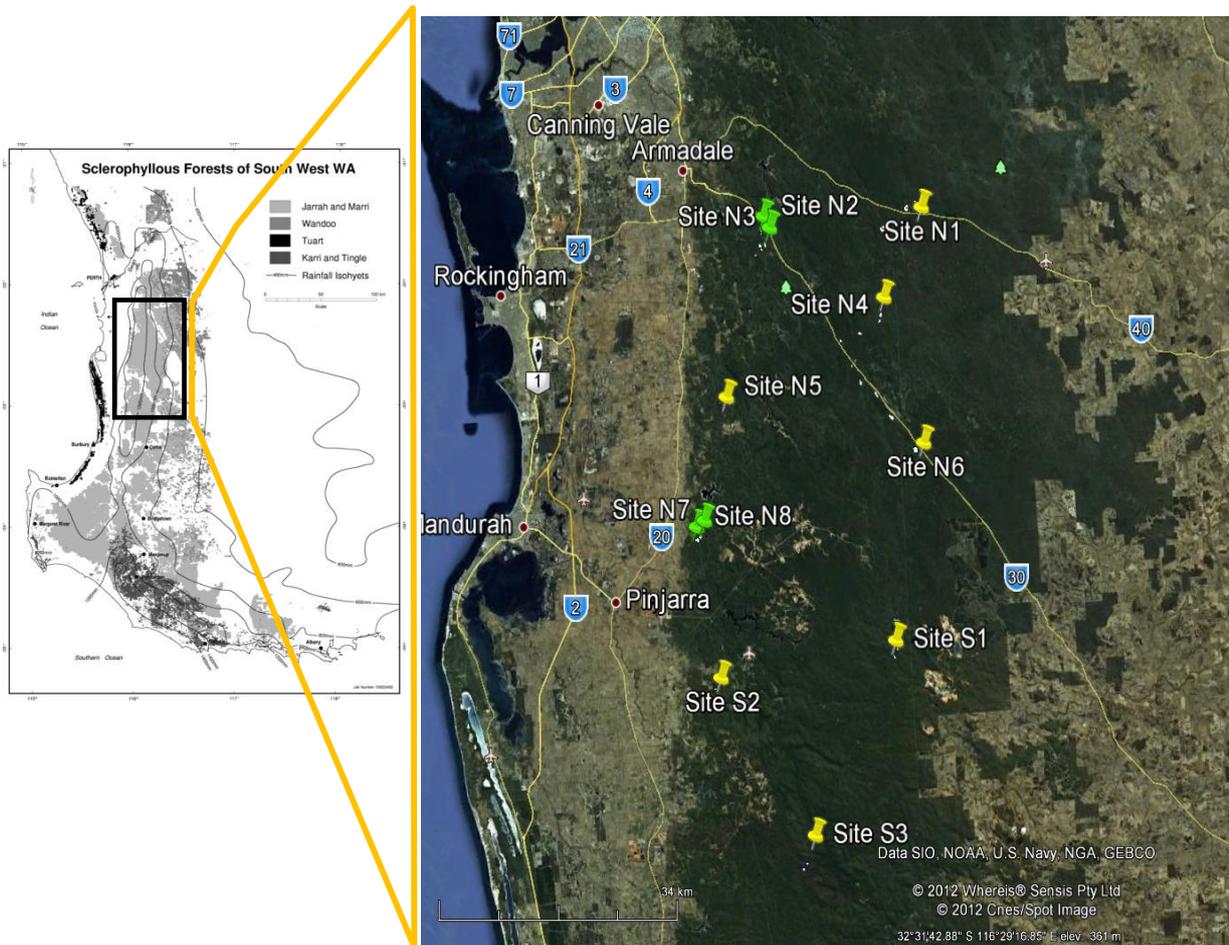


Figure 2.1. Location of the collapsed sites N2, N3, N7 and N8 (green pins) in the Northern Jarrah Forest. Inset shows location of study sites in relation to south-western Australia. The green pins are also the sites used in Chapter 3 and both the green and yellow pins indicate the collapsed sites measured in Chapter 4.

For each of the four collapsed sites (N2, N3, N7 and N8) a 10 metre buffer from the edge of the collapsed site was marked out using ArcPad: ArcGIS v10 and then outside the buffer a 30 m wide area of healthy unaffected trees (referred to as intact area) was delineated. The buffer was used to avoid sampling trees along the edge of the collapsed sites (Figure 2.2) and the 30 m limit was delineated to avoid possible overlapping with an adjacent collapsed sites and to give a similar sampling area as for the collapsed sites.

2.2.2. Sample point selection

Within each of the collapsed sites and adjacent intact areas, the fGIS v1 forest cruze program (Wisconsin DNR-Division of Forestry) was used to generate 20 random points on a 40 m x 40 m grid within collapsed and adjacent intact areas at each site. However, due to time constraints, only 6 of the 20 random points were sampled. Effort was taken to ensure the six chosen sample points were representative across the collapsed and intact areas (Figure 2.2). A differential GPS (± 0.4 m) was used to locate each sample point in the forest.

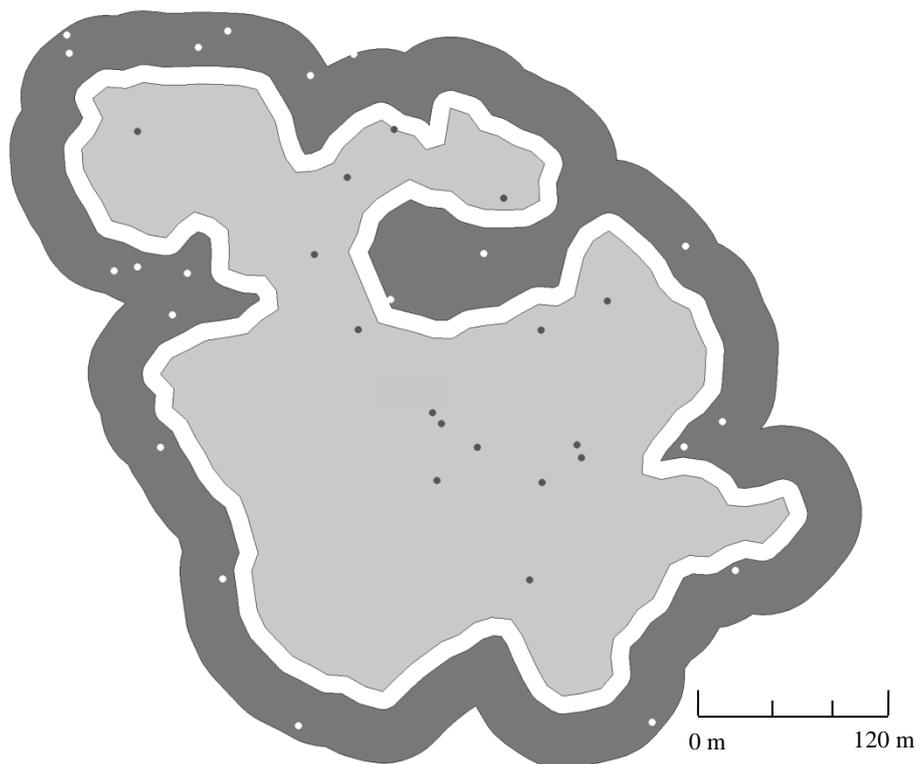


Figure 2.2. A collapsed area (light grey), with 10 m buffer zone (white) and a surrounding intact area (dark grey) in this case site N2. Also shown are the random points (dark grey for collapsed area and white for intact area) used for sampling.

2.2.3. Sampling methods

The point-centred quarter method of tree sampling was used to select four trees at each sample point (Mitchell 2007). First, the area surrounding each of the six random points

was divided into four quarters using a compass (Sunto MC2, Finland) to mark North, South, East and West making NE, SE, SW and NW quadrats, respectively. Then the nearest tree (jarrah or marri) with a diameter over bark at breast height (DOBH) >10 cm in each quarter was selected for sampling, to give a total of 24 trees sampled within each of the intact and collapsed areas on each site. Consequently, a total of 192 trees were sampled for *P. semipunctata*. The distance from the random point to the four trees selected was measured. The modified randomised point centred quarter method (Mitchell 2007) was then used to determine the density of trees per site (\bar{r}).

$$\bar{r} = \frac{\sum_{i=1}^n \sum_{j=1}^4 R_{ij}}{4n}$$

where n the number of sample points at a collapsed site

4n the number of samples or observations with one for each quarter

i a particular sample point, where i = 1...n

j a quarter at a sample point, where j = 1...4

R_{ij} the point-to-tree distance at point i in quarter j

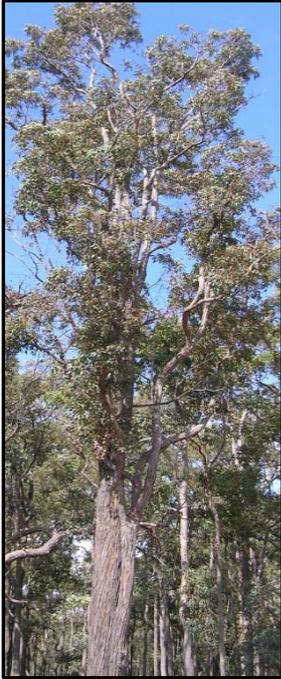
where the density (λ) of trees per site in trees per hectare was calculated as; $\lambda = 10,000 / \bar{r}^2$ (Mitchell 2007).

For each of the sample trees the diameter at breast height over bark at 1.37 m (DBHOB) was measured using tree callipers (Haglof, Sweden) and the health of each tree was estimated using a tree health score from 1 (healthy) to 5 (long dead) (Table 2.1, Figure 2.3).

Table 2.1. Tree health scores*

Score	Description
1	>90 % of tree green and healthy with full crown
2	40 to 90 % of tree green and healthy with part of crown missing
3	<40 % tree green and healthy with no crown present (not including coppice and epicormic shoots)
4	tree recently dead (intact bark, fine branches present)
5	tree long dead grey appearance (trunk lost bark, fine branches missing)

*adapted from Worrall et al., (2008).



(a)



(b)



(c)



(d)



(e)

Figure 2.3. Example of trees with (a) health score 1= >90 % green and healthy with full crown, (b) health score 2= 40 to 90 % green and healthy with part of crown missing, (c) health score 3= <40 % green and healthy with no crown present (not including coppice and epicormic shoots), (d) health score 4= tree recently dead (intact bark, fine branches present), and (e) health score 5= tree long dead with grey appearance (in foreground) (trunk lost bark, fine branches missing).

Emergence holes (m^{-2}) was calculated by counting the number of emergence holes created by *P. semipunctata* to a height of 2 m and dividing by the surface area of the tree calculated to 2 m (Curry 1981; Fierke et al., 2005). In order to reveal emergence holes that were obstructed by bark, the outer bark was scraped away prior to counting. Emergence holes of *P. semipunctata* were easily distinguished from other woodborers that occur in the NJF by their diameter. The emergence holes of *P. semipunctata* are 8-12 mm in diameter (and confirmed from preliminary observations of emergence holes where *P. semipunctata* adults had emerged from jarrah and marri trees in the NJF, Figure 2.4), whilst emergence holes for the introduced bark beetle *Ips grandicollis* Eichhoff were 2 mm and for the pin hole borer *Atractocerus kreuslerae* Pascoe (Coleoptera, Lymexylidae) and the ambrosia beetle *Xyleborus saxeseni* Ratzeburg <1 mm (Curry 1981; Major and Abbott 1989). The diameter of the emergence hole of *P. semipunctata* is similar to *P. acanthocera* (Figure 2.4 a and b) except for the external appearance of a bullseye. The frass plug leads to the pupal cell and is absent once the adult has emerged (Farr 2010).



Figure 2.4. Emergence hole of (a) *Phoracantha semipunctata* in the bark of jarrah and (b) entry to the pupal cell of *P. acanthocera* in the sapwood of marri. Scale next to emergence hole is in mm.

2.2.4. Statistical analysis

The effect of treatment area on tree health was compared by determining the proportion of trees with a health score of 1 compared to the proportion of trees with health scores 2 -5 and evaluated by the Pearson chi-squared test. The effect of treatment area and tree health on Emergence holes (m^{-2}) of *P. semipunctata* were tested for normality of residuals and no transform was necessary and then analysis of variance (ANOVA) completed using the statistical program SPSS 18 (Anon 2011). Treatment means were compared by LSD at $P=0.05$ using Duncan Multiple Range test and means (\pm SE) are shown as appropriate.

2.3. Results

2.3.1. Effect of drought on the jarrah forest

There was a significantly ($\chi^2=59.29$, $n=1$, $P<0.001$) greater proportion (9x) of trees in the intact area with a health score of 1 compared to trees in the collapsed area, where 93 % had lost some or all of their canopy (Figure 2.5). There was no significant ($P>0.050$) difference in the proportion of trees in the intact area with a health score of 2 (i.e. lost 15 - 95 % of canopy) compared to trees in the collapsed area. There was a significantly ($P<0.050$) smaller proportion ($1/6^{\text{th}}$) of trees in the intact area with a health score of 3 (i.e. had lost all canopy) compared to trees in the collapsed area. Less than 1 % of the trees in the intact area had recently died (health score 4) with no long dead trees (health score 5) present. While in the collapsed area 18 % of trees had recently died (health scores 4) and 6 % of trees were long dead (health score 5) (Figure 2.5).

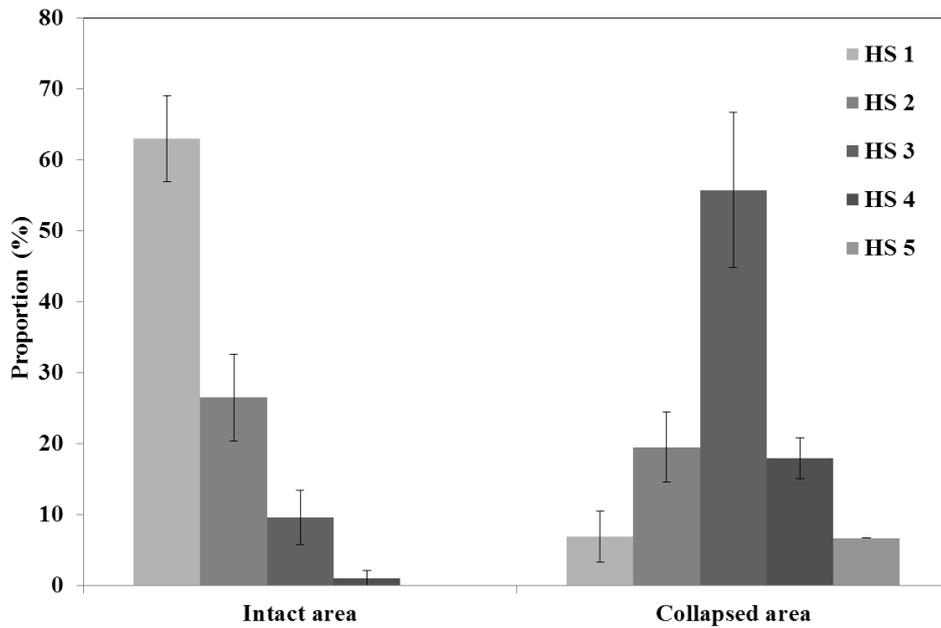


Figure 2.5. Proportion (mean \pm SE) of trees in each health score (1 healthy to 5 long dead) (HS 1 to HS 5) as a percentage of the total number of trees measured for intact area and collapsed area averaged across all collapsed sites N2, N3, N7 and N8.

2.3.2. Effect of drought on *P. semipunctata*

There was no significant ($P > 0.050$) difference of emergence holes (m^{-2}) between the four sites ($F = 1.23$, $P = 0.299$) (Table 2.3). While emergence holes (m^{-2}) were fifty-nine times higher ($F = 39.13$, $P < 0.001$) for trees in the collapsed areas compared to trees in the intact areas across all sites (Figure 2.6, Table 2.2). Also the number of trees with emergence holes (m^{-2}) in the intact areas was significantly ($\chi^2 = 70.40$, $n = 1$, $P < 0.001$) different compared to trees in the collapsed areas.

Table 2.2. Analysis of variance of adult *Phoracantha semipunctata* emergence holes (m^{-2}) comparing intact or collapsed areas for the collapsed sites N2, N3, N7 and N8,

Source of variation	d.f.	m.s.	<i>F</i>	<i>P</i>
Site	3	29.05	1.23	0.299
Treatment area	1	35.45	39.13	<0.001
Site x Treatment area	3	920.83	1.51	0.215

Table gives degrees of freedom (d.f.), means squared (m.s.), f values (*F*) and associated probabilities (*P*) where treatments were intact area vs collapsed area.

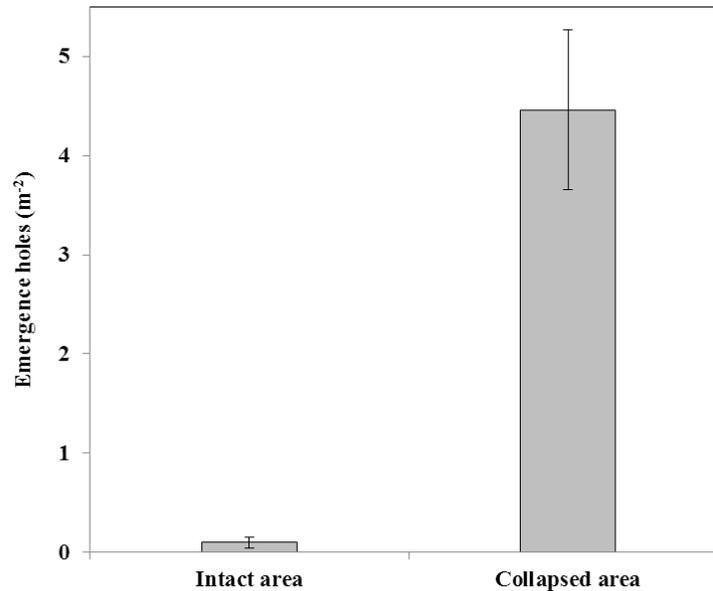


Figure 2.6. *Phoracantha semipunctata* emergence holes (m⁻²) (mean ± SE) (measured by counting the number of emergence holes made in the bark by adults measured from the first 2 m of tree height) in intact area and collapsed area averaged for the four collapsed sites N2, N3, N7 and N8. LSD ($P<0.050$) for comparing intact area and collapsed area =1.379, n =184.

For trees with a health score of 1 or 2 no *P. semipunctata* emergence holes were present in the intact area and there were less than 1 emergence hole/m² present in the collapsed area (Figure 2.7). Whereas for trees with a health score of 3 there were less than 1 emergence holes (m⁻²) in the intact area with significantly ($F= 3.952$, $P<0.002$) higher (13 times) emergence holes (m⁻²) in the collapsed area (Figure 2.7). Within the collapsed area emergence holes (m⁻²) in trees with a health score of 4 was significantly ($P<0.050$) higher (2.5 times) than for trees with a health score of 3. There was also no significant ($P>0.050$) difference of emergence holes (m⁻²) measured to 2 m tree height, with equal number of emergence holes (m⁻²) occurring on the northern and southern sides of the tree ($F=0.03$, $P=0.856$).

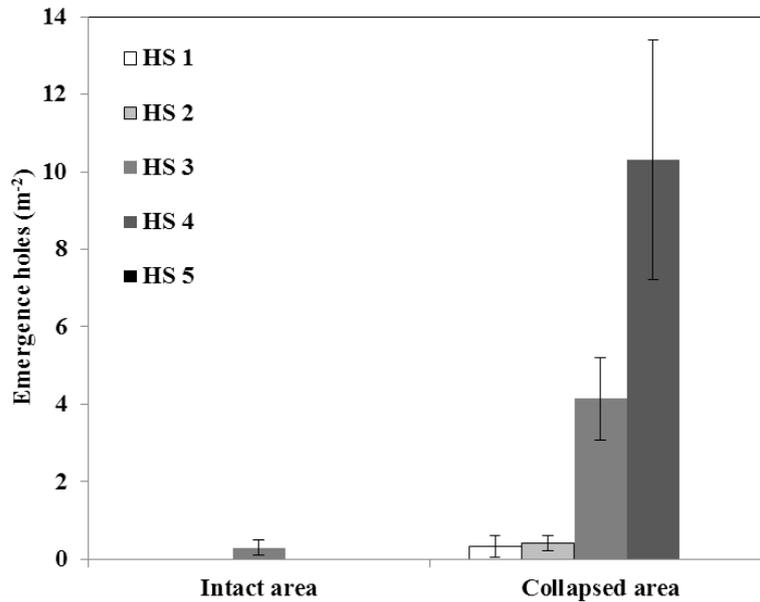


Figure 2.7. *Phoracantha semipunctata* emergence holes (m^{-2}) (mean \pm SE) (measured by counting the number of emergence holes made in the bark by adults measured from the first 2 m of tree height) for each health class (1 healthy to 5 long dead (no trees were found) (for HS 1 n=65, HS 2 n=47, HS 3 n=58 and H4 n=15) for intact areas and collapsed areas averaged across all collapsed sites N2, N3, N7 and N8. For health score x treatment area interaction LSD ($P < 0.050$) = 3.952, n = 27.

2.4. Discussion

The presence of *P. semipunctata* was strongly associated with drought affected trees that had lost their canopy and these were concentrated within collapsed areas. This demarcation has not been reported before for *P. semipunctata* in the NJF. A similar response has been recorded for the twolined chestnut borer *Agilus bilineatus* (Coleoptera: Cerambycidae) where infestation was significantly higher in oak (*Quercus* spp.) trees which experienced crown dieback compared to trees with healthy crowns (Muzika et al., 2000). In plantation grown *Eucalyptus* in California larval survivorship of *P. semipunctata* was high in stressed trees and cut logs that were artificially infested (Hanks et al., 1999). Also in northern Queensland plantation grown *Eucalyptus* that were drought stressed had high levels of *P. semipunctata* in trees (Lawson 2003). Concentrations of southern pine beetle have been found in susceptible habitat patches of southern yellow pine *Pinus taedia* (Coulson and Stephen 2006). Woodborers tend to be patchily

distributed in forests (Haack and Slansky 1987). In the NJF this appears to be related to the high concentration of drought affected trees which were more susceptible to borer attack.

The association of high concentration of *P. semipunctata* in drought affected patches of the NJF could have been due to insects responding to the damage of trees from the drought or the insects contributed to the damage of the trees affecting their health. A number of reports have indicated that *P. semipunctata* adults are attracted to trees that are stressed (Chararas 1969; Drinkwater 1975). The larvae can cause major destruction partially (Hanks et al., 1999) or completely destroying the entire cambium and sapwood layer of *Eucalyptus* (Duffy 1963) resulting in the death of trees including plantation *Eucalyptus* in Tunisia (Chararas 1969). These reports tend to suggest that initially there is a need for weakened trees for ovipositing and larval development (Hanks et al., 1993). Once the tree is infested it is further weakened by larval feeding which increases susceptibility to further attack by later generations, increases the amount of damage until it is sufficient to kill the tree (Duffy 1963). In the case of the NJF it may have been that the drought weakened the trees allowing infestation by *P. semipunctata* which may further weakened the trees and subject them to further infestation.

There was a clear distinction of adult *P. semipunctata* population levels within and outside collapsed areas of the forest. The numbers of *P. semipunctata* emergence holes (m^{-2}) in the intact surrounding areas may be an indication of the background population levels in the NJF. The number of 4.5 emergence holes (m^{-2}) in the collapsed sites was similar to 2 to 6 emergence holes (m^{-2}) reported by Hanks et al., (1993) on *Eucalyptus* plantation logs in California. However, the collapsed area was where most of the borers were found it is expected the average level of *P. semipunctata* across the NJF will be much less and

approaching 0.5 emergence holes (m^{-2}). In contrast, density of red oak borer *Enaphalodes rufulus* Haldeman (Coleoptera: Cerambycidae) found in oak (*Quercus* spp.) trees in Arkansas were much higher at 12.5 emergence holes (m^{-2}) (Fierke et al., 2007) than in the NJF. It appears that in a Mediterranean climate a sclerophyll forest can only support low numbers of borers before trees become adversely affected by *P. semipunctata* leading to tree decline.

The inability of *P. semipunctata* to move into the intact area surrounding the collapsed area may indicate lack of sufficient suitable hosts or stressed trees being hidden by healthy trees, poor semiochemical signals or erratic flight patterns. Sight recognition and semiochemicals released from stressed or recently dead trees (Barata and Araujo 2001) are critical for *P. semipunctata* to find suitable hosts (Drinkwater 1975). This may indicate that *P. semipunctata* is unable to visualise stressed trees in the intact area as they were few in number and therefore may have been hidden from view by healthy trees. Alternatively, the few stressed trees in the intact area did not produce sufficient semiochemical odours to attract adults whose flight pattern became erratic (Barata and Araujo 2001) and were unable to find a host. Preliminary observations in the present study using light traps observed that the flight patterns of an individual *P. semipunctata* was erratic (data not presented). Therefore, in the intact areas where there were few stressed trees the likelihood of finding a suitable host tree to mate and oviposit is low.

Findings from the present study that *P. semipunctata* emergence holes (m^{-2}) appeared approximately 12 to 14 months after the drought and occurred almost exclusively in trees affected by the drought. This strongly points to *P. semipunctata* infesting trees during the exceptionally hot summer of 2010/11 and taking advantage of the weakened condition of trees at this time. In studies overseas *P. semipunctata* was found to attack trees mainly

during spring and summer (Paine et al., 2009). *Phoracantha semipunctata* were particularly concentrated in trees that had recently died and lost their entire canopy. As a result *P. semipunctata* may have contributed to the dying condition of these trees accelerating tree decline.

Tree collapse was concentrated in distinct patches within the NJF and appears to be a similar response to a number of drought-induced tree mortality events in relation to climatic stress worldwide (Allen et al., 2010). Increasing borer activity causing hydraulic failure and carbon starvation in trees amplifies the effects of drought (McDowell et al., 2008). In the NJF, explosion of *P. semipunctata* numbers due to the abundance of stressed trees in a confined area caused increased damage to trees exacerbating tree decline. As trees in the intact area had experienced some loss of canopy this indicates that the effect the 2010 drought appears to be extending in a limited amount beyond the collapsed area and into the intact area. This process if it continues in response to drought there would be likely a significant increase in area of collapsed sites, with a possible reduction in the species diversity in the NJF as has occurred across northern Arizona from subsequent droughts in 1996 and 2002 with a pinyon–juniper woodlands becoming dominated by juniper (Mueller et al., 2005). Further study is needed to investigate the health of the NJF in response to further *P. semipunctata* infestations under conditions of the expected increased frequency of droughts in south-western Australia (Bates et al., 2008). The effect of high infestation by *P. semipunctata* on drought affected jarrah and marri trees, in terms of *P. semipunctata*'s life stages and tree characteristics will be presented in Chapter 3.

CHAPTER 3

Within-tree population dynamics of *Phoracantha semipunctata* (Coleoptera: Cerambycidae) in drought stressed trees in the Northern Jarrah (*Eucalyptus marginata*) Forest.

3.1. Introduction

Cerambycid woodborers are polyphagous and can cause major damage in forests reducing the value of salvageable timber and also increase tree mortality, with many becoming serious pests in Europe and North America (Evans et al., 2004; Costello et al., 2011). One example of a cerambycid woodborer causing considerable damage is the Asian longhorned beetle (*Anoplophora glabripennis* Motschulsky), which has been recently introduced to Europe and North America and has been responsible for 30 % mortality with a \$600 billion impact predicted in the USA (Evans et al., 2004; Hanks 2006; Hu et al., 2009). Also following drought a number of outbreaks of Cerambycids have been reported (Allen et al., 2010). For example, *Enaphalodes rufulus* Haldeman which was associated with a prolonged drought between 1990–2002 contributed to the destruction of 1.8 million hectares of oak (*Quercus* spp.)-hickory forest in the Ozark and Ouachita Mountains of Arkansas in the USA (Haavik et al., 2012).

Tree characteristics and host preference are important in determining within-tree population dynamics (Haavik and Stephen 2010; Haavik et al., 2012). In *Quercus rubra* L. *E. rufulus* showed a preference for infesting red oak over white oak (Haavik et al., 2012). The relationship between physical tree characteristics and woodborer behaviour has been studied for emerald ash borer *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae) in ash (*Fraxinus* spp.) trees in North America which preferred trees with diameters of between 4 and

13 cm, a critical bark thickness of 1.5 to 5 mm and had decreased gallery density at greater than 7 m tree height (Timms et al., 2006). Bark type and texture characteristics of trees are important in locating ovipositing positions in *Agrilus liragus* Barter and Brown (Coleoptera: Buprestidae) (Barter 1957). There is little or no such evidence of the effect of these physical factors reported for Cerambycids.

The genus *Phoracantha*, a prominent group of Cerambycids, occurs in *Eucalyptus* forests throughout Australia (Wang 1995). In south-western Australia the main *Phoracantha* species are the bulls eye borer *P. acanthocera* Macleay which infests native stands of healthy karri (*E. diversicolor*) trees reducing their value (Farr et al., 2000) and the tuart longicorn borer (*P. impavida* Newman), which ringbarks stems causing considerable damage to mature tuart (*E. gomphocephala* D.C.) trees along the south-western coast (Curry 1981). In Queensland and New South Wales the two hole borer *P. solida* Blackburn and the Eucalyptus longhorned borer *P. semipunctata* Fabricius infests Australian plantation eucalypts causing damage (Lawson 2003). Susceptibility of *Eucalyptus* trees to *Phoracantha* spp. attack depends both on the species of *Eucalyptus* and the species of *Phoracantha*. For example, 7 out of 24 *Eucalyptus* taxa were most susceptible to *P. solida* in Queensland (Lawson 2003).

Phoracantha semipunctata has been identified as a potential serious pest of forests in south-western Australia subject to drought (Kliejunas et al., 2003). Following the 2010 drought in south-western Australia, one of the driest years on record, and the appearance of patches of trees in the NJF showing effects of severe stress (Matusick et al. accepted) *P. semipunctata* was observed invading trees (Chapter 2). *Phoracantha semipunctata* has caused the death of a number of young jarrah (*Eucalyptus marginata*) trees in revegetated bauxite mine pits in the jarrah forest and has been associated with dead dying or dead trees (Curry 1981; Majer and Abbott 1989) and the destruction of cambium and phloem (Duffy 1963). *Phoracantha*

semipunctata has over 30 hosts of *Eucalyptus* that it infests (Duffy 1963; Wang 1995) with a preference for some hosts over others. For instance, in plantations in California *P. semipunctata* preferred to oviposit in logs of *E. trabutii* Wilm (a *E. camaldulensis* hybrid) compared to *E. cladocalyx* F., *E. grandis* Hill ex Maiden and *E. terreticornis* Small although at high larval densities in *E. trabutii* increased larval competition and caused a high level of larval and pupae mortality (Hanks et al., 1993). Also the size of adults appears to determine the success of larvae in different aged trees, with larger adults able to survive in older fallen *Eucalyptus* logs compared to logs that were recently felled (Hanks et al., 1995). In the NJF no such studies have compared the host preference of *P. semipunctata* for jarrah and marri.

Drought events are likely to become more frequent and severe in south-western Australia and are projected to impact on south-western Australia's forests (Maher et al., 2010). The association between *P. semipunctata* and drought highlights the importance of understanding the biology and ecology of *P. semipunctata*. The aim of this study was to determine the relationship between *P. semipunctata* infestation and tree characteristics as it is affected by jarrah and marri trees in the Northern Jarrah Forest. The hypothesis tested was that *P. semipunctata* was distributed evenly within infested trees.

3.2. Methods

3.2.1. Sample tree selection

Eighty trees, which experienced canopy collapse (health class 3 or 4 [Chapter 3]), were selected from four sites, including two sites in the Wungong catchment, located in the north of the NJF, and two sites in the south of the NJF. All four sites represent typical upland sites in the northern jarrah forest composed of a mixture of jarrah and marri (*Corymbia calophylla*) in the overstory. At each site 10 jarrah and 10 marri trees with a diameter at breast height over

bark (DBHOB) between 10 cm and 45 cm were selected. This DBHOB range was used to ensure trees dissected were of a manageable size and comparable to other studies (Sanchez-Martinez et al., 2010). Locations of trees at the paired sites were recorded using a GarminGPSMap handheld receiver (Garmin Olathe, Kansas).

3.2.2. Harvesting and tree measurements

Sample trees were then harvested between March and April approximately 12-14 months after the initial collapse following the 2010 drought. Trees were felled as close to the ground as possible and tree height was measured. The entire tree was then cut into 1 m billets and each billet was numbered. Sectioning was stopped at 5 cm DOB as preliminary observations showed that *P. semipunctata* damage below this diameter in jarrah and marri was negligible. The diameter over bark (DOB) was measured over the outer bark at a position half way along each billet using 50 cm callipers (Haglof, Sweden). The surface area (m²) of a billet was calculated using the DOB and the length of the billet (1 m). This area was used to calculate *P. semipunctata* population measurements on an area basis. The cut end of each billet was photographed (Olympus® Camedia C-770 UltraZoom) for location of heartwood galleries to determine the distance larvae travelled into the heartwood. Bark thickness was measured using vernier callipers at two points around the circumference of each billet for selected trees.

3.2.3. P. semipunctata population measurements

The loose outer bark on each 1 metre billet for the whole tree was removed using a brush hook (Gerber® Portland, Oregon USA) to reveal adult emergence holes. Adult emergence holes (referred to as emergence holes) were identified by their oval shape and size (approximately 5 mm) and a lack of frass. All emergence holes were counted on each billet, then the entire bark of each odd numbered billet was removed to the sapwood using a brush

hook (Gerber®) machete or a small axe to reveal and count the number of clutch points (the position where ovipositing of eggs occurred) and neonate (1st instar) larval galleries. Clutch points were identified by neonate larval galleries radiating from a focal point (Figure 3.1).



Figure 3.1. Clutch point and neonate larval galleries as seen in sapwood of jarrah at site N2. The number of larvae that emerged from this clutch point was 39.

Each odd numbered billet was then split using log splitters and axes into 2 to 10 sections depending on the billet diameter to reveal larval galleries in the heartwood (Figure 3.2). Larvae, pupae or adults both dead and alive were collected from galleries, counted and placed in vials and 70 % ethanol solution was added and then on return to the laboratory were stored at 2 °C. Also any larval predators of Cerambycids were noted and collected.



Figure 3.2. Felled jarrah tree showing billets and method of splitting billets for within tree sampling.

Larvae, pupae and adults collected from sectioned billets (Figure 3.3) were identified as *P. semipunctata* using descriptions and keys in Duffy (1963), Wang (1995) and Morelli and Sanchez (2002) (reported in literature review, section 1.5). Larvae length and width of the pronotum were measured using vernier callipers with a dissecting microscope (Olympus®).



Figure 3.3. The mature larvae (left), pupae (middle) and adult (right) of *P. semipunctata* collected from sectioned billets of felled trees.

3.2.4. *P. semipunctata* feeding damage

For each odd numbered billet larval feeding damage was measured by placing a 10 cm x 10 cm grid printed on transparency paper (Figure 3.4) at three random locations on the sapwood surface, followed by recording the number of squares with larval feeding damage (represented as the percentage (%) of larval feeding). For selected billets of jarrah and marri trees the length of 12 pupal chambers was measured. For standing drought affected marri trees where bark had recently fallen off the trunk, the length of 10 larval feeding galleries in the sapwood were measured from a clutch point to its entry point into the heartwood.

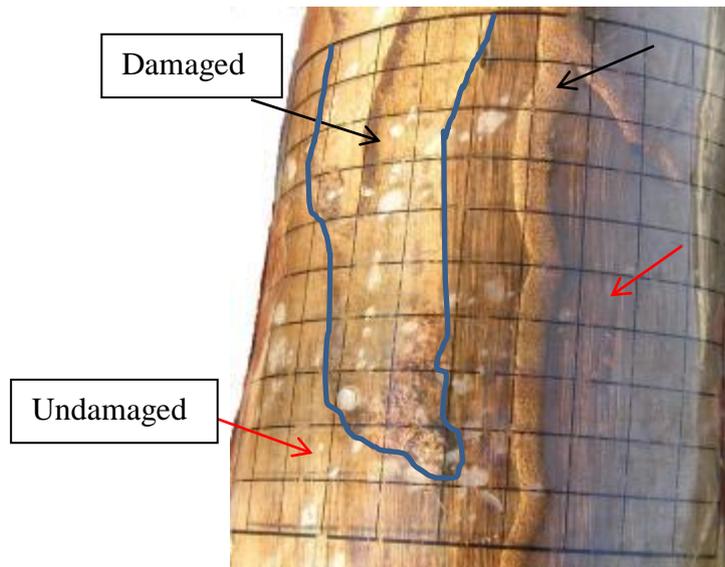


Figure 3.4. Transparent 10 cm x 10 cm grid used to measure larval damage to the sapwood after outer bark removal. Black arrows indicate damage and red arrows indicates where the sapwood was undamaged.

Although not the main purpose of the study, wood samples (80 cm x 30 cm) were collected during tree dissections from galleries showing dark staining, possibly indicating the presence of ophiostomatoid (blue stain fungi) (Matusick and Hardy pers comm.) using chisels and hammers. The samples were, placed in plastic bags, transported to the lab and placed in moisture chambers to culture the fungus for further investigation with identification being the responsibility of other parties.

3.2.5. Data analysis

At each of the four sites tree and *P. semipunctata* characteristics were compared for trees divided into 1 m billets (for up to 15 billets per tree, with the first billet at the base of the tree and subsequent billets increasing tree height until billet diameter was ≤ 5 cm) for 10 trees of jarrah and marri. Sites were not random and were treated as factors in the analysis as were species and billets with trees as replicates. Analysis of variance (ANOVA), using SPSS[®] 18.0 (Statistical Package for the Social Science, USA, IBM[®] Anon 2011) was used to test for differences between treatments of site, species and billet number on two levels, I) -sites,

species, billet height and all interactions, II) -individual analysis for each site comparing species and billet height and their interaction. Residuals were tested for normality and no transformation was necessary. For each analysis level tests for significance was made at $P < 0.050$ and if significant, treatment means were then compared by $LSD_{0.05}$ using the Duncan Multiple Range test and means (\pm SE) and are shown as appropriate in the results. Correlations between variables were analysed using generalised linear regression analysis using a t-test and a correlation coefficient (r^2). Where two variables were compared to the same independent variable a test of significance was completed using regression analysis at $P < 0.050$ in SPSS.

3.3. Results

3.3.1. Tree measurements

Jarrah and marri trees selected for sampling were not significantly different in height ($F=0.010$, $P=0.929$) and DBHOB ($F=0.480$ $P=0.491$) within sites with an average tree height of 11.32 m and an average DBHOB of 20.1 cm. Trees were significantly ($F=3.510$, $P < 0.020$) different in height between sites with the average height for jarrah and marri trees at site 166, 14 % taller than trees at the other three sites, while DBHOB was not significantly ($F=0.940$, $P=0.426$) different between sites (Table 3.1).

Table 3.1. Height (mean \pm SE) and diameter (mean \pm SE) of jarrah and marri trees selected at collapsed sites.

Site	Jarrah		Marri		Mean	
	height (m)	DBHOB (cm)	height (m)	DBHOB (cm)	height (m)	DBHOB (cm)
N2	10.12 \pm 0.68	19.8 \pm 2.8	10.62 \pm 0.46	17.7 \pm 1.7	10.37 \pm 0.40	18.7 \pm 1.6
N3	10.83 \pm 0.88	18.8 \pm 1.8	11.94 \pm 0.78	20.2 \pm 3.3	11.39 \pm 0.59	19.5 \pm 1.8
N7	11.21 \pm 0.96	19.1 \pm 0.35	10.84 \pm 0.46	21.3 \pm 1.3	11.03 \pm 0.29	20.7 \pm 1.0
N8	12.10 \pm 0.85	20.6 \pm 1.8	12.91 \pm 0.71	23.6 \pm 2.5	12.51 \pm 0.55	22.2 \pm 1.6
Mean	11.34 \pm 0.84	19.6 \pm 1.4	11.30 \pm 0.60	20.7 \pm 1.7	11.32 \pm 0.46	20.1 \pm 1.6

Billet diameter for both jarrah and marri trees significantly ($F=247.99$, $P<0.001$) decreased with increasing height above the ground. Species of trees had the same diameter over bark (DOB) at 1 metre height with DOB of marri decreasing significantly ($F=19.32$ $P<0.001$) more (1.49 cm m^{-2}) than jarrah (1.02 cm m^{-2}) with increasing height (Table 3.2). The average diameter (cross sectional area) of marri was $13.83 \pm 1.61 \text{ cm}$ ($0.434 \pm 0.050 \text{ m}^{-2}$) and jarrah was $15.31 \pm 1.14 \text{ cm}$ ($0.481 \pm 0.036 \text{ m}^{-2}$) (Figure 3.5). There was a strong negative correlation between billet diameter and height of tree (Figure 3.5).

Table 3.2. Analysis of variance of DOB comparing sites (N2, N3, N7 and N8), species (jarrah and marri) and height.

Source of variation	d.f.	m.s.	<i>F</i>	<i>P</i>
Site	3	433.78	10.96	<.001
Species	1	16.46	0.42	1.000
Site x species x height	3	281.93	7.12	<.001
Species x height	22	764.95	19.32	<.001
Site x Species x height	66	524.74	13.25	<.001

Table gives degrees of freedom (d.f.), means squared (m.s.), f values (F) and associated probabilities (P).

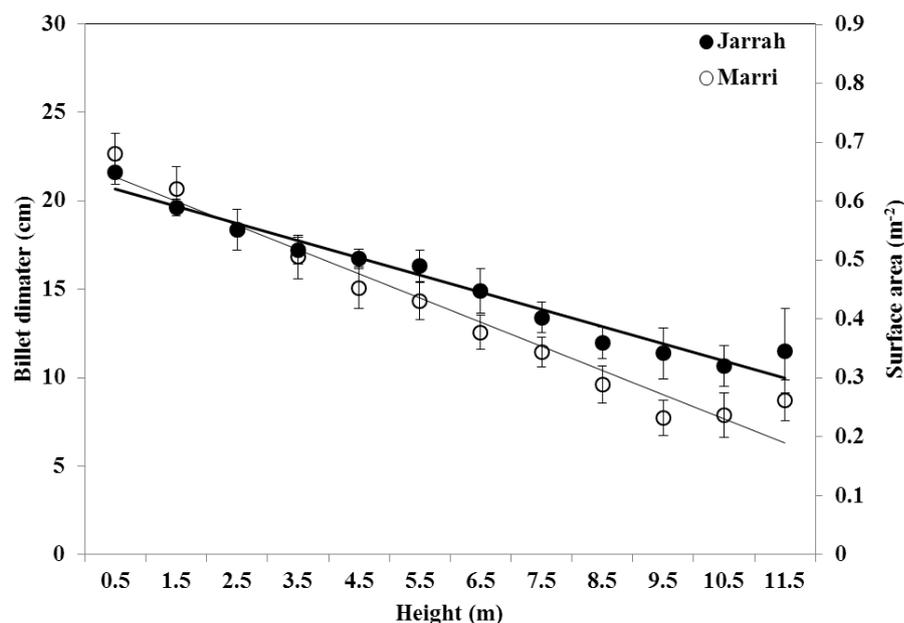


Figure 3.5. Relationship (mean \pm SE) between billet diameter (cm) and surface area (cm^2) and tree height for jarrah (\bullet) and marri (\circ) averaged between the four sites jarrah, $y = -0.97x + 21.64$ $r^2 = 0.9615$, $P<0.001$ marri, $y = -1.37x + 22.73$ $r^2 = 0.9575$, $P<0.001$.

Bark thickness averaged 10.52 ± 0.68 mm in jarrah and 12.73 ± 0.84 mm in marri and was significantly ($t_{30}=-1.35$, $P<0.043$) higher (1.2×) in marri compared to jarrah. There was a positive linear relationship between bark thickness and billet diameter $y = 0.0049x + 0.032$ $r^2 = 0.3723$ ($t_{116}=88.29$, $P<0.001$).

3.3.2. *P. semipunctata* population measurements

Across the four sites emergence holes per tree ranged from 0 to 429 with mean values (\pm SE) of 76 ± 13 , and 97 ± 19 for jarrah and marri, respectively. Whilst, clutch points per tree ranged from 0 to 24 with 8 ± 1 and 9 ± 1 for jarrah and marri, respectively. Larval galleries per tree in the sapwood ranged from 0 to 378 with 76 ± 12 and 96 ± 20 for jarrah and marri, respectively and mature larvae per tree in the heartwood ranged from 0 to 128 with 22 ± 5 and 8 ± 3 for jarrah and marri, respectively. There was a significant effect of site on emergence holes (m^{-2}) ($F=4.40$, $P=0.007$), clutch points (m^{-2}) ($F=4.66$, $P=0.005$), larval galleries ($F=4.23$, $P=0.009$) and mature larvae ($F=21.99$, $P=0.001$). There was only a significant effect of tree species across all sites for emergence holes (m^{-2}) ($F=5.47$, $P=0.023$) and larvae ($F=21.99$, $P=0.001$) (Table 3.3).

Table 3.3. Analysis of variance comparing *Phoracantha semipunctata* population characteristics of emergence holes (m⁻²), clutch points (m⁻²), larval galleries (m⁻²) and mature larvae (m⁻²) across sites N2, N3, N7 and N8 and between jarrah and marri. Larval galleries refer to galleries formed by larvae in the sapwood and mature larvae refer to galleries formed in the heartwood by mature larvae.

Source of Variation	d.f.	m.s.	<i>F</i>	<i>P</i>	m.s.	<i>F</i>	<i>P</i>
		<u>Emergence holes (m⁻²)</u>			<u>clutch points (m⁻²)</u>		
Site	3	595.8	4.40	0.007**	3.9387	4.66	0.005**
Tree species	1	740.7	5.47	0.023*	0.3457	0.41	0.525
Site x Species	3	217.1	1.60	0.198	4.1262	4.88	0.004**
		<u>larval galleries (m⁻²)</u>			<u>mature larvae (m⁻²)</u>		
Site	3	535.9	4.23	0.009**	77.31	5.37	0.002**
Tree species	1	385.5	2.69	0.106	316.89	21.99	<.001***
Site x Species	3	340.1	3.05	0.035*	31.89	2.21	0.095

d.f.; degrees of freedom, m.s.; means square, *F*; variance ratio and *P*; significance level of * (*P*<0.05), ** (*P*<0.01) and *** (*P*<0.001).

On an individual site basis *P. semipunctata* population response per m² of tree surface area in jarrah and marri varied with the site. At site N2 there was no significant (*F*=0.05, *P*<0.831) difference in emergence holes (m⁻²), clutch points (m⁻²) (*F*=0.16, *P*<0.695), larval galleries (m⁻²) (*F*=0.05, *P*<0.830) and mature larvae (m⁻²) (*F*=1.83, *P*<0.210) between jarrah and marri (Figure 3.6a-d, Table 3.4 a-d). At site N3, there was a significant (*F*=7.09, *P*<0.026) difference of mature larvae (m⁻²) between jarrah and marri with 3 times as many larvae in jarrah compared to marri (Figure 3.6d, Table 3.4b). At site N7 there was a significantly (*F*=9.60, *P*<0.013) higher (3×) number of emergence holes (m⁻²), clutch points (m⁻²) (*F*=11.70, *P*<0.008) (2.4×) and larval galleries (*F*=43.43, *P*<0.001) (2.8×) in marri compared to jarrah (Figure 3.6a-c, Table 3.4c). Also there was significantly (*F*=16.83, *P*<0.003) more mature larvae (m⁻²) with 5 times as many in jarrah compared to marri (Figure 3.6 d, Table 3.4c) at site N7. At site N8 there were significantly (*F*=8.37, *P*<0.018) more (2×) emergence holes (m⁻²) in marri compared to jarrah (Figure 3.6a, Table 3.4d).

Table 3.4. Analysis of variance comparing *P. semipunctata* population characteristics as determined by emergence holes (m⁻²), clutch points (m⁻²), larval galleries (m⁻²) and mature larvae (m⁻²) for sites (a) N2, (b) N3, (c) N7 and (d) N8 for jarrah and marri. Larval galleries refer to galleries formed by larvae in the sapwood and mature larvae refer to galleries formed in the heartwood by mature larvae.

Source of Variation	d.f.	m.s.	F	P	m.s.	F	P
(a)							
Species	1	<u>emergence holes (m⁻²)</u> 19.2	0.05	0.831	<u>clutch points (m⁻²)</u> 0.16	0.16	0.695
Species	1	<u>larval galleries (m⁻²)</u> 7.6	0.05	0.830	<u>mature larvae (m⁻²)</u> 52.95	1.83	0.210
(b)							
Species	1	<u>emergence holes (m⁻²)</u> 130.89	1.91	0.200	<u>clutch points (m⁻²)</u> 1.05	0.86	0.378
Species	1	<u>larval galleries (m⁻²)</u> 15.50	0.07	0.794	<u>mature larvae (m⁻²)</u> 107.64	7.09	0.026*
(c)							
Species	1	<u>emergence holes (m⁻²)</u> 987.20	9.60	0.013*	<u>clutch points (m⁻²)</u> 11.00	11.70	0.008**
Species	1	<u>larval galleries (m⁻²)</u> 1473.48	43.43	<0.001***	<u>mature larvae (m⁻²)</u> 246.98	16.83	0.003**
(d)							
Species	1	<u>emergence holes (m⁻²)</u> 254.56	8.37	0.018*	<u>clutch points (m⁻²)</u> 0.5195	0.66	0.437
Species	1	<u>larval galleries (m⁻²)</u> 0.10	0.00	0.975	<u>mature larvae (m⁻²)</u> 4.99	1.56	0.244

with d.f.; degrees of freedom, m.s.; means square, F; variance ratio and P; significance level of * ($P < 0.05$), ** ($P < 0.01$) and *** ($P < 0.001$).

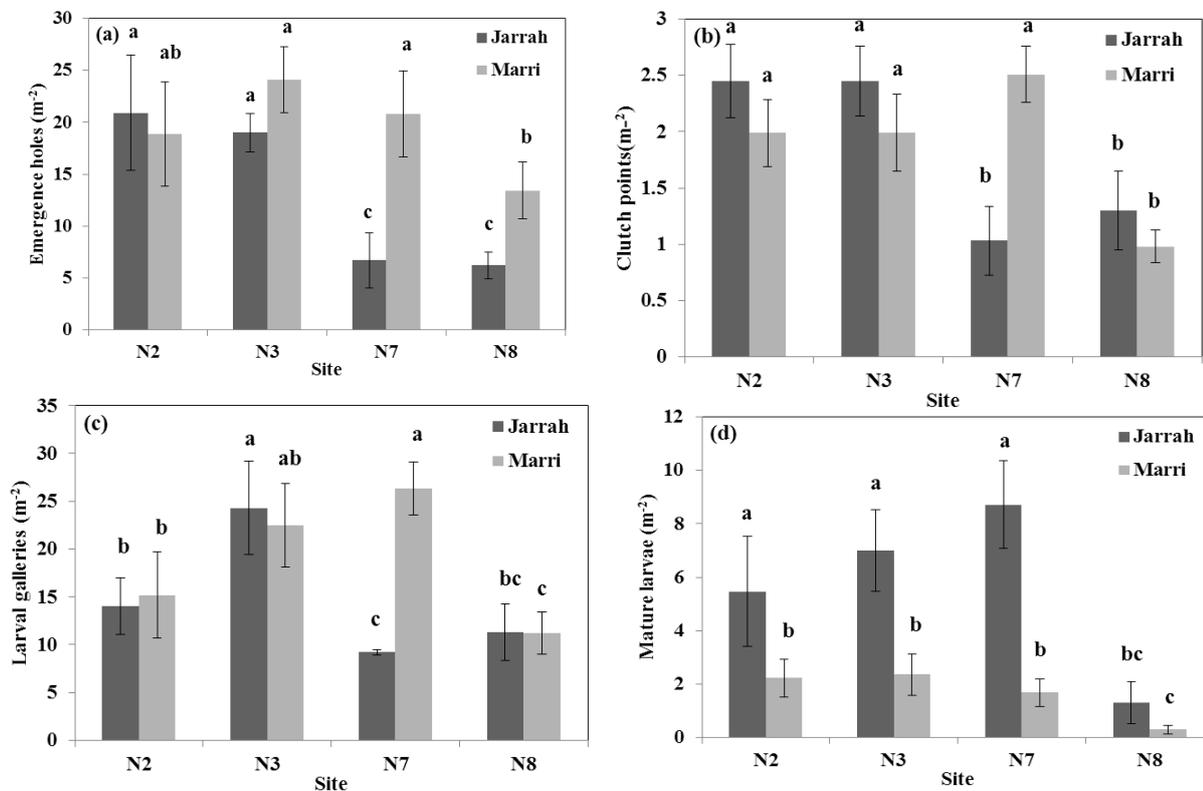


Figure 3.6. The effect of tree species (jarrah and marri) on *P. semipunctata* population characteristics (mean \pm SE) (a) emergence holes (m⁻²), (b) clutch points (m⁻²), (c) larval galleries (m⁻²) and (d) mature larvae (m⁻²) measured per m² at four different sites north (N1, N2) and south (N3, N4). Larval galleries refer to galleries formed by larvae in the sapwood and mature larvae refer to galleries formed in the heartwood by mature larvae. Means marked with different letters are significantly different, means separation test $P < 0.050$.

Emergence holes (m⁻²) in jarrah and marri trees at the four collapsed sites generally decreased from the base to the top of the tree with jarrah at sites N2 and N3 and marri at site N3 the only trees where emergence holes (m⁻²) remained above 5 from 8 to 12 m above ground (Figure 3.7 a-d). These results may have been biased at site N2 by the occurrence of several large trees with large diameters at 8-12 metres with high emergence holes (m⁻²) (Figure 3.7a). Emergence holes (m⁻²) at site N2 was significantly ($F=2.20$, $P < 0.017$) different between jarrah and marri and peaked in jarrah trees near 5 m and again at 10 m height above ground (Figure 3.7a Table 3.5). At site N3 emergence holes (m⁻²) was significantly ($F=2.20$, $P < 0.017$) different between jarrah and marri with a pronounced peak in the number of adult emergence holes at 6 m for jarrah, and was a maximum in marri at 1 m and then decreased by 2.7 fold at 12 m (Figure 3.7b, Table 3.5). Emergence holes (m⁻²) were not significantly

($P > 0.05$) different between jarrah and marri at site N7 ($F = 1.15$, $P < 0.323$) for different heights of trees (Figure 3.7, Table 3.5). However, for site N8 emergence holes (m^{-2}) was significantly ($7.56 < .001$) higher ($3.3 \times$) on average for marri compared to jarrah. A minor peak (increase of 5) emergence holes (m^{-2}) occurred at 3 m above ground in jarrah and marri trees at site N7 and site N8 (Figure 3.7). Emergence holes (m^{-2}) remained constant to 7 m height above ground being on average 15 times higher in marri compared to jarrah trees at collapsed site N8.

Table 3.5. Analysis of variance of adult emergence holes (m^{-2}) for different heights in jarrah and marri trees for sites (a) N2, (b) N3, (c) N7 and (d) N8.

Source of variation	d.f.	m.s.	v.r.	F pr.
(a)				
Tree Species	1	8950.6	20.86	<.001***
Height	11	2116.4	4.93	<.001***
Tree Species x height	11	945.4	2.20	0.017*
(b)				
Tree Species	1	144.5	0.58	0.446
Height	11	646.2	2.60	0.004**
Tree Species x height	11	646.9	2.61	0.004**
(c)				
Tree Species	1	9441.8	58.82	<.001***
Height	11	880.6	5.49	<.001***
Tree Species x height	11	185.1	1.15	0.323
(d)				
Tree Species	1	1865.70	35.14	<.001***
Height	11	59.74	1.13	0.344
Tree Species x height	11	401.55	7.56	<.001***

d.f.; degrees of freedom, m.s.; means square, F; variance ratio and P; significance level of * ($P < 0.05$), ** ($P < 0.01$) and *** ($P < 0.001$).

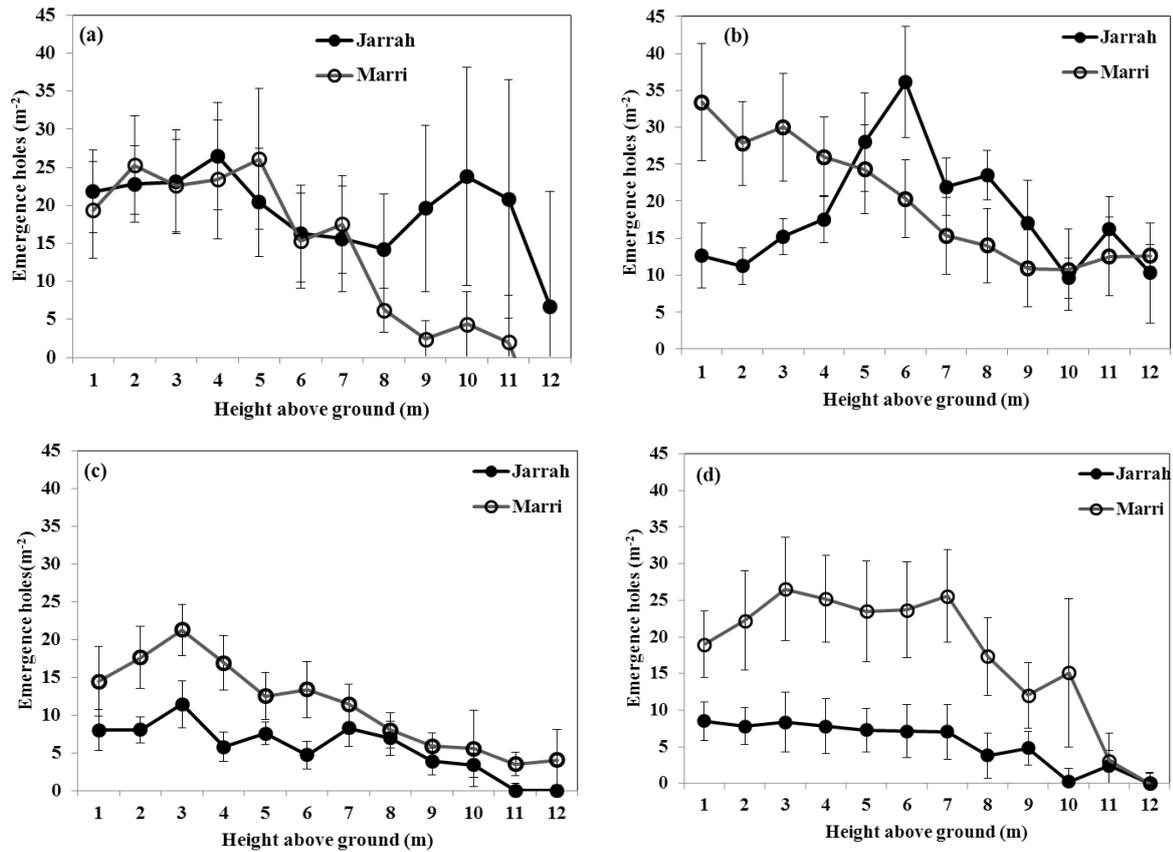


Figure 3.7. Relationship between mean adult *P. semipunctata* emergence holes (m⁻²) for jarrah and marri and height at collapsed sites (a) N2, (b) N3, (c) N7 and (d) N8. LSD for site N2=13.92 ($P<0.05$), site N3=13.92 ($P<0.05$) site N7=13.92 ($P<0.05$) and site N8=13.92 ($P<0.05$).

Emergence holes (m⁻²) of *P. semipunctata* from jarrah and marri was positively correlated with billet diameter reaching a maximum of 14 emergence holes (m⁻²) for a billet diameter of 18 cm (Figure 3.8). Regression analysis showed that the relationship between emergence holes (m⁻²) and billet diameter between jarrah and marri were not significantly ($t_{16}=-1.35$, $P<0.194$) different and was best fitted ($F=37.06$ and $P<0.001$) by a quadratic equation $y = -9.07 \times 10^{-2} x^2 + 3.29x - 15.747$ $r^2 = 0.8598$ (Figure 3.8). For billets between 5-10 cm in diameter 55 % contained emergence holes (m⁻²), between 10-15 cm in diameter 74 % contained emergence holes (m⁻²), between 15-20 cm in diameter 86 % contained emergence holes (m⁻²), billets ranging between 20-25 cm diameter 96 % contained emergence holes (m⁻²) and all billets between 30 and 49 cm in diameter contained emergence holes (m⁻²).

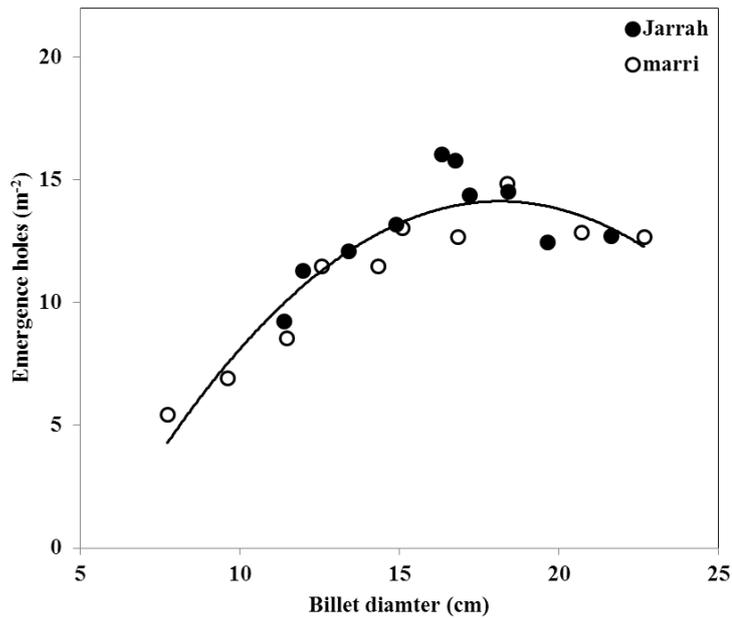


Figure 3.8. Relationship between emergence and billet diameter (DOB) for jarrah (●) and marri (○) trees averaged across all sites. Best fit regression equation: $y = -9.07 \times 10^{-2} x^2 + 3.29x - 15.747$ $r^2 = 0.8598$, $P < 0.001$.

Emergence holes summed for the whole tree, were found to be linearly related to the emergence holes measured at DBHOB (Figure 3.9; $R^2 = 0.7827$, $df = 79$, $P < 0.001$). This relationship was not different for jarrah and marri.

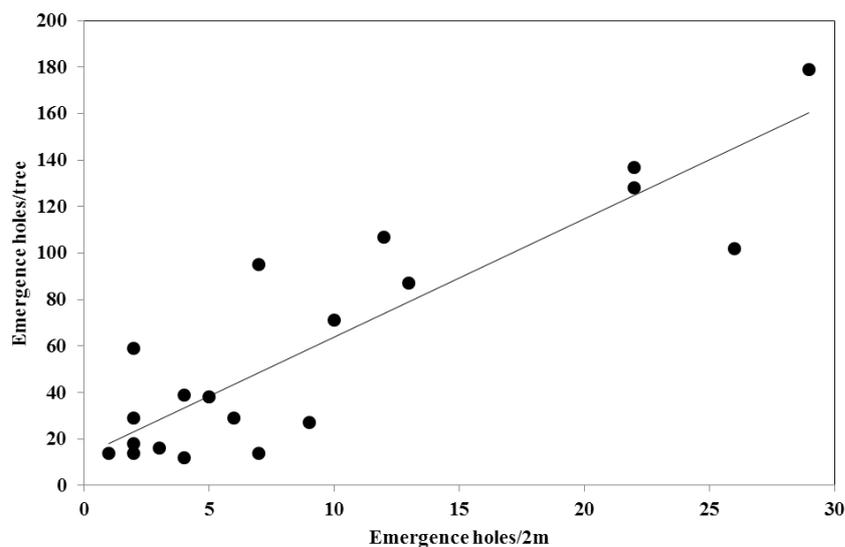


Figure 3.9. Relationship between total emergence holes/tree (measured as the number of exit holes made in the bark by adults of each billet and summed for the tree) and emergence holes made in the first 2 metres for trees at collapsed site N8. Best fit regression equation $Y = 5.0763X + 13.033$ ($R^2 = 0.782$, $P < 0.001$). This regression could be used to provide a quick estimation of total emergence holes of a tree from numbers at DBHOB.

3.3.3. *P. semipunctata* damage of sapwood and heartwood

Across the four sites damage to the sapwood caused by *P. semipunctata* ranged from 0 to 99 % (mean 48.2 % \pm 4.92 SE). For average damage of the trees at site N7 there was significantly ($F=3.21$, $P=0.029$) more (1.5 \times) damage to marri compared to jarrah (Figure 3.10, Table 3.6).

Table 3.6. Analysis of variance comparing average damage to sapwood (%) across sites N2, N3, N7 and N8 and between species of jarrah and marri.

Source of Variation	d.f.	m.s.	<i>F</i>	<i>P</i>
Site	3	1045.6	2.16	0.102
Tree species	1	48.0	0.10	0.754
Site x Species	3	1556.4	3.21	0.029*

d.f.; degrees of freedom, m.s.; means square, *F*; variance ratio and *P*; significance level of *($P<0.05$).

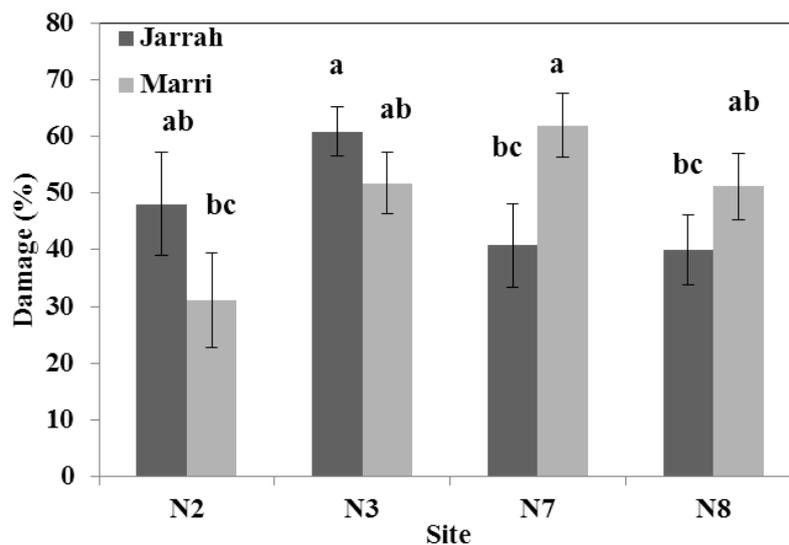


Figure 3.10. The effect of tree species (jarrah and marri) on *P. semipunctata* damage (%) to sapwood (mean \pm SE) at different sites N2, N3, N7 and N8. Means marked with different letters are significantly different, means separation test $P<0.05$.

Damage was observed to extend several feet in a straight line or turn radially (Figure 3.11).

Length of sapwood galleries for marri was 55.3 ± 4.4 cm.



Figure 3.11. Sapwood galleries of *Phoracantha semipunctata* in jarrah.

Damage levels from larval feeding galleries in jarrah and marri sapwood at the four collapsed sites generally decreased between 30 to 50 % from 3 m height to the top of the tree. The highest levels of damage of 100 % occurred in jarrah trees at site N2 at 11 metres height whereas the highest level of damage for marri trees of 76 % occurred at sites N7 and N8 at 3 metres (Figure 3.12). There was a significant difference between species for each of sites N2 ($F=39.97$, $P<0.001$), and N3 ($F=39.97$, $P<0.001$) where there was on average 25 % and 4 % respectively more damage to jarrah compared to marri (Figure 3.12 a-b, Table 3.5a-b). For sites N7 ($F=39.97$, $P<0.001$) and N8 ($F=39.97$, $P<0.001$) there was on average 21 % and 20 % respectively more damage to marri compared to jarrah (Figure 3.12 c-d, Table 3.7c-d).

Table 3.7. Analysis of variance of *Phoracantha semipunctata* sapwood damage (%), comparing species (jarrah and marri) height for sites (a) N2, (b) N3, (c) N7 and (d) N8.

Source of variation	d.f.	m.s.	v.r.	F pr.
(a)				
Species	1	47170	39.97	<0.001***
Height	11	2899	2.46	0.040*
Species x height	11	2873	2.43	0.042*
(b)				
Species	1	4874	5.21	0.025*
Height	11	2830	3.03	0.014*
Species x height	11	978	1.05	0.396
(c)				
Species	1	20005	30.58	<0.001***
Height	11	5040	7.71	<0.001***
Species x height	11	961	1.47	0.208
(d)				
Species	1	13079	16.41	<0.001***
Height	11	698	0.88	0.500
Species x height	11	6517	8.18	<0.001***

d.f.; degrees of freedom, m.s.; means square, F; variance ratio and P; significance level of * ($P < 0.05$), ** ($P < 0.01$) and *** ($P < 0.001$).

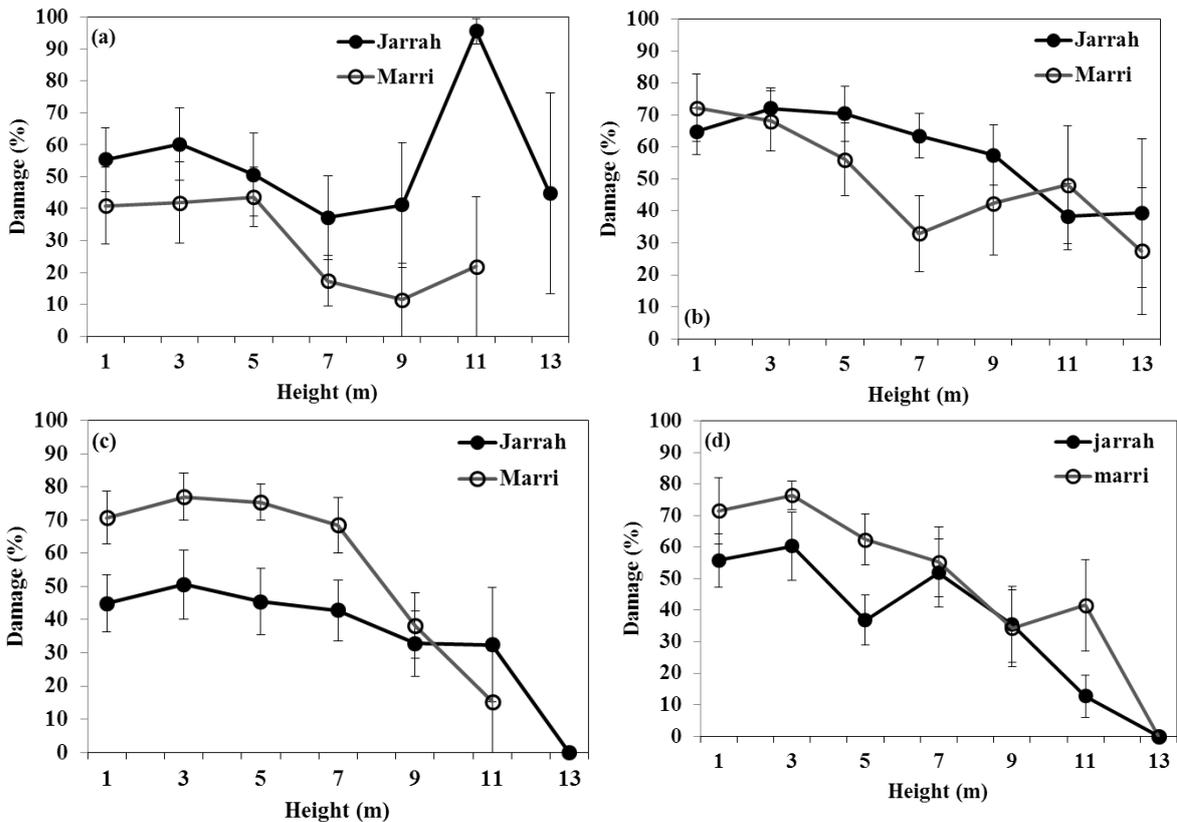


Figure 3.12. Relationship between *Phoracantha semipunctata* sapwood damage (%) for jarrah (●) and marri (○) and height at collapsed sites (a) N2, (b) N3, (c) N7 and (d) N8. LSD for site N2=13.92 ($P < 0.05$), site N3=13.92 ($P < 0.05$) site N7=13.92 ($P < 0.05$) and site N8=13.92 ($P < 0.05$) comparing, species at different heights.

The mean length of individual larvae in the heartwood of jarrah was 30.01 ± 0.54 mm long (n=60) and in marri was 30.01 ± 0.58 mm (n=52) and were not significantly ($t_{54}=5.56$, n=52, $P=0.639$) different, while pronotum width of larvae in marri was 9.29 ± 0.09 mm and was significantly ($t_{54}=1.98$, n=52, $P=0.000$) wider (8 %) than in jarrah with a width of 8.61 ± 0.09 mm. The size of pupal chambers (Figure 3.13) in the heartwood of jarrah was 4.53 ± 0.42 cm and these were not significantly ($t_{90}=5.56$, n=52, $P=0.455$) different from pupal chamber width of 4.92 ± 0.33 cm in marri.



Figure 3.13. Heartwood galleries of *Phoracantha semipunctata* in jarrah. Arrow indicates the position of the pupal chamber.

There was a positive relationship between *P. semipunctata* damage to the sapwood and emergence holes (m^{-2}) reaching a maximum of 75 % for emergence holes reaching $35 m^{-2}$.

There was no significant ($t_{76}=-0.90$, $P<0.372$) difference in sapwood damage between species (Figure 3.14).

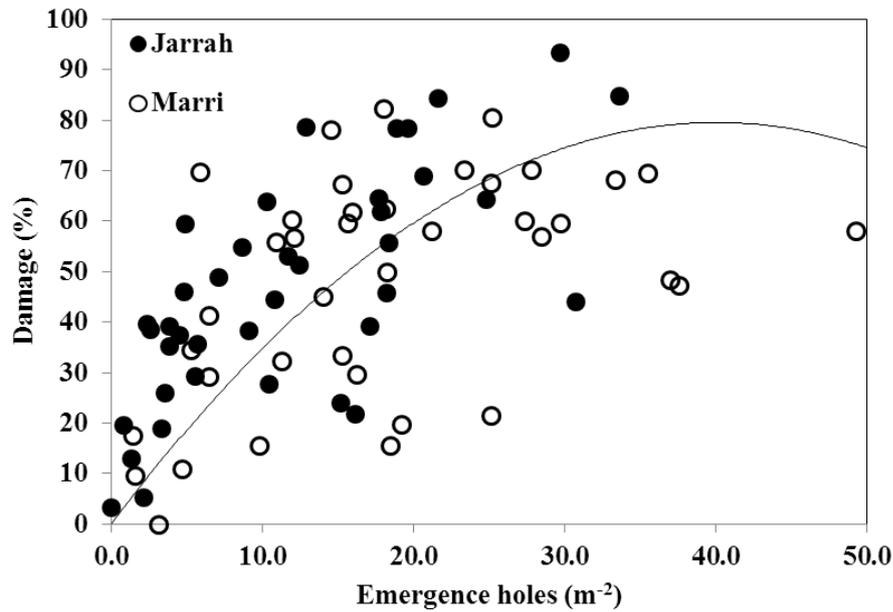


Figure 3.14. Relationship between average *Phoracantha semipunctata* damage (%) and average emergence holes (m²) for 80 trees (jarrah (●) and marri (○)) sampled from sites N2, N3, N7 and N8. Best fit regression equation was $y = -0.0496x^2 + 3.9731x$ ($R^2 = 0.2009$).

In heartwood galleries where some larvae and pupae that had died were associated with fungi (Figure 3.15c) and (with the appearance of *Ophiostoma* yet to be identified) growing in wood tissue surrounding larval chambers. Also dark red staining of dry kino was observed in heartwood galleries and pupal chambers (Figure 3.15a and b) of both jarrah and marri trees from all four collapsed sites. It was also observed only in jarrah that some *P. semipunctata* larvae and pupae had been infected by a parasitoid where small cream coloured larvae had developed within the pupae (Figure 3.15d).



Figure 3.15. Pupal chambers in the heartwood of four different trees (a) filled with kino and a live larvae present, (b) stained and partially filled by kino, (c) containing an adult *Phoracantha semipunctata* which has been consumed by a fungus and (d) with parasitic larvae (arrowed) emerging from a pupae of *P. semipunctata*.

The ratio between emergence holes (m^{-2}) (0.78 ± 0.14) was not significantly ($t_{25}=2.06$, $P=0.524$) different and the number of larval galleries (m^{-2}) 10.5 ± 1.11 was not significantly different ($t_{28}=2.05$, $P=0.544$) between jarrah and marri. On one occasion at site N2 for a sampled jarrah tree there were no emergence holes in the bark and no larvae were found in the heartwood although there were 3 clutch points and 20 larval galleries in the sapwood with 13 % damage.

3.4. Discussion

Destructive sampling of jarrah and marri trees in the NJF have shown that *P. semipunctata* infestations varied depending on a complex interaction of tree height and tree species giving a

range of responses at different sites. With higher levels of infestation (i.e. more clutch points) occurring for marri than jarrah at the southern sites and no difference in infestation levels at the northern sites. This preference of *P. semipunctata* for marri over jarrah was consistent with the higher numbers of clutch points, neonate larvae galleries in sapwood) and a higher number of adults (i.e. emergence holes (m^{-2})). In jarrah the opposite occurred where low infestation levels was associated with less clutch points, less larval galleries and less adults. The presence of more larvae remaining in the heartwood of jarrah compared to marri tends to indicate that larvae in jarrah were slower to develop (i.e. pupate and emerge as adults) and therefore *P. semipunctata*'s life cycle maybe longer in jarrah. The relationship developed between total emergence holes and emergence at DBHOB for jarrah and marri is a quick and non-destructive technique for estimating total exit holes per tree from a single measurement at DBHOB and will save considerable time and effort required in future studies that are monitoring *P. semipunctata* within-tree population densities over time across the NJF.

Tree characteristics of billet size and tree height were strongly associated with the level of infestation by *P. semipunctata* for jarrah and marri. High infestation of *Phoracantha semipunctata* occurred closer to the base of the tree for jarrah and marri where trees had a large diameter (15-22 cm) and thicker bark (10-14 mm). The differences in tree characteristics of diameter decreasing with height between jarrah and marri determined where infestations levels decreased in these species, being at a lower height for marri compared to jarrah. The importance of the billet diameter characteristic supports findings for Cerambycids (Linsley 1959, Hanks et al., 1999; Timms et al., 2006). The thicker bark of marri compared to jarrah may have encouraged more *P. semipunctata* to oviposit in marri trees. Differences in bark thickness have also been recorded for other eucalypts. For example, *E. obliqua* has twice as thick bark compared to *E. cypellocarpa* (Chattaway 1953). *P. semipunctata* development may have been more successful in the larger billets as these provided more protection from

predators (Paine et al., 2009), enabling them to avoid extremes of temperature and provided higher nutrition (Timms et al., 2006). *P. semipunctata* prefers to oviposit in strips of dry bark overlaying green bark (Duffy 1963) and larger billets would have provided more cracks and crevices for females to oviposit her eggs. As bark in jarrah and marri in the present study was less than 1.5 cm in thickness, this would have allowed *P. semipunctata*'s ovipositor, 2 cm in length (Hanks et al., 1993), to be able to penetrate the bark sufficiently to lay its eggs next to the inner bark to ensure that eggs are oviposited in the sapwood.

This large amount of damage to sapwood in both jarrah and marri was similar to findings for *P. semipunctata* in *Eucalyptus* plantations in Tunisia and South Africa where virtually the entire cambium layer was destroyed killing the trees (Chararas 1969; Drinkwater 1975). However, the damage level in jarrah and marri reported in the present study did not completely girdle the trees and may have weakened the trees but was not sufficient to kill them. It is possible given the time lapse of approximately 12 months between when drought symptoms first occurred and when emergence holes were measured in the NJF and given the generation time of *P. semipunctata* of approximately 9 months (Chen et al., 2012) that some of the trees were reinfested. This reinfestation may have been in response to being weakened and partially girdled during the first infestation as proposed by Duffy (1963). Differences in the percentage of sapwood damaged by *P. semipunctata* larval feeding between jarrah and marri varied with location, being higher for marri than jarrah in the southern sites. These differences in the sapwood damage between tree species may be related to the lower durability rating (measured in terms of the time taken for insect and pathogen to destroy the timber) of marri being half that of jarrah (Anon 2012) indicating marri wood is easier to consume than jarrah. Other factors such as carbohydrate levels and cellulose, which are different in other *Eucalyptus* species (Merchant et al., 2006), may have been important but were not measured. Slower decreases in damage for jarrah compared to marri with tree height

appear to be related to the preference of *P. semipunctata* for larger billets. As billet size decreased more slowly for jarrah than marri this appears to be controlling the different way that damage changed with tree height for these tree species.

Apart from billet size and bark thickness the occurrence of high emergence holes (m^{-2}) in stressed jarrah and marri trees in this study may be related to reduced kino production, turgidity of the bark and low bark moisture content causing decreased resistance to *P. semipunctata* attack. In plantation grown *Eucalyptus* high bark moisture and not resin flow in healthy trees prevented them from being attacked by *P. semipunctata* (Hanks et al., 1991b, 1999). However, in jarrah and marri trees in the present study dry kino resin was observed to be present in a number of the split billets and may have reduced infestation. Depending on site conditions, jarrah and marri may have developed different bark moisture levels which may have controlling *P. semipunctata* infestation levels and warrants further study. Visual cues are another factor involved in host location and infestation levels (Barata and Araujo 2001; Timms et al., 2006). Smaller billet size occurring near the top of marri and jarrah trees tree may have presented a smaller target to adult *P. semipunctata* reducing their likelihood to locate this part of the tree. Also as *P. semipunctata* flies in a random fashion (Barata and Araujo 2001) it may have been more likely to land on larger billets when mating and for oviposition.

Infestation of jarrah and marri trees by *P. semipunctata* is a complex interaction between tree characteristics, particularly tree diameter changes with height and host species and explains many of the differences observed in *P. semipunctata* infestation found between jarrah and marri. The high level of infestation and damage by *P. semipunctata* larvae destroying phloem, cambium and sapwood tissues found in the present study may have limited water transport and photosynthates leading to a weakening of the trees and an increase in their

susceptibility to further insect attack by succeeding *P. semipunctata* generations. The variation in *P. semipunctata* infestation levels depending on location of sites could be further investigated in terms of stand density, species mix, tree age, presence of parasitoids. These measurements could provide a better understanding of the behaviour of *P. semipunctata* throughout the NJF. Relationship between infestation levels at DBHOB and total tree infestation could be used to predict the levels of infestation within jarrah and marri trees, without the need to fell trees. This relationship was examined in Chapter 4.

CHAPTER 4

Site and tree characteristics influencing the distribution of *Phoracantha semipunctata* in the northern jarrah (*Eucalyptus marginata*) forest.

4.1. Introduction

Drought is a particular disturbance agent that has been shown to cause an increase in woodborer populations (Allen et al., 2010; Burke et al., 2011) in forests and contribute to forest die-offs (Anderegg et al., 2012). In Europe the jewel beetles (Coleoptera: Buprestidae) including *Agrilus* spp population outbreaks have been associated with trees weakened by drought (Evans et al., 2004). There is also evidence that vulnerability of forests to attack from *Agrilus* spp. and *Phaenops cyanea* Fabricius (Coleoptera: Cerambycidae) will increase from climate change as these beetles are favoured by increased temperatures (Evans et al., 2004). The exotic emerald ash borer *Agrilus planipennis* Fairmaire has been responsible for the decline of millions of ash (*Fraxinus* spp.) trees in North America (Ghandi and Herms 2010) killing their hosts by destroying sap connections between roots and shoots (Timms et al., 2006). Its population outbreaks may be triggered by stress events such as drought (Kamal et al., 2010). Historic drought events in the 1930 and 1950's in USA were associated with increases in *Enaphalodes rufulus* Haldeman (Coleoptera: Cerambycidae) infestations of northern red oak (*Quercus rubra* L.) in North America (Dwyer et al., 1995). More recently a number of droughts between 1990 and 2006 have seen widespread oak mortality and this has been attributed to increased infestations *E. rufulus* populations (Coulson and Stephen 2006; Haavik 2006; Haavik et al., 2012). High infestations of *A. planipennis* destroying the sapwood have

caused widespread death of ash (*Fraxinus* spp.) trees (Ghandi and Herms 2010). The distribution of *E. rufulus* during drought varied depending on the timing of borer life cycles and was influenced by stand maturity and increased in years of low soil moisture availability (Haavik 2006). Also, outbreak numbers of *E. rufulus* were highest in northern red oak *Q. rubra* trees with crown dieback, on ridges and south facing slopes, increased with forest stand density and decreased with species diversity (Fierke et al., 2007).

The northern jarrah forest (NJF) in the southwest of Australia has historically experienced severe drought periods over the last 40 years (Smith et al., 2000; Bates et al., 2008; Yesertener 2010). In particular, more recent droughts in 2007 and 2010 (driest year in 107 years, Bureau of Meteorology 2010) have resulted in extensive canopy mortality in the NJF (Davison 2011, Matusick et al., accepted). Decreases in rainfall have also been implicated in groundwater reductions leading to tree decline east of the NJF in wandoo (*Eucalyptus wandoo* Blakely) woodlands (Smith 2003). This decline of wandoo has been associated with the girdling of branches by the borer *Cisseis fascigera* Obenberger (Coleoptera: Buprestidae) (Hooper et al., 2010).

Little is known of the impact of recent droughts (2007 and 2010) on woodborer population's forestwide in south-western Australia. Increases in the bull's eye borer *Phoracantha acanthocera* Macleay (Coleoptera: Cerambycidae) have been associated with karri (*Eucalyptus diversicolor* F. Muell.) and marri (*Corymbia calophylla*) trees on poor quality drier sites (Farr et al., 2000). In the present study, the *Eucalyptus* longhorned borer *P. semipunctata* Fabricius has been identified taxonomically as occurring in the NJF as an endemic borer (Chapter 1). Studies have shown that *P. semipunctata* favours stressed or dying *Eucalyptus* trees in plantation in Australia (Pook 1980; Lawson 2003) and in California, USA (Hanks et al., 1999). While observational studies in WA have

indicated that *P. semipunctata* infests jarrah and marri trees in the NJF (Curry 1981) no estimates of infestation levels across its' distribution in the NJF have been recorded. The aim of the present study was to determine population levels of *P. semipunctata* at a number of collapsed sites and borer distribution across the NJF following the 2010 drought. The study examines the relationship between, forest health, site factors and stand (tree density and species composition) characteristics associated with *P. semipunctata* populations and tested the hypothesis that the level *P. semipunctata* emergence is equally distributed throughout collapsed sites within the Northern Jarrah Forest.

4.2. Methods

4.2.1. Site selection

Following a recent aerial survey (Matusick et al., accepted) thirty sites were identified and their perimeters defined from ground truthing (explanation see Chapter 2). Out of these 30 sites, eleven sites (Figure 4.1, Table 4.1), were chosen for sampling *P. semipunctata* emergence holes. There were 8 sites (N1-N8) located in the northern half and 3 sites (S1-S3) in the southern half of the NJF. Half of the 8 northern sites are the same sites used in Chapters 2 and 3. The areas of these sites, calculated using ArcGIS v10, ranged between 1 to 14 ha (Table 4.1) and were characterised by an overstorey predominantly composed of jarrah and marri with some sheoak (*Allocasuarina fraseriana* (Miq.) L.A.S.Johnson). In the NJF the understorey in the northern area is composed of *Hakea*, *Leptospermum*, *Hibbertia*, *Xanthorrhoea preissii* and in the southern region composed of *Hakea*, *Hibbertia* and *Hypocalymma* and *Lambertia*.

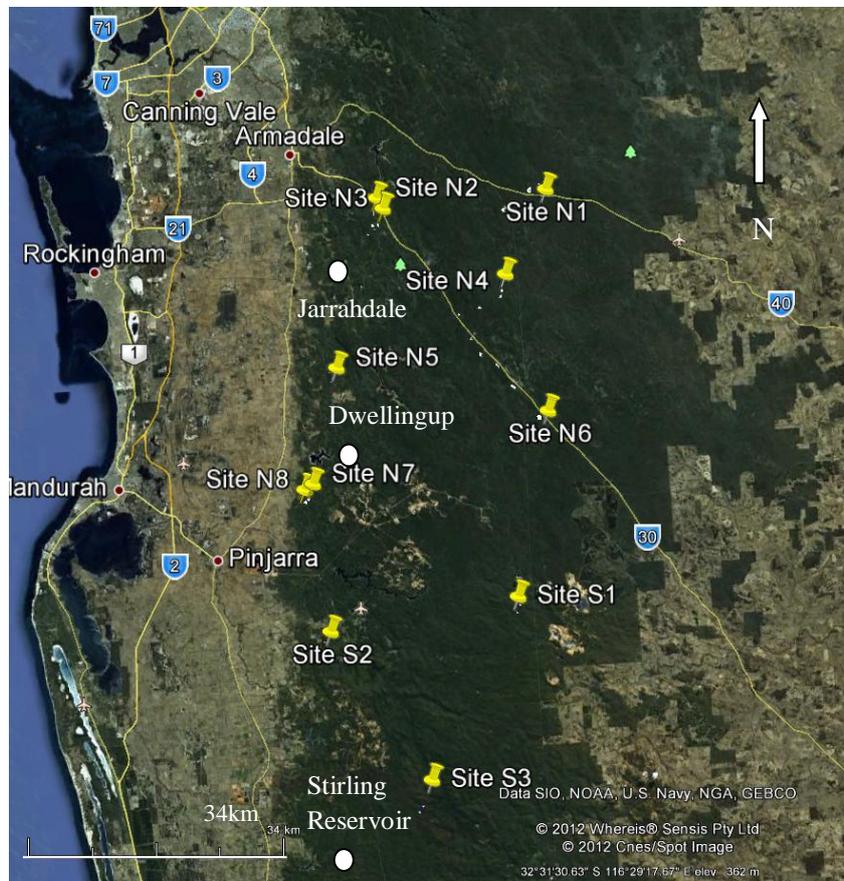


Figure 4.1. The location of the 11 collapsed sites with major jarrah forest townships.

Table 4.1. Coordinates of collapsed sites sampled in the NJF.

Site	Latitude and Longitude coordinates	
N1	32°12'50.71"S	116°20'45.66"E
N2	32°13'36.96"S	116° 8'1.24"E
N3	32°14'32.70"S	116° 7'55.49"E
N4	32°19'54.03"S	116°17'50.46"E
N5	32°25'34.09"S	116° 3'4.78"E
N6	32°29'0.91"S	116°20'20.82"E
N7	32°33'45.76"S	116° 0'32.41"E
N8	32°33'58.41"S	116° 0'17.67"E
S1	32°42'48.87"S	116°17'19.18"E
S2	32°44'3.57"S	116° 1'1.46"E
S3	32°56'36.60"S	116° 8'0.88"E

4.2.2. Site characteristics

Site characteristics were determined from rainfall and evaporation contours (Gentili 1989), soil characteristics were determined from a number of sources including soil maps (McArthur et al., 1977; CSIRO 1980 and ASRIS 2012), elevation and slope from

GoogleEarth and field notes and site area calculated using fGIS (Wisconsin DNR-Division of Forestry).

4.2.3. Forest stand characteristics and canopy health measurements

Within each collapsed site 20 random points were generated using fGIS forest cruise software and of these five points were chosen for sampling as detailed in Chapter 2.

The effect of drought on trees was estimated using a health score, rated from 1 (healthy) -5 (long dead) as detailed in Chapter 2 (Table 2.1). Also additional measurements of the recovery of trees following the drought was estimated from green height percentage (G_H), measured as the height of the tree to which green foliage or resprouts was present as a percentage of the total tree height, the percentage of the total green foliage composed of living resprouts (epicormic shoots), dead sprouts, as the percentage of the total sprouts that had died and remaining crown as a percentage of the original crown present.

4.2.4. Adult *P. semipunctata* measurements

Adult *P. semipunctata* numbers were measured by counting the number of emergence holes in the bark from the base of the tree to a height of 2 m for the north and south aspects. The detailed methods used are described in Chapter 2. Numbers of emergence holes were divided by the surface area of the tree to 2 m to give emergence holes (m^{-2}). The density of *P. semipunctata* per hectare was calculated by multiplying the average number of emergence holes per tree averaged for all sample points at a site by the density of trees per hectare at a collapsed site.

4.2.5. Data analysis

Sites were selected to cover environmental heterogeneity of the NJF from Armadale in the north to Stirling Reservoir in the south and data were analysed using collapsed sites as replicates (n=11). Site, stand and tree characteristics were estimated from five random plots at each of the 11 collapsed sites. The following relationships between adult *P. semipunctata* infestation levels/m² of tree surface and area of collapsed sites, density of trees, percentage of jarrah and marri, health score (1 healthy to 5 long dead, see Table 4.3), diameter over bark at breast height (DBHOB), green proportion (G_H), percentage canopy remaining and percentage green and dead epicormic shoots (resprouts). These were summarised in graphs and compared at $P < 0.05$ using t-test (at $P < 0.050$) with means (\pm SE) are shown as appropriate. Data were blocked using site and analysed using multivariate correlation, stepwise linear and least squares regression at the site level using SPSS[®] 18.0 (Statistical Package for the Social Science, USA, IBM[®] 2011). Other site variables analysed by linear regression were estimates calculated using ArcGis v10. For each variable a mean and standard error was calculated from the five plots at each collapsed site.

4.3. Results

4.3.1. Site and stand characteristics

Soils at the collapsed sites are lateritic podsollic soils predominantly ironstone gravels with sandy matrixes of the Australian Soil classification type Uc 4.1 with underlying country rock (granite) or classification type Uc4.2 with underlying clay loams (coloured B horizon) (McArthur et al., 1977; CSIRO 1980). Several collapsed sites had bare areas with granite outcrops (sites N2, N6, S3) and site N7 with areas of exposed rock present and site N8 with concreted gravel (Table 4.2). Most sites were sloping with site N8 on a

ridge top. Rainfall in the west of the NJF varied from 1200 mm to 1300 mm and in the east ranged from 800-900 mm (Table 4.2) with little or no variation in rainfall from north to south. Evaporation ranged from 575 in the south to 700 in the north (Table 4.2). Site N1 had 22 % higher evaporation of 700 mm/year compared to site S3.

Table 4.2. Site physical characteristics

Site	Area (in hectares).	Rainfall/ Evaporation* (mm)	Elevation (m)	Slope	Soil description
N1	14.21	800/700	320-350	slightly sloping	sandy gravel less than 30 cm over clay.
N2	6.65	1200/680	300-329	mainly flat below ridge	shallow sandy loam over granite with predominant rocky outcrops.
N3	4.19	1200/680	300-329	sloping site	moderately deep sandy to loamy gravel over and cemented gravel with cemented outcrops.
N4	6.60	900/690	310-330	sloping	small cemented outcrops.
N5	0.85	1300/670	elevated >470	sloping site	red shallow loamy duplex.
N6	12.63	900/690	375-385	on a small ridge line	predominant rocky outcrops.
N7	2.90	1200/660	300-310	undulating	red shallow loamy duplex
N8	2.94	1200/660	290-300	ridge top	red shallow loamy duplex with central rocky area of concreted gravel.
S1	5.33	850/675	340-330	slopes to the SE	no rock outcrops gravelly
S2	1.26	1300/650	235-275	on the mid slope	sand over clay.
S3	4.10	1150/575	280-320	mid slope to lower valley	predominant rocky outcrops.

*Rainfall and evaporation at sites was estimated from isohyet and pan evaporation contours presented by (Gentilli 1989). Rainfall has decreased by 30 % at Pinjarra adjacent to the NJF in the last 25 years (Bates et al., 2008) and similar decreases would be expected for rainfall presented in this table.

4.3.2. *P. semipunctata* density and tree health

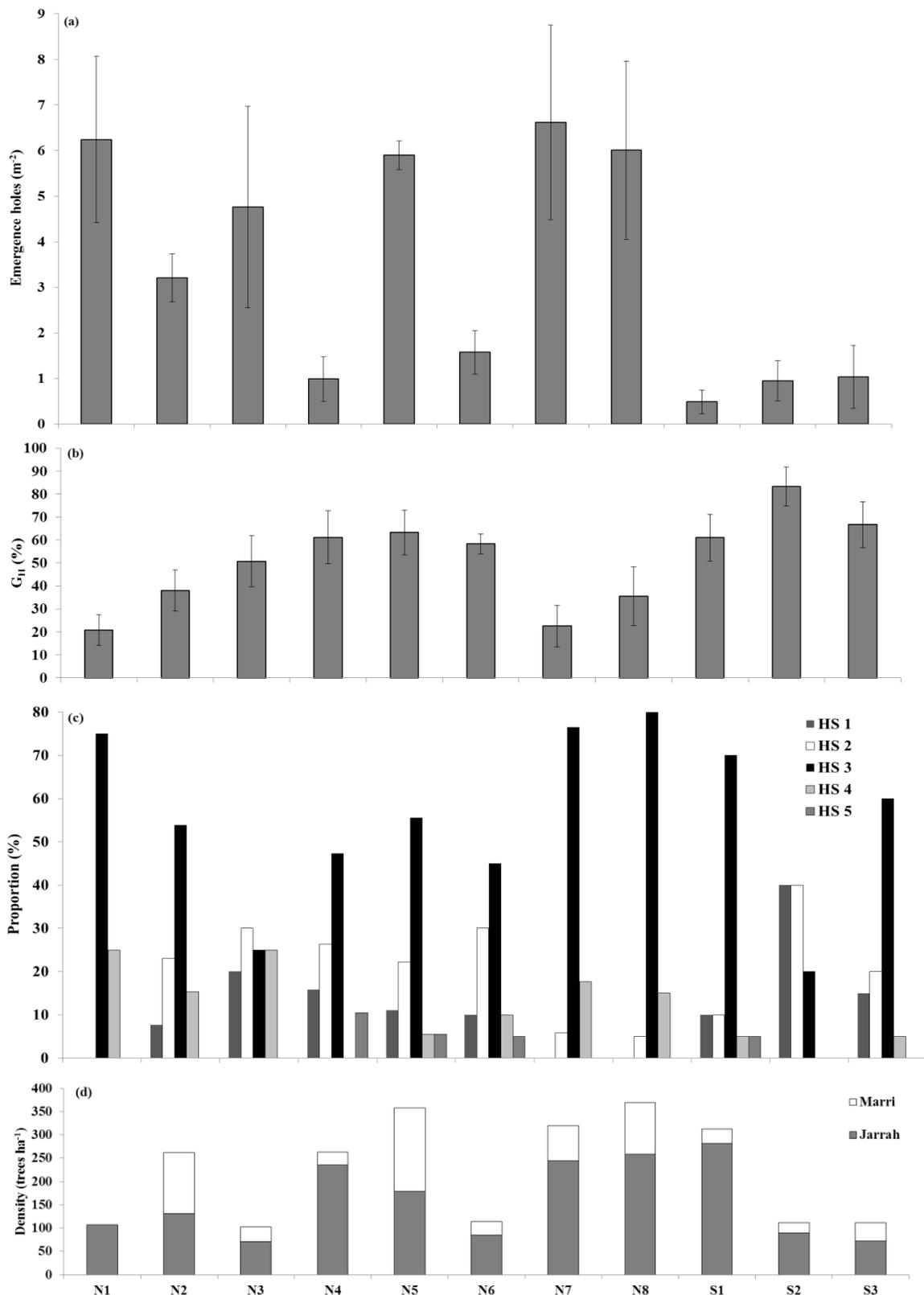


Figure 4.2. The (a) mean \pm SE of emergence holes (m^{-2}) (measured by counting the number of emergence holes made in the bark by adults measured from the first 2 m of tree height), (b), mean \pm SE green height G_H (where increases in percentage G_H indicated green foliage occupied more of the tree's height), (c) proportion (%) of trees in each health class (1 healthy to 5 long dead) (HS 1 to HS 5) as a percentage of the total number of trees and (d) density (trees/ha) of jarrah and marri trees in all collapsed sites (N1-N8, S1-S3).

Total emergence holes (m^{-2}) at the 11 collapsed sites sampled varied and were higher (average $5.40 \pm 0.62 \text{ m}^{-2}$) at sites N1, N2, N3, N5, N7, N8 compared to being lower (average of $1.07 \pm 0.17 \text{ m}^{-2}$) at sites, N4, N6, S1, S2 and S3 (Figure 4.2a). The highest numbers of *P. semipunctata* emergence holes (m^{-2}) occurred at sites in the northern section (N1-N3, N5, N7 and N8) of the sampling area towards the east and south along the scarp to Nanga brook, while the lowest numbers of emergence holes (m^{-2}) occurred south east along the Albany Highway and to the north of Stirling Reservoir (Figure 4.3).

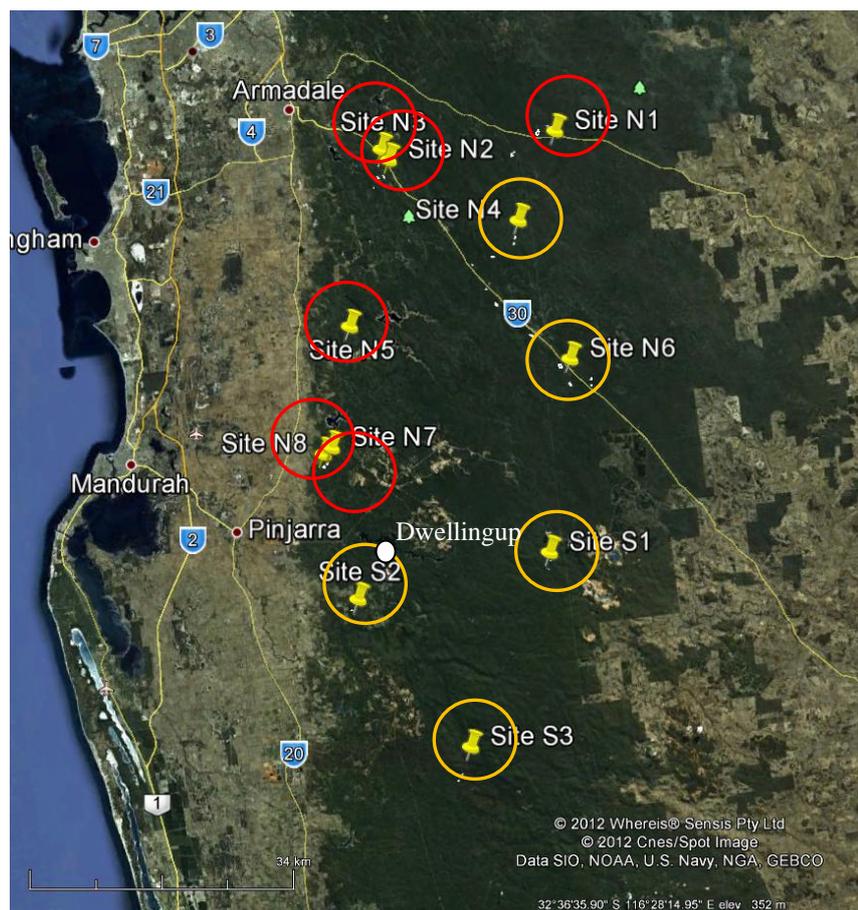


Figure 4.3. Collapsed sites (circled red) are indicated where the highest numbers of *Phoracantha semipunctata* densities/ha occurred and sites (circled orange) with lowest numbers of *P. semipunctata* in the NJF.

Green height (G_H) (proportion of the height of the tree where there was green foliage) reached a maximum of 80 % at only S2, with trees at sites N1, N2, N7 and N8 being

significantly ($F=6.077$, $P<0.001$) shorter with a G_H averaging 38.7 ± 8.16 compared to sites N3, N4, N5, N6, S1, S2 and S3 averaging 65.8 ± 4.50 (Figure 4.2b).

Tree health across the 11 collapsed sites sampled were not consistent with a north-south climatic gradient in the NJF. At each of the 11 collapsed sites few trees (15 %) retained all of their canopy (health score of 1). At most sites trees with a health score of 3 (which had lost all of their canopy) were in the majority. At sites, N1, N7 and N8 70 % to 80 % of trees had lost all of their canopy and had no trees with a health score of 1 (Figure 4.2c). Site N3 had the highest proportion (>20 %) of dead trees and site S2 did not have any dead trees. The location of the most stressed sites were N1 in the north east near the Brookton Highway and N7 and N8 near Nanga Brook to the west of the Darling Scarp and the healthiest sites N4, N6, S2 and S3 which had the highest proportion of healthy trees with few dead trees ranging from 5 % to 10 % occurred along the Albany Highway to the north and south of Dwellingup.

Trees at some sites (N1, N2, N3, N5 and N8) were significantly ($\chi^2=24.52$, $n=10$, $P<0.006$) less healthy (i.e. trees with health score from 2 to 5 compared to trees with a health score of 1) than trees at other sites (N4, N6, S1-S3).

Tree densities varied considerably between sites with sites N1, N3, N6 and S2 and S3 having a lower density averaging 124.5 ± 14.6 trees ha^{-1} than sites N2, N4, to N5, N7, N8, and S1 with an average of 358.3 ± 13.4 trees ha^{-1} (Figure 4.2d). Jarrah was the dominant species at all collapsed sites except sites N2 and N5 where there was an almost equal density of jarrah and marri (Figure 4.2d).

DBHOB varied between the collapsed sites with trees for example, at sites N6 being 37 % larger than trees at site N4. The DBHOB decreased linearly with increased density of trees/ha ($t_9=11.25$, $P<0.030$) (Figure 4.4). Jarrah had a significantly ($t=3.21$, $P<0.001$) larger DBHOB being 31.176 ± 2.109 than marri being 25.080 ± 3.583 . It also appears that sites with high proportion of jarrah had the largest DBHOB. For example, trees at site N1 where only jarrah was present (100 %) had 62 % larger diameter compared to trees at site N8 which had 70 % jarrah. Considerable variation in terms of site characteristics (some with major rock outcrops others with duplex loamy soils), area (1 to 14 hectares) and rainfall (800-1300 mm on average), stand characteristics (103- 383 trees ha⁻¹, proportion of jarrah 45 to 100 %) and tree health (retaining some of their canopy to almost complete loss of canopy).

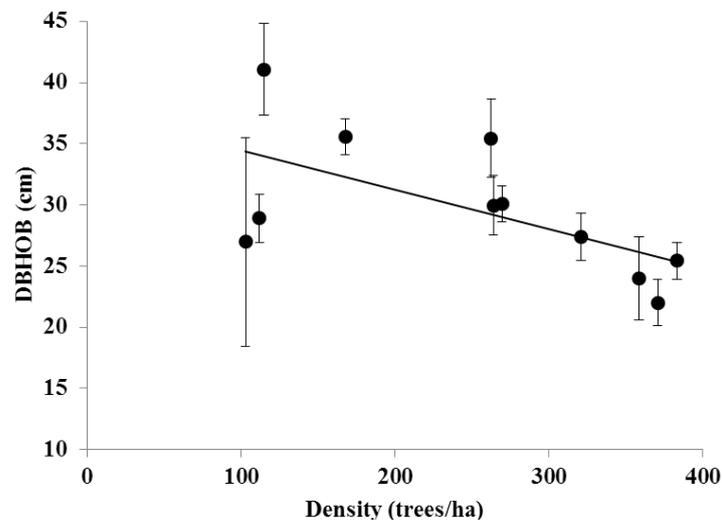


Figure 4.4. The relationship between DBHOB and density for trees at 11 collapsed sites (N1-N8, S1-S3) in the NJF (n=11). Best fit regression equation $Y=-0.0321x + 37.661$ ($R^2 = 0.3712$).

4.3.3. Factors related to *P. semipunctata* emergence hole numbers

G_H (%) (Figure 4.2b) and canopy % remaining were best correlated with health score (R^2 of -0.90), and with canopy % remaining (R^2 of -0.97) (Table 4.3). Health was the most strongly negatively correlated ($P<0.001$) variable with G_H and canopy % remaining (Table

4.3). Epicormic shoots was negatively correlated ($P<0.006$) with G_H (%) (Table 4.3, Figure 4.5). DBHOB was highly negatively correlated ($P<0.007$) with tree density (Table 4.3, Figure 4.4). Canopy % remaining was the most strongly positively correlated variable ($P<0.001$) with G_H . Epicormic shoots was strongly positively correlated ($P<0.002$) with health score (Table 4.3).

Table 4.3. Correlation matrix showing pair-wise comparisons of tree health variables and adult *P. semipunctata* emergence holes for 11 collapsed sites sampled in the NJF.

Variables evaluated	Adult <i>P. semipunctata</i> (m ⁻²)	Health score (1-5)	G_H (%)	Canopy % remaining	Epicormic shoots (%)	Dead epicormic shoots (%)	Density (trees ha ⁻¹)
Adult <i>P. semipunctata</i> (m ⁻²)							
Health score	0.66						
G_H (%)	-0.79***	-0.90***					
Canopy % remaining	-0.59	-0.97***	0.91***				
Epicormic shoots (%)	0.59	0.87**	-0.66	-0.83**			
Dead shoots (%)	0.06	0.24	-0.36	-0.31	-0.13		
Density (trees ha ⁻¹)	0.29	0.14	-0.07	0.00	0.2	-0.55	
DBHOB (cm)	-0.26	-0.08	-0.02	-0.01	-0.36	0.79**	-0.82**

G_H =green height (%). Numbers in bold indicate variables with $R^2 \geq 0.75$, where P; significance level of * ($P<0.05$), ** ($P<0.01$) and *** ($P<0.001$).

Epicormic shoots occupied 100 % of the foliage of trees up to a G_H of 50 % and then occurred in lower proportions down to 45 % as G_H approached 100 % (Figure 4.5) where more of the original crown remained (data not shown).

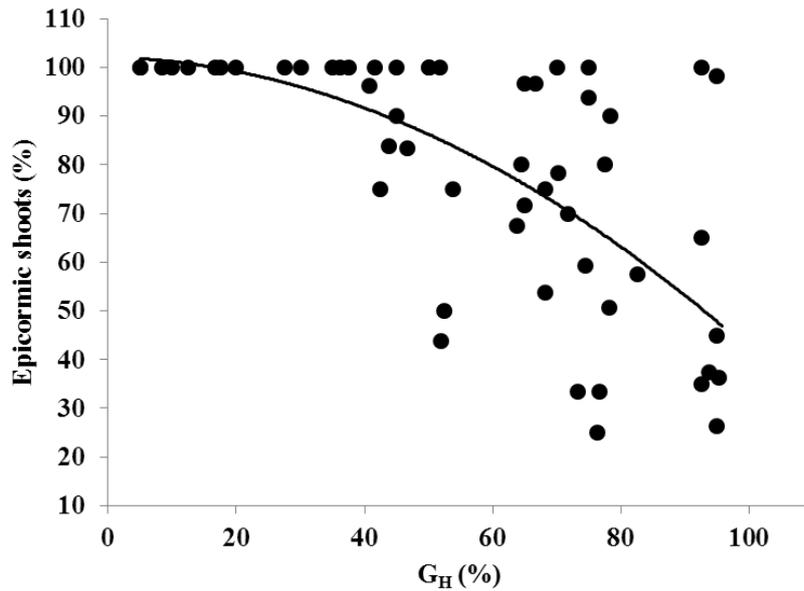


Figure 4.5. The relationship between epicormic shoots (%) and green height (G_H %) (for 11 collapsed sites, (N1-N8, S1-S3) sampled in the NJF (n=55). Best fit regression equation $Y = -0.0092x^2 + 0.2944x + 97.858$ $R^2 = 0.5703$.

4.3.4. Adult *P. semipunctata* emergence holes and tree health

Numbers of emergence holes (m^{-2}) in trees that had lost all or part of their canopy or had died (health score of 2 -5) were significantly ($t_{10}=4.89$, $P<0.001$) higher (24 ×) than in healthy trees (health score 1) (Figure 4.6). A similar analysis comparing jarrah and marri for these two groups of health scores found no significant ($P>0.056$) differences averaged across the whole jarrah forest with 6.2 emergence holes (m^{-2}) in marri and 2.4 emergence holes (m^{-2}) in jarrah.

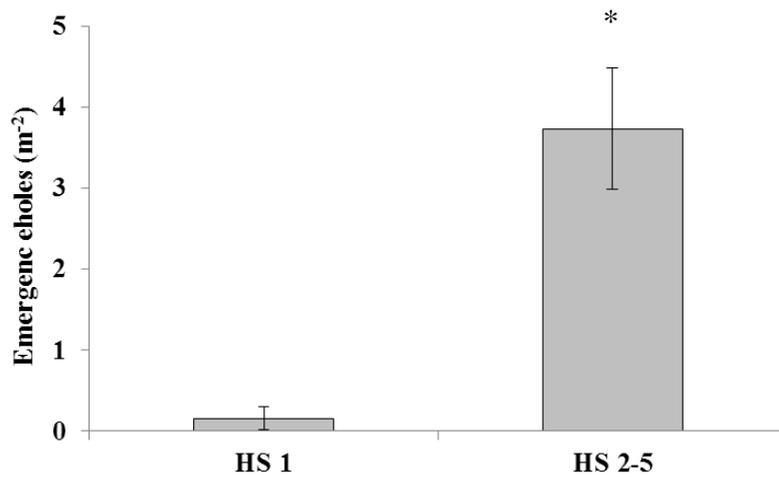


Figure 4.6. Adult *P semipunctata* emergence holes (m⁻²) (mean ± SE) (measured by counting the number of emergence holes made in the bark by adults measured from the first 2 m of tree height) for healthy trees with a health a score of 1 (HS 1) and trees that had lost part or all of their canopy or had died (HS 2 -5) (n=55). Columns with asterisks are different at $P < 0.050$, resulting from t-test.

Emergence holes (m⁻²) was best negatively correlated ($P < 0.001$) with G_H (Table 4.3). The number of emergence holes (m⁻²) decreased logarithmically ($t_9 = -3.85$, $P = 0.004$) with green height (G_H). When G_H was 100 % there were no emergence holes (m⁻²) and when G_H had decreased to approximately 20 % the number of emergence holes (m⁻²) of *P. semipunctata* increased exponentially to a maximum of 15 emergence holes (m⁻²) (Figure 4.7). The relationship between emergence holes (m⁻²) and canopy % remaining ($R^2 = -0.59$) was not as strong as between emergence holes (m⁻²) and G_H ($R^2 = -0.79$). Epicormic shoots was strongly positively correlated with canopy % remaining ($R^2 = 0.83$) (Table 4.3). No correlations were found ($P > 0.05$) between density of emergence holes (m⁻²) and percentage of dead epicormic shoots.

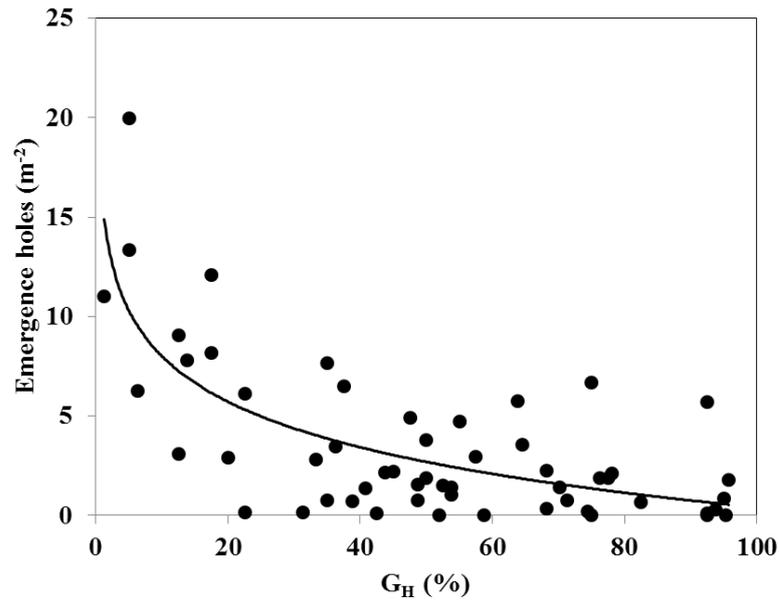


Figure 4.7. Relationship between *Phoracantha semipunctata* emergence holes (m^{-2}) and green height (G_H %), Best fit regression equation $Y = -3.301\ln(x) + 15.606$ ($R^2 = 0.5218$), for the 11 collapsed sites in the NJF ($n=55$). Where percentage G_H is the height of the tree to which foliage was present as a percentage of the total tree height.

4.3.5. Adult *P. semipunctata* emergence holes and stand characteristics

Although DBHOB and tree density were negatively correlated (Figure 4.3) and stand density varied throughout the NJF, no correlations were found ($t_9=P>0.05$) between density of *P. semipunctata* emergence holes (m^{-2}) and tree density or DBHOB at the 11 collapsed sites.

An estimate of the number of adults emerged (ha^{-1}) calculated from the number of emergence holes per 2 m tree height the total number of emergence holes per tree was calculated using the relationship $Y = 5.07X + 13$ (from Chapter 3) where X is the number of emergence holes for first 2 m of tree height. The total number of adult emergence (ha^{-1}) was calculated by multiplying number of adults per tree by the density of trees per hectare for each site. Adults emergence (ha^{-1}) was significantly ($P<0.001$) different between the

collapsed sites (Figure 4.8). There were an average emergence holes of $9434 \pm 1972/\text{ha}$ (or $85.75 \pm 15.18/\text{m}^3$) in the NJF over the study period (Figure 4.8).

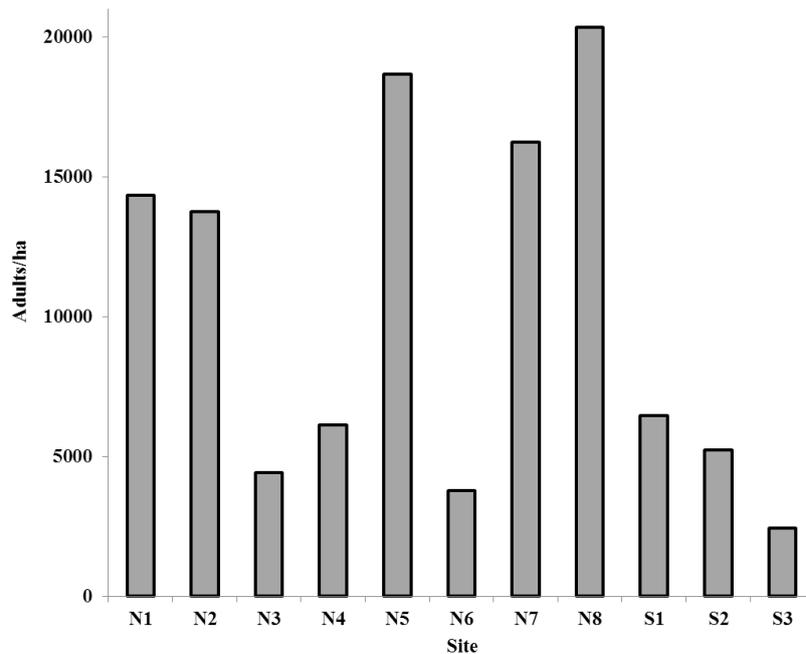


Figure 4.8. Number of adult *P. semipunctata* density/ha (measured by counting the number of emergence holes made in the bark by adults measured from the first 2 m of tree height) (mean \pm SE) at the 11 collapsed sites (N1 to N8 and S1 to S3) sampled in the NJF.

4.3.6. Adult emergence and site characteristics

At the collapsed sites N1, N4, N6 and S1 with 30 % less rainfall and 10 % higher evaporation than the other 7 collapsed sites only N1 had high *P. semipunctata* infestation with trees being less healthy with G_H of 20 % (Table 4.2, Figure 4.2a-b). Trees at this site were only in health classes of 3 and above with no healthy trees and were all jarrah. Soils across collapsed sites varied considerably (Table 4.2) and those with rocky outcrops (sites N2, N6 and S3) had moderately low *P. semipunctata* infestation (Figure 4.2a), those on ridges (sites N7 and N8) or having sandy soils (site N1) had high *P. semipunctata* infestation, while sites N2, N4, S1, S2 and S3 which were sloping sites tended to have low *P. semipunctata* infestation.

4.4. Discussion

The variation in the average number of emergence holes between collapsed sites throughout the NJF was uneven. This did not solely depend on their geographical position (latitude or longitude in the NJF) and was closely related to the health of trees at a site. The strong negative correlation between *P. semipunctata* infestation and G_H (%) and a high proportion of trees with a health score of 3 (having lost all of their canopy) across the 11 sites supports the findings from Chapter 2 that trees that were more drought affected were more susceptible to secondary agents of insects, as they had higher infestations of *P. semipunctata*. This effect of tree health on *P. semipunctata* levels was most evident when comparing site N1 in the north east of the NJF with low rainfall and high evaporation and site S3 with higher rainfall and lower evaporation. These observations agree with those of Haavik (2006) and Haavik et al., (2012) which showed increases in numbers of *E. rufulus* in northern red oak (*Q. rubra*) forests in USA.

The tree health score classes, green height (G_H %), canopy % remaining and percentage epicormic shoots were highly correlated amongst the collapsed sites sampled and appear to be good measures of the effect of the major drought event in 18 months earlier in 2010. These methods of assessing health were preferred to the use of direct techniques for measuring water stress such as pre-dawn leaf water potential or chlorophyll fluorescence parameter (Stone 2001), which only provide data on the water status of the trees at the time of measurement. As most trees suffering from *P. semipunctata* infestation had produced epicormic shoots an indication that these trees were recovering from the drought. Following a drought it takes time for trees to dieback with the gradual death of distal component of the branch system to the trees boles (Pook 1980). There is also a delay in the effect of drought on borers (Hebertson and Jenkins 2008) with the life cycle taking up

to 15 months for *P. semipunctata* (Gonzalez 1992; Paine et al., 2009) to produce emergence holes and live adults. In the present study, the use of G_H or canopy % remaining provided an accurate picture of the effect of the drought on the trees and in turn the resulting effect on *P. semipunctata* infestations. Using this method the study was able to show a clear relationship between the effects of the 2010 drought and *P. semipunctata* infestation 18 months after the drought occurred.

The highest percentage of epicormic shoots (over 70 %) indicate that most trees that had been drought affected had recovered by producing epicormic shoots. Resprouting has been generally associated with trees recovery following a stress event such as fire (Boer et al., 2008) and is also a drought recovery mechanism of jarrah (Abbott et al., 1989). In the present study callusing over of *P. semipunctata* galleries in the sapwood was observed in trees where the bark had fallen off and had been infested by *P. semipunctata*. Callus formation may have been stimulated by wounding of the phloem and the production of allelochemicals as occurs in oak trees (Dunn et al., 1990) and tends to indicate that insect damage may initiate the new shoot growth. This recovery from drought may only be short term, as dead sprouts were also present in trees that were resprouting. This tends to indicate that trees which had recovered following the 2010 drought may have subsequently received insufficient rainfall to maintain their water balance with 2011/ 2012 having lower than average rainfall. Alternatively, the large damage to the sapwood (over 60 %) by *P. semipunctata* (Chapter 3) following the drought collapse could have contributed significantly to the subsequent death of trees. Studies by Chararas (1969) and Drinkwater (1975) on cambium damage caused by *P. semipunctata* on *Eucalyptus* species have caused trees to die. There is usually a delay in the time it takes for trees to die as observed for *E. rufulus* in the northern red oak (Coulson and Stephen 2006). The tendency for older and larger trees to survive *P. semipunctata* attack (Evans et al., 2004) may lead to

a change in composition of the forest towards older trees. Reductions of oak tree densities following *E. rufulus* attack (Fierke et al., 2007) may also apply in the NJF with a thinning of trees. For younger trees the stem is often completely girdled by larvae activity of *P. semipunctata* often leading to their death (Evans et al., 2004). If the trend of increased drought events occurs in the NJF in the next 5 years trees may become severely stressed over a larger area and it is possible that they may become heavily infested by *P. semipunctata* with more intense secondary effects of these borers on tree decline.

High levels of *P. semipunctata* infestation were not generally associated with sites in the drier eastern side of the NJF with low rainfall (less than 900 mm) where trees would be expected to be severely drought affected. However, it is also likely that trees at these sites may have developed better adaptations to drought such as deeper sinker roots, so are less prone to drought stress when conditions are drier. The only exception was a high *P. semipunctata* infestation in the most northern site (N1) which has a sandy soil, receives the least annual rainfall and the trees suffered severe canopy loss. Similar results have been found for *P. acanthocera* where higher populations were attributed to poor quality low rainfall sites (Abbott et al., 1991; Farr et al., 2000). The high rainfall sites on the western side of the NJF were associated in the north with high levels of *P. semipunctata* infestation and in the south with low levels of *P. semipunctata* infestation. This tends to indicate some other site and stand factor other than rainfall was controlling the health of trees and *P. semipunctata* infestation levels at a site. The tendency for trees on the western side of the NJF to be more stressed (poorer health) despite having the highest average rainfall may be that trees are least adapted to drought than on the eastern side due to greater soil depth and increased clay content to store water. In the light of climate change trees in these western areas may become more vulnerable to the effects of drought. Further studies

are needed on the water relations of jarrah and marri in the NJF and localised response to drought.

The higher levels of *P. semipunctata* infestation occurred at sites with sandy soils and on ridges where soils were shallow (<30 cm). These soils would be expected to have low soil water storage and given the drought conditions of 2010, trees on these sites may have run out of water earlier than less drought affected sites encouraging higher levels of *P. semipunctata* infestation. The sites associated with low *P. semipunctata* infestation had granite outcrops, indicating shallow soils (CSIRO 1980) and had larger diameter trees (having a higher DBHOB) and had a greater proportion of healthy trees with some of their canopy % remaining. The healthier trees at these sites may have been due to the granite acting as catchment preventing water from draining through the soil profile, conserving the limited rainfall and providing stored soil water. Also the granite may have also restricted deep root development encouraging more lateral root development allowing the trees to source water from a larger area. These different types of root systems have been reported in jarrah (Dell and Wallace 1981). The presence of concreted gravel at some sites appears to be associated with high *P. semipunctata* infestation and poor tree health. The soils at these sites may have reduced water storage limiting the ability of trees to penetrate this layer to reach the clay subsoil (Bleby et al., 2009), leading to loss of tree health and increased *P. semipunctata* infestation. Variations in levels of *P. semipunctata* infestation were related to different in site characteristics in the NJF. In the southern sites, the deeper more clayey soils on the slopes allowed for accumulation of water from runoff producing healthier trees and lower *P. semipunctata* infestation. For *E. rufulus* infestations in the Ozark National Forest in Arkansas depended on site topographical differences such as ridge and slopes encouraged the predominance of more favoured host oak species (Fierke et al., 2007).

Density of trees at sites was a poor predictor of *P. semipunctata* infestation. Sites varied in their density and may have been due to past logging practices in the NJF over the last 100 years (Stoneman and Schofield 1989) or site conditions. The variation would be expected to alter the water balance at a site with a high density of trees with a high demand for water leading to more tree stress compared to sites with low density of trees (Stoneman and Schofield 1989). No positive relationship was found between *P. semipunctata* infestation and tree density although sites with high stand density tended to have high *P. semipunctata* infestations. Infestations of *P. semipunctata* tended to increase for sites with a high proportion of marri and may lead to a change in the species mix at sites in the NJF as has occurred in oaks infested by *E. rufulus* in Arkansas (Fierke et al., 2007).

This study has shown that the distribution of *P. semipunctata* is complex and does not generally follow a North to South or West to East gradient but depends heavily on the health of the trees at a site. Although further sites may be needed to clarify this result. As soils vary considerably across the NJF (CSIRO 1980) the way these characteristics affect the health of the trees in response to drought may determine *P. semipunctata* infestation levels. In this study, variations in site characteristics were defined by soil depth, slope, presence or absence of sand, granite outcrops and duricrust. While stand variations were determined by tree density, size and species mix. This study has provided a relationship between *P. semipunctata* infestation and tree health using various measures such as health scores, G_H and canopy % remaining which would be useful for predicting areas in the NJF that are likely to have high infestations of *P. semipunctata* following periods of drought. To develop a model of *P. semipunctata* distribution and numbers in collapsed sites in the NJF would involve use of satellite imagery to determine tree health using an NDVI image. Such a model has been developed for *E. rufulus* in red oak forests (Aquino et al., 2008).

To produce such a model will also involve taking soil cores to determine the soil profile, depth and moisture to work out the soils water holding capacity. This information could be combined with the use of long term climate change models to predict future rainfall and evaporation patterns to predict areas where trees will be under the most stress. From the positive relationship found in this study between *P. semipunctata* numbers and health score (tree stress) likely places in the NJF where high infestation of *P. semipunctata* will occur in the future can be determined. This information could be combined into a land change analysis of the NJF using GIS programs.

CHAPTER 5

***Phoracantha semipunctata* (Coleoptera, Cerambycidae) colonisation patterns and larval success in water stressed marri trees induced by ringbarking at two sites impacted by drought in the Northern Jarrah (*Eucalyptus marginata*) Forest.**

5.1. Introduction

Ringbarking (girdling) is the complete removal of a strip of bark including the cambium, phloem and sometimes xylem around the circumference of a tree. This disrupts translocation of carbohydrates from leaves to roots starving them of carbon (Schepper and Steppe 2011). If girdling disrupts the xylem it may limit water supply from roots to leaves increasing plant water stress similar to the effects of drought and in most cases eventually killing the trees. Ringbarking has been used to study the response of woodborers to carbon deficiency and stress and results have been variable. For example, a study in America found 20 or 100 times more two lined chestnut borers (m^{-2}) (*Agrilus bilineatus* Weber) were caught in traps on girdled compared to non-girdled trees (Coate 1976). Also ash trees *Fraxinus* spp. L. with manuka oil lures attached to them attracted higher emerald ash borer *Agrilus planipennis* Fairmaire numbers compared to girdled trees (Marshall et al., 2009). Sections of exposed sapwood created during ringbarking of Scots pine (*Pinus sylvestris* L.) were attacked by woodborers (Liley 2005). Cut log experiments by Hanks et al. (1999) for *P. semipunctata* showed that there was a negative relationship between woodborers survival and bark moisture. Cell lignification and fortification by the production of lignin and the deposition of chemical compounds in xylem vessels at wound

sites has been reported as a critical defence mechanism against Buprestid woodborer attack in oaks (*Quercus* spp.) (Dunn et al., 1990). Also a wound response of formation of a (necrophylactic) periderm at the boundaries of the damaged cells creates an impervious surface barrier region, limiting borer development and rejuvenating damaged cells (Robinson et al., 2004). Ringbarking has been used to study plant response such as enhancing flower development (Schepper and Steppe 2011).

The aim of this experiment was to use ringbarking to impose stress in marri (*Corymbia calophylla* Hill) trees within intact forest to encourage response of *P. semipunctata*, and to determine whether there is a critical bark moisture level controlling infestation to test the hypothesis that *P. semipunctata* equally visit healthy and ringbarked (stressed) trees.

5.2. Methods

5.2.1. Experimental sites, tree selection, health rating and harvest

Sixteen pairs of marri trees were selected in the intact area surrounding two collapsed sites N2 (32°12'50.71"S, 116° 7'55.49"E,) and N3 32°13'36.96"S, 116° 8'1.24"E) which were located in the Wungong catchment of the NJF (Figure 2.1, Chapter 2). Each pair of trees was selected with less than 10 m separating them and a DBHOB between 10 to 25 cm, one tree was ringbarked with the other an untreated control. Trees were ringbarked in May by making two cuts 15-20 cm apart with the first cut at 10 cm above the ground. Cuts were 4-8 cm deep into the bark reaching the heartwood around the entire circumference at the collar of a tree by use of chainsaw. The bark and outer sapwood were then chiselled out to remove the cambium and sapwood tissues (Figure 5.1). At each harvest four pairs of trees were planned to be felled at 6 weekly intervals from May to November. However, at the planned harvest dates of late July, September and October, no borer infestation was

observed, so only two pairs of trees were harvested at each time. The remaining trees will be harvested post-Honours.



Figure 5.1. A marri tree showing the ringbarked section of the collar.

Pairs of trees (ringbarked and control) were harvested at approximately 5 cm from the ground using a chainsaw (Stihl®) and tree height was measured. Trees were then sectioned into 1 m lengths until the diameter over bark (DOB) was less than 5 cm (see Chapter 3). The diameter over bark (DOB) was measured half way along the billet using 50 cm callipers (Haglof, Sweden). Exit holes of *P. semipunctata* were counted by removing the loose outer bark of each billet with pocket knives and a Gerber®. The cut end of each billet was also examined for any heartwood galleries made by *P. semipunctata* larvae.

5.2.2. Tree moisture and *P. semipunctata* sampling

Eight pairs of trees (ringbarked and untreated), were dedicated to tree health and bark moisture measurements. At the time of felling trees bark moisture, photographs were taken to compare colour and condition of crown over time and tree health was rated using health scores described in Chapter 2 (Section 2.2). On each of the eight pairs of trees two sticky traps for monitoring *P. semipunctata* visitation were attached by stapling a section (25 cm long) of fine nylon mesh (Nylex®) around the circumference of the tree trunk at heights of 1 and 3 m, and a layer of Tanglefoot® (Tangletrap paste formula) was applied covering

the mesh. Traps were inspected at each sampling time and Coleopteran insect presence noted. Bark moisture was measured by taking a core approximately 50 cm above the ground (in ringbarked trees this was above the ringbark). Subsequent cores were taken approximately 20 cm apart around the trees circumference. Cores were taken at similar heights on each tree. Before each core was taken the loose bark was removed with a Gerber®. The depth of each core extended to the heartwood. Samples were stored in 80 mL acrylic vials, kept cool and transported back to the laboratory where wet weight was recorded. Samples were then dried at 80°C for 72 hours. Bark moisture was calculated on a fresh weight basis.

5.3. Results

5.3.1. Harvest tree, and P. semipunctata measurements

Over the 5 months post ringbarking the trees tree did not show any borer activity with no emergence holes, clutches, sapwood damage or larval presence of *P. semipunctata* were recorded in the felled trees. During the second visit (July) the leaves of two of the sixteen ringbarked trees had a few leaves that had begun to curl or had turned yellow indicating they were beginning to stress (Figure 5.2). The canopy of the control trees did not show this browning.



Figure 5.2. Canopy of ringbarked marri tree showing some yellow leaves.

After 5 months one ringbarked tree had canopy death (brown leaves). This was felled and on dissection no clutches or sapwood galleries of *P. semipunctata* were found. This tree had small white larvae approximately 2-4 mm long similar to bark beetle larvae (Coleoptera: Scolytidae). A number of the felled trees, which had been split into billets, had evidence of kino present. There was no significant ($P < 0.05$) change in the bark moisture levels between the ringbarked trees at both sites (Figure 5.3) for the duration of the trial.

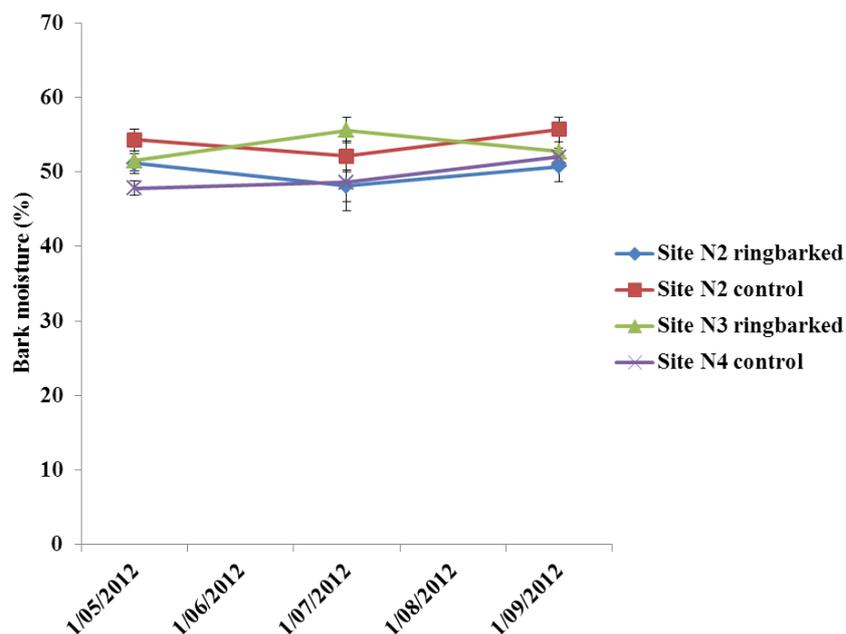


Figure 5.3. Bark moisture (\pm SE) in ringbarked and control marri trees.

5.3.2. Insect visitation

On the third visit (10/09/2012) to site N3, lower and upper pair of traps in trees with intact crowns seven adults of a *Phoracantha* spp. (Cerambycidae) were collected. This was identified as an unknown *Phoracantha* spp. other than *P. semipunctata*. Distinguishing features of the unknown *Phoracantha* spp. were long antennae, brown elytra colour and two yellow discs on the base of their elytra that was different to the elytral pattern of *P. semipunctata* (Chapter 1.5) (Figure 5.4). The *Phoracantha* spp. were shorter being 13.44 ± 1.10 mm long (n=7) approximately half the size of *P. semipunctata* found at sites N2 and N3 in the NJF (Chapter 3).

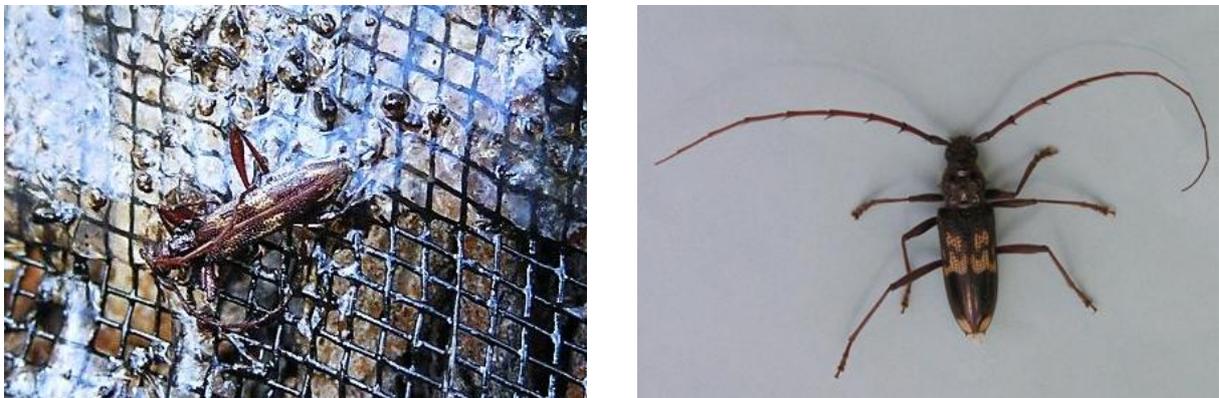


Figure 5.4. *Phoracantha* spp. found on the sticky trap of a ringbarked tree and *P. semipunctata* from split billets (on the right). Not to scale.

5.4. Discussion

The lack of *P. semipunctata* on ringbarked trees appears to be consistent with these trees showing very little signs of drought stress during the 5 months following ringbarking of trees. This response is consistent with trees being able to maintain their water balance. As the entire phloem and secondary xylem was severed during ringbarking preventing uptake of soil water by the tree, trees maintained turgor by other means. Several possible explanations are possible and include; (a) trees shift water across and around the severed xylem vessels of the ringbarked section through primary xylem, (b) as showers were

frequent during the winter months and rainfall was below average, ringbarked trees may have extracted water from the soil that had infiltrated the soil months earlier, (c) wet bark and leaves may have contributed to water absorbed by the tree and (d) trees were simply utilising water stored in the trees tissues. However, these mechanisms of hydration to maintain turgor may have been sufficient if transpiration was low as would be expected in the winter months. Transpiration in jarrah and marri can be as low as 2-2.5 cm per day (Veneklas pers com). At least in the short term it appears that marri were responding very slowly to the effects of ringbarking as only a few trees showed some signs of stress. Other changes during ringbarking such as disrupting translocation of carbohydrates from leaves to roots starving them of carbon (Schepper and Steppe 2011; Johnson et al., 2007) do not appear to have taken effect following ringbarking as the majority of trees appeared to be healthy although in fact they had down regulated of photosynthesis (Flexas et al., 2004) and were drying out sufficiently slowly to remain green.

It was found in this study, that at least in the short term, *P. semipunctata* was not infesting ringbarked trees. Given the strong relationship between *P. semipunctata* infestation and drought stressed trees (Chapter 2 and Chapter 4) (Hanks et al., 1999). it appears that the ringbarked trees were (a) not sufficiently stressed to attract adults, (b) there were insufficient numbers of adult *P. semipunctata* in the area of the ringbarked trees or (c) *P. semipunctata* were less active in the winter months (d) the trees as a result of the ringbarking and possible accumulation of carbohydrates above the ringbark area may have been releasing different semiochemicals to those required to attack *P. semipunctata*. Specific semiochemicals appear to be important in attracting woodborers such as artificially droughted Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst) are known to have high monoterpene and resin acids (Turtola et al., 2003). Also monoterpenes are known to be host finding cues for woodborers (Marshall et al., 2001).

In addition, sesquiterpenes found in stressed ash are volatiles that are attractive to the emerald ash borer *Agrilus planipennis* (Coleoptera: Cerambycidae) (Marshall et al., 2001).

As visual cues are important in attracting *P. semipunctata* (Barata and Araujo 2001) the ringbarked trees may not have been visually attractive to *P. semipunctata*. Also as ringbarked trees were scattered throughout the intact areas surrounding collapsed sites, stressed trees may not have been at threshold numbers (i.e. above 30 % of dead trees (Chapter 2) were sufficient to attract *P. semipunctata* in intact' areas with over 50 % canopy loss needed to induce high infestation (Chapter 4).

CHAPTER 6

General Discussion

This is the first detailed study to illustrate a strong association between the Eucalyptus longhorned borer *Phoracantha semipunctata* infestations and declining health of jarrah (*Eucalyptus marginata* Donn Ex Smith) and marri (*Corymbia calophylla* Hill) trees following a major drought event in the NJF of south-western Australia. It clearly demonstrates that (a) the focus of infestation by *P. semipunctata* is concentrated in patches of forest that were severely drought affected compared to surrounding forest, (b) *P. semipunctata* attacks jarrah and marri trees that have lost part or all of their canopy or had recently died, (c) during *P. semipunctata*'s life cycle, larval stages feed on sapwood and heartwood destroying the cambium layer and vascular tissue, and through this cause a high level of damage to jarrah and marri trees (d) infestation levels of *P. semipunctata* within a drought affected tree were disproportionate being concentrated in the larger, lower sections of the tree with marri being more susceptible than jarrah. Furthermore, this study has provided a detailed survey of the levels of infestation across the NJF and has shown this to be uneven and dependant on the susceptibility of the location to drought. Through these finding this study has contributed to a greater understanding of the ecology of *P. semipunctata* following severe drought in the NJF. It also poses a number of questions that need to be asked including;

- Are *P. semipunctata* passive insects that merely respond to drought without killing trees or do they actively kill trees?
- Do *P. semipunctata* in the NJF behave differently to *P. semipunctata* in plantations? (i.e. endemic compared to exotic).
- Have *P. semipunctata* reached outbreak levels?
- Can *P. semipunctata* behaviour be modelled?

- How *P. semipunctata* distribution changes with increasing drought events? (Do borers disperse from collapsed sites throughout the NJF or do they remain in the collapsed site)?

These questions will be discussed below.

6.1. Response of *P. semipunctata* to drought

Phoracantha semipunctata infestations were clearly associated with severely stressed trees that had major canopy loss or had died following the 2010 drought event (Chapter 4). Given the level of damage to the cambium and phloem tissue from *P. semipunctata* and the drought it would be expected that these trees would die, whereas many resprouted and continued to grow. However, woodborers vary in the way they respond to a disturbance event such as drought. There are those that attack trees irrespective of the health of the host such as defoliators including Christmas beetles *Anoplognathus chloropyrus* Leach (Carne et al., 1974) and repeated defoliation by these insects can kill the tree (Morrison 2007). Most Cerambycids spend their life cycle consuming dead trees (Cocquempot and Lindlelow 2010). There are beetles that attack healthy trees and do not kill them outright but weaken them including the bullseye borer *P. acanthocera* Macleay in karri (*E. diversicolor* F.Muell.) and marri trees (Farr et al., 2000) and the Asian longhorn borer *Anoplothora glabripennis* Motschulsky attacking poplar (*Populus*) (Hue et al., 2009). There are beetles that attack and kill healthy trees including members of the genus *Dendroctonus* (Burke et al., 2011). There are also beetles that attack stressed trees but do not kill them such as *Ips lecontei* Swaine (McMillin and DeGomez 2008), or beetles that attack trees and kill them such as the southern pine beetle *Dendroctonus frontalis* Zimmermann attacking *Pinus taeda* L. (Dodds and Stephen 2002) and finally borers that attack stressed trees and kill them (Hanks et al., 1991; Muzika et al., 2000; Coulson and Stephen 2006). In the present study, *P. semipunctata* was found to only attack trees that had been stressed by drought and had experienced partial (40

%) to a complete loss of canopy. These trees were subsequently severely damaged by *P. semipunctata* with destruction of up to 60 % of phloem, cambium and xylem tissues. Only a small percentage (<20 %) of these trees died with most (74 %) recovering as indicated by the production of epicormic shoots 18 months after the drought (Chapter 4) which may have been stimulated by death of the trees crown during the 2010 drought.

Phoracantha semipunctata may have hindered recovery of the trees from drought by destroying cambium and sapwood tissues that would have otherwise resprouted. By reducing the vigour and growth of trees it would make them more susceptible to future droughts. There was some indication that tree recovery was becoming affected by the damage to sapwood caused by *P. semipunctata*, with the appearance of dead epicormic shoots (Chapter 4). This tends to indicate that the damaged vascular system was insufficient to maintain water balance to the new epicormic shoots. Therefore, recovery may be short lived, particularly if another drought event occurs soon after the initial drought. With trees becoming increasingly stressed they will become more vulnerable to repeated *P. semipunctata* attack causing further damage. This process tends to indicate a Manion decline spiral effect (Manion 1991) where the inciting factors in this case drought, predisposes trees to *P. semipunctata* attack, and in turn makes the trees more vulnerable to future drought. It appears that *P. semipunctata*, endemic to the NJF, is behaving similar to *P. semipunctata* in exotic *Eucalyptus* plantations in Mediterranean regions where it has caused extensive tree mortality (Chararas 1969; Drinkwater 1975) and in *E. globulus* and *E. rudis* plantations in California (Paine et al., 2009).

6.2. Outbreak levels

Levels of infestation of *P. semipunctata* within collapsed sites following the drought may have been unprecedented, with 18 times that in the surrounding intact areas (Chapter 2). At

these levels considerable damage occurred to the sapwood of trees and may have contributed to the death of these trees but was not the sole cause of the collapse. It is possible that in the future more larval feeding will further damage the remaining intact sapwood. As a result populations could increase to outbreak levels. Once populations reach outbreak levels they have the potential to cause widespread damage to forests (Coulson and Stephen 2006). In the case of drought there could be a major shift in populations of *P. semipunctata* and this would have dramatic effects on forest health in the NJF in the years to come. At normal levels *P. semipunctata* do not normally attack healthy trees but this can change under high (>50 larva/metre) populations levels, as shown in controlled experiments by Hanks et al., (1999) on *E. rudis*, leading to *P. semipunctata* attacking healthy trees. For example, in North America following a drought event in ash forests levels of *A. planipennis* dramatically increased causing widespread forest decline (Evans et al., 2004). Also when population levels of the red oak borer *E. rufulus* were low in the past they did not severely damage or kill trees but following recent droughts population levels of this borer have been considerably higher reaching outbreak levels (Riggins et al., 2009) and have caused high oak mortality of drought stressed trees (Coulson and Stephen 2006).

6.3. Modelling tree infestation levels

Poor tree health was shown to be the main factor determining the susceptibility of trees to *P. semipunctata* infestation. However, the intensity of *P. semipunctata* infestation in a tree varied depending on differences in behavioural response of *P. semipunctata* to jarrah and marri. Infestation at a site depended on the level of drought and the tree characteristics of diameter at breast height over bark (DBHOB), height and tree species. A model has been proposed to describe how these factors influence *P. semipunctata* levels (Figure 6.1). The model takes into the account the effect of tree health (canopy remaining or % G_H) on

controlling high and low infestation. For different levels of drought, infestation increases when insects switch from jarrah to marri giving a 20 % higher rate of infestation. A host preference factor has been described in Hanks et al., (1993) with higher larval feeding occurring in more preferred hosts. Also in the present study, infestation increased in larger diameter trees and was dependent on height and tree species (Chapter 3). The study also related level of *P. semipunctata* infestation with the health of the trees which was in turn dependant on site characteristics in the NJF. This information could then be used to predict levels of *P. semipunctata* infestation as it varies depending on site, DBHOB and tree species. Insect risk models have been used to calculate probability of Spruce bark beetle (*Ips typographus* L.) outbreaks on Norway spruce (*Picea abies* Karst) based on basal tree area (Zolubas et al., 2009). Measurements made in the present study of DBHOB for jarrah and marri and the level of infestation could be used to apply a similar model for *P. semipunctata* in the NJF.

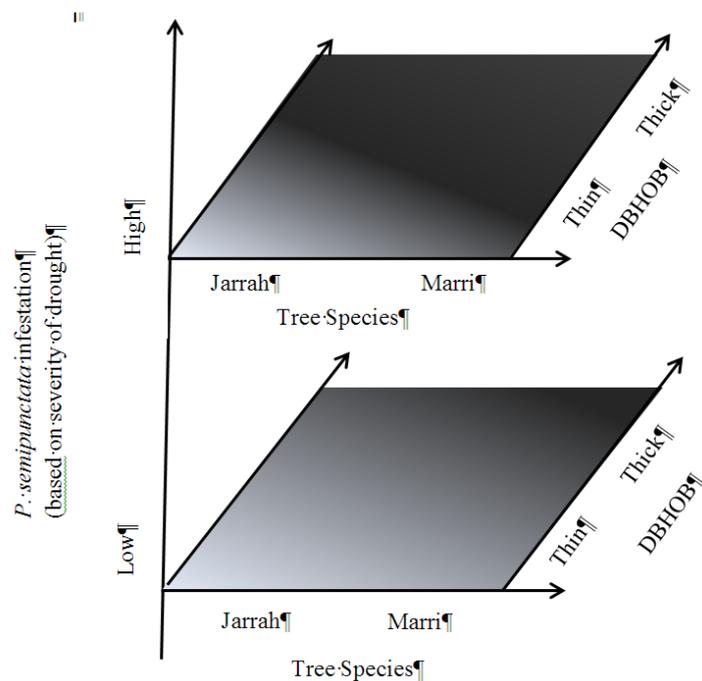


Figure 6.1. Schematic diagram of the way in which drought, stem diameter at breast height (DBHOB) and species type control *P. semipunctata* infestation. The level of infestation is represented by the shaded surface where increasing density of shade indicates higher infestation.

6.4. Dispersal

The present study has demonstrated a confinement of *P. semipunctata* infestation to collapsed sites where a large number of drought affected trees were present with very little infestation in the adjacent surrounding intact area (Chapter 2). It is known that beetles have good dispersal abilities and have effective mechanism for locating hosts (Haack and Stansky 1987). *Phoracantha semipunctata* has good dispersal ability and is able to find stressed and weakened *Eucalyptus* (Hanks et al., 1998) using olfactory and sight recognition strategies (Barata and Araujo 2001). However, in the present study, the intact areas immediately surrounding each collapsed site had very little infestation despite there being over 30 % drought affected trees present. There are two possible reasons for this contrast in infestation levels in the present study (Barata and Araujo; Hanks et al. 1998). One explanation is that before the 2010 drought as *P. semipunctata* was at a low (non-out-break) endemic population levels, as occurs in *Ips typhographus* in Spruce forests (Zolubus et al., 2009), living in the few stressed trees in the intact area. Following the 2010 drought these beetles moved into the collapsed area, and started to infest the large number of stressed trees close together and population levels rapidly increased. This ‘oasis effect’ has been known to occur where outbreaks of insects can be triggered by the appearance of lush growth or stressed hosts (Schowalter 2012). This explanation seems likely given the characteristic of Cerambycids that attack weakened or dying trees is their strong ability to disperse throughout the forest to find suitable larval hosts (Hanks et al., 1995). Alternatively the population levels were already building up in trees in the collapsed area given that the area is more likely to have had previous stress history. For instance, Davison (2011) reported stressed sites in the Jarrahdale area following a mild drought in 2007. The presence of some stressed trees as a result of earlier droughts in collapsed sites may have provided suitable hosts allowing population levels of *P. semipunctata* to increase. Following the 2010 drought the high level of *P.*

semipunctata in the collapsed sites may put pressure on populations to move out of the collapsed sites and into the intact areas beyond that measured in the present study. Further monitoring post drought is needed to answer these questions.

6.5. Distribution

This study has shown that the distribution of *P. semipunctata* emergence holes between collapsed sites across the NJF was uneven, tending to be higher in the north and lower in the south, and was directly related to the health of trees at these locations (Chapter 4). Given that the soils and topography vary considerably throughout the NJF (CSIRO 1980) it is to be expected that site to site variation will be large and this is reflected in the uneven *P. semipunctata* distribution in the NJF. Several stand and site factors seemed to be important in determining whether a site is drought prone as observed by high levels of tree stress (i.e. loss of canopy). These included sites with sandy soils with lateritic cap rock and little slope (Chapter 4). With a predicted increase in the frequency of droughts and drier conditions expected in south-western Australia (IPCC 2007; Bates et al., 2008) there is the possibility that the occurrence of many more of these collapsed sites will occur in drought prone locations in the NJF. It may take several generations for woodborers to build up to epidemic levels in these newly formed collapsed sites.

6.6. Future Research

The methods used in the current study have been useful for providing a basis for understanding *P. semipunctata* population levels in the NJF. Further studies using these techniques to assess *P. semipunctata* activity over several generations would increase our knowledge of this insect's response to drought events and the future population levels to be expected in the NJF. This study provided important information about the location and size

of clutch points, larval feeding intensity in phloem, sapwood and heartwood and adult emergence in the NJF. Although detailed information is available on the timing of these life cycle phases of *P. semipunctata* from overseas studies, environmental conditions and tree hosts are different in south-western Australia. Given the dependence of larval development on ambient air temperatures (Chararas 1969) and species of host (Hanks et al., 1993) the predicted higher temperatures in the future for south-western Australia generation times are likely to decrease and infestation levels rise. Research is urgently needed to be able to predict these changes in life cycle of *P. semipunctata* in jarrah and marri, especially under changing temperature and drought conditions.

This study, was the first quantitative assessment of *P. semipunctata* activity following a major drought event in the NJF, and has shown a strong relationship between tree health and infestation. Further studies are required to examine the interactions between drought stress and host defence to *P. semipunctata*. For example, whether bark moisture or kino production or other defence mechanisms are the critical factors in providing resistance against *P. semipunctata*. The decrease in *P. semipunctata* infestation with tree height measured in the present study was attributed to stem diameter and may have also influenced changes in systemic acquired resistance mechanisms throughout the tree.

The present study showed a concentration of infestation in collapsed areas with very low levels of infestation in the surrounding areas despite drought affected trees being present. Understanding the movement and fate of the high numbers of *P. semipunctata* produced in collapsed sites and whether succeeding generations disperse into the surrounding healthy forest or remain in the collapsed site and eventually die out is important. This information is critical to be able to map the distribution of *P. semipunctata* across the NJF and correlate this distribution with drought affected patches. The use sticky traps or panel traps with and

without pheromones and light traps placed at intervals out from the collapsed sites would be useful techniques that could be employed here.

The ability of jarrah and marri to resprout following heavy infestation and the occurrence major damage to cambium and sapwood indicates these species are able to survive major drought events and insect attack. It would be interesting to determine if there is a critical level of infestation and damage from which trees do not recover. This relationship would provide an understanding of the possible consequences of increased *P. semipunctata* infestation during more frequent drought events.

6.7. Management practices

Given the current climate trajectory and future climate projections of increased frequency of droughts, it may not be possible to affect the outcome in terms of forest decline by controlling insect infestation. However, management of *P. semipunctata* populations will most likely slow down the inevitable effects of drought on the forest. The present study has shown that *P. semipunctata* concentrates in collapsed sites and that population levels varied in these collapsed sites throughout the NJF. Knowing the location of the highest *P. semipunctata* infestation areas this information could be used to ground truth GIS data layers and produce a land change model or similar. From this model other sites of high *P. semipunctata* infestation risk would be identified. Using this information would allow for development of an efficient management program. Further refinements of the land change model could be made from relationships developed observed in this study between *P. semipunctata* infestation and tree characteristics and differences between jarrah and marri. Another relationship developed in this study that would allow a quick assessment of *P. semipunctata* densities per hectare were variations of tree density between sites and a linear regression between numbers of *P.*

semipunctata emergence holes up to 2 m high and total emergence holes per tree (Chapter 3).

Based on the present study a number of management options are proposed:

- Rearing and then releasing native parasitic wasps into the forest as biological control agents of *P. semipunctata* larvae as observed following sectioning of felled jarrah trees (Chapter 3).
- Use of sticky traps containing both a pheromone and an insecticide to attract, trap and kill adult *P. semipunctata*. Construct and place artificial trees in the forest with traps attached or positioned adjacent to attract and kill adult *P. semipunctata*. Spraying with insecticide is known to prevent mortality of Pines from Cerambycid attack (Burke et al., 2011).
- High priority drought affected sites could be thinned to conserve soil moisture to limit the effects of drought on trees. This would reduce susceptibility of the trees to *P. semipunctata* attack as only stressed trees were attacked and this in turn would reduce the population levels in the NJF which may prevent an outbreak occurring following other severe drought events. Site thinning practises can be favourable (Breda et al., 2005) or change the soils to a state that is unfavourable for tree growth (Jurskis 2005).
- Other management practices that could be implemented are the felling and removal of severely stressed and in particular dead trees-which had the highest number of emergence holes (m^{-2}). This would reduce *P. semipunctata* population levels and help to limit future population outbreaks similar to the infestation levels found in the present study following the 2010 drought.

This study has shown that drought induced tree mortality or severe changes in tree health result in high *P. semipunctata* infestation levels especially in stands with a concentration of collapsed trees. Infestations were found to cause a high level of vascular damage that was

most likely contributing to tree decline. These infestations were found to have a preference for marri compared to jarrah and for trees with larger basal diameter.

In terms of the Hypotheses given in Chapter 1:

Hypothesis 1 that *Phoracantha semipunctata* equally infest stressed and healthy trees was shown to be incorrect and that this borer mainly infests stressed and recently dead trees.

Hypothesis 2 that *Phoracantha semipunctata* are distributed evenly within infested trees was shown to be incorrect and that the highest infestations by this borer occur towards the base of jarrah and marri trees and where their diameter ranges from 15 to 22 cm.

Hypothesis 3 that *Phoracantha semipunctata* population levels are equally distributed throughout collapsed sites within the Northern Jarrah Forest was shown to be incorrect and that the highest levels of emergence holes made by this borer tend to occur in the NE and western regions of the NJF.

Hypothesis 4 that *Phoracantha semipunctata* equally visit healthy and ringbarked (stressed) trees was shown to be incorrect and that this borer did not visit healthy and ringbarked (stressed) trees.

REFERENCES

- Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H. (Ted), Gonzalez, P., Fensham, R., Zhangm, Z., Castro, J., Demidova, N., Lim, Jong-Hwanm, Allardm G., Running, S. W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management* 259, 660–684. doi:10.1016/j.foreco.2009.09.001.
- Abbott, I., Dell, B., Loneragan, O., 1989. The Jarrah Plant. Chapter 4. In: Dell, B., Havel, J.J., Malazcuk, N., (Eds.). *The Jarrah Forest a Complex Mediterranean Ecosystem*. pp. 41-51. Kluwer Academic Publishers, Dordrecht.
- Abbott, I., Smith, R., Williams, M., Voutier, R., 1991. Infestation of regenerated stands of karri (*Eucalyptus diversicolor*) by bullseye borer (*Tryphocaria acanthocera* Cerambycidae) in Western Australia. *Australian Forestry* 54, 66-74.
- Amman, G.D., Ryan, K.C., 1991. Insect infestation of fire-injured trees in the greater Yellowstone area. USDA, Forest Service, Intermountain Research Stations, Research Note INT-398.
- Anderegg, W.R.L., Kane, J.M., Anderegg, L.D.L., 2012. Consequences of widespread tree mortality triggered by drought and temperature stress. *Nature Climate Change* 2(9), 1-7. doi: 10.1038/NCLIMATE1635.

Anon., 2012. Timber Advisory Notes. http://www.fpc.wa.gov.au/content_migration/plantations/species/species_notes.aspx#durability.

Anon., 2011. IBM SPSS® 18th edition. <http://www01.ibm.com/software/au/analytics/spss/products/statistics/index.html>.

Anselmi, N., Giorcelli, A., 2007. Factors influencing the incidence of *Rosellinia necatrix* Prill. in poplars. *Forest Pathology* 20(3), 175-183. doi: 10.1111/j.1439-0329.1990.tb01128.x

Asbjornsen, H., Goldsmith, G.R., Alvarado- Barrientos, M.S., Rebel, K., Van Osch, Floortje, P., Rietkerk, M., Chen, J., Gotsch, S., Toboń, C., Geissert, D.R., Gońmez-Tagle, A., Vache, K., Dawson, T.E., 2011. Ecohydrological advances and applications in plant–water relations research: a review. *Journal of Plant Ecology* (4), 3-22 doi: 10.1093/jpe/rtr005.

Austin, A.D., Dangerfield, P.C., 1997. A New Species of *Jarra* Marsh and Austin (Hymenoptera: Braconidae) with Comments on Other Parasitoids Associated with the Eucalypt Longicorn *Phoracantha semipunctata* (F.) (Coleoptera: Cerambycidae). *Australian Journal of Entomology* 36, 327-331.

Barter, G.W., 1957. Studies of the bronze birch borer, *Agrilus anxius* Gory, in New Brunswick. *The Canadian Entomologist* 89, 12- 36.

Barata, E.N., Araújo, J., 2001. Olfactory orientation responses of the eucalyptus woodborer, *Phoracantha semipunctata*, to host plant in a wind tunnel. *Physiological Entomology* 26, 26-37.

- Barata, E.N., Picket, J.A., Wadhams, L.J., Woodcock, C.M., Mustaparta, H., 2000. Identification of host and non host semiochemicals of eucalyptus woodborer *Phoracantha semipunctata* by gas chromatography – electroantennography. *Journal of Chemical Ecology* 26(8), 1877–1895.
- Barrett, R., Tay, E.P., 2005. *Perth Plants: A field guide to bushland and coastal flora of King Park and Bold Park, Perth, Western Australia*. Kings Park and Botanic Gardens Authority (publ.).
- Bates, B.C., Hope, P., Ryan, B., Smith, I. Charles, S., 2008. Key findings from the Indian Ocean Climate Initiative and their impact on policy development in Australia. *Climate Change* 89, 339-354, Springer Science + Business Media B.V.
- Battisti, A., 2006. Insect populations in relation to environmental change in forests of temperate Europe. In *Invasive forest insects, introduced forest trees, and altered ecosystems*, edited by T.D Paine, 127-140. Dordrecht, The Netherlands: Springer.
- Beard, J.S., (1981). *Vegetation survey of Western Australia*. Swan. 1: 1000 000 Vegetation Series.
- Bell, B., Heddle, J., 1989. Floristic, morphologic and vegetational diversity. Pages 53-66 in Dell, B., Havel, J.J., and Malajczuk, N. editors. *The Jarrah Forest. A Complex Mediterranean Ecosystem*. Kluwer Academic Publishers, Dordrecht.
- Blanchard, R.O. Tattar, T.A., 1997. *Field and Laboratory Guide to Tree Pathology*. 2th ed. USA: Academic Press.

- Bleby, T.M., Colquhoun, I.J., Adams, M.A., 2009. Architectural plasticity in young *Eucalyptus marginata* on restored bauxite mines and adjacent natural forest in south-western Australia. *Tree Physiology* 29, 1033–1045. doi: 10.1093/treephys/tpp044.
- Boer, M.M., Macfarlane, C., Norris, J., Sadler, R.J., Wallace, J., Grierson, P.F., 2008. Mapping burned areas and burn severity patterns in SW Australian eucalypt forest using remotely-sensed changes in leaf area index. *Remote Sensing of Environment* 112, 4358–4369. doi: 10.1016/j.rse.2008.08.005.
- Breda, N., Granier A., Aussenaca, G., 1995. Effects of thinning on soil and tree water relations, transpiration and growth in an oak forest (*Quercus petraea* (Matt.) Liebl.). *Tree Physiology* 15, 295-306.
- Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C D., Balice, R.G., Romme, W.H., Jude, H., Kastens, M., Floyd, L., Belnap, J., Anderson, J.J., Myers, O.B., and Meyer, C.W., 2005. Regional vegetation die-off in response to global-change-type drought. *PNAS* 102(42), 15144-15148. doi: 10.1073/pnas.0505734102.
- Brokaw, N.V.L., Scheiner, S.M., 1989. Species Composition in Gaps and Structure of a Tropical Forest. *Ecology* 70(3), pp. 538-541. <http://www.jstor.org/stable/1940196>.
- Bureau of Meteorology., 2010. Perth in 2010: One of the hottest and driest years on record. Australian Government, Bureau of Meteorology. <http://www.bom.gov.au/climate/current/annual/wa/archive/2010.Perth.shtml>.

- Bureau of Meteorology., 2011. Annual Australian Climate Statement 2010. Bureau of Meteorology. Australian Government. (Ed.), January 5, 2010. http://www.bom.gov.au/announcements/media_releases/climate/change/20110105.shtml
- Burke, J.L., Hanula, J.L., Horn, S., Audleya, J.P., and Gandhia, K.J.K., 2011. Efficacy of two insecticides for protecting loblolly pines (*Pinus taeda* L.) from subcortical beetles (Coleoptera: Curculionidae and Cerambycidae). *Pest Management Science*. doi: 10.1002/ps.3266.
- Carne, P.B. (Ed.), Cantrell, B.K., Crawford, L.D., Fletcher, M.J., Galloway, I.D., Richards, K.T., Terauds, A., 1987. *Scientific and Common Names of Insects and Allied Forms Occurring in Australia*. CSIRO Australia.
- Chararas, C., 1969. Biologie et ecologie de *Phoracantha semipunctata* F. (Coléoptère Cerambycidae xylophage) ravageur des eucalyptus en Tunisie, et methodes de protection des peuplements. *Annales Institut. National. Researches. Foresters. Tunis* 2: 1Ð37.
- Charlesworth, P., 2000. *Soil water Monitoring. Irrigation Insights*, no 1. Land and Water Australia. Canberra, ACT.
- Chattaway, M.M., 1953. The anatomy of bark. I The genus *Eucalyptus*. *Australian Journal of Botany* 1, 402-433.
- Chen, Y., Ulyshen, M.D., Poland, T.M., 2012. Differential utilization of ash phloem by emerald ash borer larvae: ash species and larval stage effects. *Agricultural and Forest Entomology* pp. 1-7. doi: 10.1111/j.1461-9563.2012.00572.x.

- Chmura, D.J., Anderson, P.D., Howe, G.T., Harrington, C.A., Halofsky, J.E., Peterson, D.L., Shawe, D.C., St Clair, B., 2011. Forest responses to climate change in the northwestern United States: Ecophysiological foundations for adaptive management. *Forest Ecology and Management* 261, 1121–1142. doi:10.1016/j.foreco.2010.12.040.
- Clark, J., 1925. Forest insects: the marri borer (*Tryphocaria hamata*). *Journal of the Department of Agriculture of Western Australia* 2, 513–517.
- Cleugh, H., Smith, M.S., Battaglia, M., Graham, P., (Eds.), 2011. *Climate change: Science and solutions for Australia* CSIRO Publishing, Collingwood VIC, Australia.
- Cocquemot, C., Lindelöw, A., 2010. Longhorn beetles (Coleoptera, Cerambycidae) Chapter 8.1. *BioRisk* 4(1), 193–218. doi: 10.3897/biorisk.4.56.
- Coder, K.D., 1999. Heat Stroke in Trees 9/99 The University of Georgia School of forest resources extension, pub For99-024.
- Comstock, J.H., Comstock, A.B., 1901. *A manual for the study of insects*. 8th edition. Comstock Publishing Company. Ithaca, N.Y.
- Cornish, P.M., Vertessy, R.A., 2001. Forest age-induced changes in evapotranspiration and water yields in eucalypt forest. *Journal of Hydrology* 242, 43-63.
- Costello, S.L., Negron, J.F., and Jacobi, W.R. 2011. Wood-boring insect abundance in fire-injured ponderosa pine. *Agricultural and Forest Entomology* 13, 373-381. doi: 10.1111/j.1461-9563.2011.00531.x.

- Coulson, R.N., Stephen, F.M., 2006. Impacts of insects in forest landscapes-implications for forest health management. In: Paine, T.D. (Eds.), Invasive forest insects, introduced forest trees, and altered ecosystems, edited by, 101-125. Dordrecht, The Netherlands: Springer.
- Crombie, D.S., Tippett, J.T., Hill, T.C., 1988. Dawn water potentials and root depth of trees and understory species in south-western Australia. *Australian Journal of Botany* 36, 621-631.
- Crowson, R.A., 1967. The Natural classification of families of Coleoptera. Nathaniel Lloyd & Co, Ltd, London.
- CSIRO., 1980. Atlas of Australian Soils, 3rd series volume 1; Soils and Land Use, CSIRO Division of National Mapping, Canberra.
- CSIRO., 1991. The Insects of Australia: A textbook for student and research workers. Volume II. Division of Entomology, CSIRO Melbourne. Melbourne University Press.
- CSIRO., 2004. Australian Insect Collection National (AICN).
http://www.ces.csiro.au/aicn/name_s/b_3253.htm.
- CSIRO, 2012. ASRIS. www.asris.CSIRO.au
- Curry, S.J., 1981. The association of insects with eucalypt dieback in Western Australia. In *Eucalypt Dieback in forests and Woodlands*. Old, K.M., Kile, G.A., Ohmart C.P. (Eds.), pp 130-133. CSIRO: Melbourne.

- Dale, V.H., Joyce, L.A., McNulty, S., Neilson, R.P., Ayres, M.P., Flannigan, M.D., Hanson, P.J., Irland, L.C., Lugo, A.E., Peterson, C.J., Simberloff, D., Swanson, F.J., Stocks, B.J. & Wotton, B.M. 2001. Climate Change and Forest Disturbances 51(9). *BioScience* 723-734.
- Davison, E., 2011. Tree deaths in native forests and rehabilitated minesites in the Wungong Catchment. Wungong Catchment Trial. Northern Jarrah Forest. Water Corporation.
- De Diego, N., Pérez-Alfocea, F., Cantero, E., Lacuesta, M., Moncaleán, P., 2012. Physiological response to drought in radiata pine: phytohormone implication at leaf level *Tree Physiology* 32(4), 435-49.
- Dell, B., Malajczuk, N., 1989. Jarrah Dieback - A disease caused by *Phytophthora cinnamomi*. In: Dell, B., Havel, J.J., Malazcuk, N. (Eds.), *The Jarrah Forest a Complex Mediterranean Ecosystem*. Chapter 6, pp. Kluwer Academic Publishers, Dordrecht. Kluwer Academic publishers, 67 -87.
- Dell, B., and Wallace, I.M., 1981. Recovery of *Phytophthora cinnamomi* from naturally infected jarrah roots. *Australian Journal of Plant Pathology* 10: 1-2.
- Dickens, D.E. and Johnson, J. 2007. *Assessing Storm Damaged Forest Stands Georgia Forestry Commission*.
- Di-Iorio, R.O., 2004. Exotic Species of Cerambycids (Coleoptera) Introduced in Argentina. Part 1. The Genus *Phoracantha* Newman, 1840. *Articuloa en Agrobiencia* 38, 503-515.

- Dodds, K.J., Stephen, F.M., 2002. Arrival and species complex of Cerambycidae on Pines attacked by southern pine beetle. *Journal of Entomological Science* 37(3), 272-274.
- Drinkwater, T.W., 1975. The present pest status of eucalyptus borers, *Phoracantha* spp., in South Africa, pp. 119-129. In: Durr, H.J.R., Giliomee, J. H. Nesor, S. (Eds.), *Proceedings of the first Congress of the Entomological Society*. pp. 119-129.
- Duerr, D.A., Mistretta, Paul.A., 2011. Insect and Disease Pests of Southern Forests, Chapter 16 In Southern Forest Future Project. Unites States Department of Agriculture.
- Duffy, E.A.J., 1963. A monograph of the immature stages of Australasian timber beetles (Cerambycidae). British Museum of Natural History London.
- Dunn, J.P., Potter D.A., Kimmerer, T.W., 1990. Carbohydrate reserves, radial growth, and mechanisms of resistance of oak trees to phloem-boring insects. *Oecologia* 83, 458–468.
- Dunn, D., Crutchfield, J.P., 2009. Insects, trees, and climate: The bioacoustics ecology of deforestation and entomogenic climate change. *Conference Proceedings of MutaMorphis*. <http://mutamorphosis.wordpress.com/2009/02/21/insects-trees-climate/>.
- Dwyer, J.P., Cutter, B.E., Wetteroff, J.J., 1995. A dendrochronological study of black and scarlet oak decline in the Missouri Ozarks. *Forest. Ecological. Management* 75, 69-75.

- Evans, H.F., Moraal, L.G., Pajares, J.A., 2004. Biology, ecology and economic importance of Buprestidae and Cerambycidae. In: Lieutier, F., Day, K.R., Battisti, A., Gregoire, J.C., Evans, H.F., (Eds.), Bark and Wood Boring Insects in Living Trees in Europe- A Synthesis. pp. 447-474.
- Eyles, A., Mohammed, C., 2002. Kino vein formation in *Eucalyptus globulus* and *E. nitens*. Australian Forestry 66(3), 206-212.
- FAO., 2009. Profiles of selected forest pests. Insect Pests, Part II Global Review of forest pests and diseases pp. 110 – 112.
- Farr, J., 2010. Bullseye borer (*Phoracantha acanthocera*) in karri. Information Sheet 37, Department of Environment and Conservation, Perth: DEC Science Division. www.dec.wa.gov.au/index.php?option=com_docman.
- Farr, J.D., Dick, S.G., Williams, M.R., Wheeler, I.B., 2000. Incidence of bullseye borer (*Phoracantha acanthocera*, (Macleay) Cerambycidae) in 20-35 year old regrowth karri in the south west of Western Australia. Australian Forestry 63(2), 107-122.
- Farrington, P., Turner, J.V., Gailitis, V., 1996. Tracing water uptake by jarrah (*Eucalyptus marginata*) trees using natural abundances of deuterium. Trees-Structure and Function 11, 9-15. 10.1007/PL00009654.

- Faucheux, M.J., 2011. Antennal sensilla of the yellow longicorn beetle *Phoracantha recurva* Newman, 1840: distribution and comparison with *Phoracantha semipunctata* (Fabricius, 1775) (Coleoptera: Cerambycidae). Bulletin de l'Institut Scientifique, Rabat, section Sciences de la Vie. 33(1), 19-29.
- Fierke, M.K., Kinney, D.L., Salisbury, V.B., Crook, D.J., Stephen, F.M., 2005. Development and comparison of extensive and intensive sampling of the red oak borer. Environmental Entomology 34(1), 184-192.
- Fierke, M.K., Kelley, M.B., Stephen, F.M. 2007. Site and stand variables influencing red oak borer, *Enaphalodes rufulus* (Coleoptera: Cerambycidae), population densities and tree mortality. Forest Ecology and Management 247, 227–236. doi: 10.1016/j.foreco.2007.04.051.
- Flexas, J., Bota, J., Cifre, J., Escalona, J.M., Galmes, J., Gulias, J., Lefi, E-K., Florinda, S., Canellas, M., Moreno, T., Carbo, M.M., Rier, D., Sampol, B., Medrano, H., 2004. Understanding down-regulation of photosynthesis under water stress: future prospects and searching for physiological tools for irrigation management Annuals Applied Biology 144, 273-283.
- Franceschi, V.R., Krekling, T., Berryman, A.A., Christiansen, E., 1998. Specialized phloem parenchyma cells in Norway spruce (*Pinaceae*) bark are an important site of defence reactions. American Journal of Botany 85, 601–615.
- French, C., 1911. A Handbook of Destructive Insects of Victoria.-with notes on the methods of prevention and examination. PartV. Government Printer Melbourne.

- Gaylord, M.L., Kolb, T.E., McDowell, N.G., Pockman, W.T., 2009. Does drought predispose trees to insect attack. 94th ESA Annual Meeting, PS 55-151. Albuquerque, New Mexico.
- Gentili, J., 1989. Climate of the Jarrah Forest. In: Dell, B., Havel, J.J., Malazcuk, N. (Eds.), The Jarrah Forest a Complex Mediterranean Ecosystem. Chapter 3. Kluwer Academic Publishers, Dordrecht. pp.23-40.
- Gonzalez, T.L., 1992. Estudio sobre intergrales termicas de *phoracantha semipunctata* Fab. (Coleoptera: Cerambycidae), insect perdorador del genero *Eucalyptus*, en Huelva (Espana). Boletin de Sanidad Vegetal, Plagas 18, 529 45.
- Grieve, B.J., 1960. Negative turgor pressure on schlerophyll plants. Australian Journal of Science 23, 375-377.
- Grieve, B.J., Helmuth, E.O., 1968. Eco-physiological studies of Western Australian plants, Proceeding of the Ecological Society of Australia. 3, 46-54.
- Haack, R.A., Slansky, F., 1987. Nutritional Ecology of Wood-Feeding Coleoptera, Lepidoptera and Hymenoptera. Chapter 15 Slansky, F., Rodroquez, J.G., (Eds.) Nutritional Ecology of Insects, Mites, and Spiders. John Wiley and Sons. pp. 449-486.
- Haavik, L. J., 2006. Outbreak and Population History of a Native Woodborer in Ozark and Ouachita National Forests, Arkansas, in Relation to Climatic Factors, Host physical Resistance and Individual Tree and Stand Characteristics. PhD Thesis. University of Kansas.

- Haavik, L.J., Stephen, F.M., 2010. Stand and individual tree characteristics associated with *Enaphalodes rufulus* (Haldeman) (Coleoptera: Cerambycidae) infestations within the Ozark and Ouachita National Forests. *Forest Ecology Management* 259, 1938-1945.
- Haavik, L.J., Frederick, S.M., 2011. Optimal Cross-Sectional Sampling Strategy for Red Oak Borer (Coleoptera: Cerambycidae) Scars with Northern Red Oaks. *Southern Journal of Applied Forestry* 35(1), 44-49
- Haavik, L.J., Jones, J.S., Galligan, L.D., Guldin, J.M., Stephen, F.S., 2012. Oak decline and red oak borer outbreak: impact in upland oak-hickory forests of Arkansas, USA. *Forestry*. doi: 10.1093/forestry/cps032.
- Hangay, G., Zborowski, P., 2010. A guide to the beetles of Australia, CSIRO Publishing. Collingwood, Victoria. pp.191-197.
- Hanks, L.M., Millar, J.G., Paine, T.D., 1991a. Evaluation of cold temperatures and density as mortality factors of the eucalyptus longhorned borer (Coleoptera: Cerambycidae) in California. *Environmental Entomology* 20(6), 1653-1658.
- Hanks, L.M., Paine, T.D., Millar, J.G., 1991b. Mechanisms of resistance in Eucalyptus against larvae of the eucalyptus longhorned borer (Coleoptera: Cerambycidae). *Environmental Entomology* 20, 1583-1588.
- Hanks, L.M., Paine, T.D., Millar, J.G., 1993. Host Species Preference and Larval Performance in the Wood-Boring Beetle *Phoracantha semipunctata* F. *Oecologia* 95(1), 22-29.

- Hanks, L.M., Gould, J., Paine, T.D., Millar, J.G., Wang, Q., 1995. Biology and Host relations of *Avetianella longoi* (Hymenoptera: Encyrtidae), an Egg Parasitoid of the Eucalyptus Longhorned Borer (Coleoptera: Cerambycidae). *Annals of entomological Society of America* 88(5), 666-671.
- Hanks, L.M., Millar, J.G., and Paine, T.D., 1996a. Body Size influences mating success of the Eucalyptus Longhorned Borer (Coleoptera: Cerambycidae). *Journal of Insect Behaviour* 9(3), 369-382.
- Hanks, L.M., Paine, T.D., Millar, J.G., 1996b. Tiny wasp helps protect eucalypts from eucalyptus long horned borer. *California Agriculture* 50(3), 14-16.
- Hanks, L.M., 1999. Influence of the larval host plant on reproductive strategies of Cerambycid beetle. *Annual Review of Entomology* pp 483-505.
- Hanks, L.M., Paine, T.D., Millar, J.G., Campbell, D., Schuch, U.K., 1999. Water relations of host trees and resistance to the phloem-boring beetle *Phoracantha semipunctata* F. (Coleoptera: Cerambycidae). *Oecologia* 1999, 400-407.
- Hanks, L.M., Paine, T.D., Millar, J.G., 2005. Influence of the larval environment on performance and adult body size of the wood-boring beetle *Phoracantha semipunctata*. *Entomologia Experimentalis et Applicata* 114, 25–34.

- Hanks, L.M., 2006. Changing relationships among biodiversity, management, and biosecurity in managed and unmanaged forests. In: Paine, T.D (Ed.), *Invasive forest insects, introduced forest trees, and altered ecosystems* 15-51. Dordrecht, The Netherlands: Springer pp. 153-159.
- Havel, J.J., 1975. Site-Vegetation Mapping in the Northern Jarrah Forest (Darling Range): 1. Definition of site vegetation types. Bulletin 86. CALM, Perth.
- Hebertson, E.G., Jenkins, M.J., 2008. Climate factors associated with historic spruce beetle (Coleoptera: Curculionidae) outbreaks in Utah and Colorado *Environmental Entomology* 37(2), 281-92.
- Hermes, D.A., Stone, A.K., Chatfield, J.A., 2004. Emerald ashborer: the beginning of the end of ash in North America? *Ornamental plants: annual reports and research reviews, 2003* Chatfield, J.A., Draper, E.A., Mathers, H.M., Dyke, D.E., Bennett, P.J., Boggs, J.F., (Eds.), pp. 62–71. OARDC/OSU Extension Special Circular 193.
- Hobbs, R.J., 1999. Restoration of disturbed ecosystems. In *Ecosystems of the world 16: Ecosystems of disturbed ground* Walker, L (Ed.), Elsevier, Amsterdam. pp. 691-705.
- Hooper, R.J., Wills, A., Shearer, B.L., Sivasithamparam, K., 2010. A redescription and notes on biology of *Cisseis fascigera* Obenberger (Coleoptera: Buprestidae) on declining *Eucalyptus wandoo* in south-western Australia. *Australian Journal of Entomology* 49, 234–244. doi:10.1111/j.1440-6055.2010.00755.x.

- Hoskovec., R., 2010. Longhorned Beetles (Cerambycidae) of the West Palaearctic region.
<http://www.cerambyx.uochb.cz/cerambyx.htm>.
- Hu, J., Angeli, S., Schuetz, S., Luo, Y., Hajek, A.E., 2009. Ecology and management of exotic and endemic Asian longhorned beetle *Anoplophora glabripennis*. *Agricultural and Forest Entomology* 11, 359–375. doi: 10.1111/j.1461-9563.2009.00443.x.
- Imms, A.D., 1967. A General Textbook of Entomology- Including the Anatomy, Physiology, Development and Classification of Insects. Butler and Tanner Ltd. pp. 808-809.
- IPCC., 2007. IPCC Fourth Assessment Report Climate Change 2007: Synthesis Report, An Assessment of the Intergovernmental Panel on Climate Change.
http://www.ipcc.ch/publications_and_data/publications_ipcc_fourth_assessment_report_synthesis_report.htm.
- Ivory, M.H., 1977. Preliminary infestations of the pests of exotic forest trees in Zambia, *Commonwealth Forest Review* 56, 47-56.
- Jacobs, K, Seifert, K.A., Harrison, K.J., Smith, G., Kirisits, T., 2002. Ophiostomatoid fungi associated with invasive *Tetropium* spp. (Fabr.) (Coleoptera:Cerambycidae) in Atlantic Canada. U.S. Department of Agriculture Interagency Research Forum.
- Jankowiak, R., Rossa, R., Bilanski, B., 2007. Contribution to pathogenicity by three blue-stain fungi associated with the pine sawyer beetle (*Monochamous galloprovincialis*) (Coleoptera: Cerambycidae) to Scots pine in Poland. *Phytopathology Polish*. 46, 37-46.

- Jankowiak, R., Rossa, R., 2007. Filamentous fungi associated with *Monochamous galloprovincialis* and *Acanthocinus aedilis* (Coleoptera: Cerambycidae) in Scots pine. Polish. Botany Journal 52(2), 140-143.
- Johnson, K., Maier, C., Sanchez, F., Anderson, J., Linder, S., 2007. Physiological girdling of pine trees via phloem chilling: proof of concept Plant, Cell and Environment 30, 128–134. doi: 10.1111/j.1365-3040.2006.01610.x.
- Kallarackal, J., Somen, C.K., 1997. Water use by *Eucalyptus tereticornis* stands of differing density in southern India. Tree Physiology. 17, 195-203. doi: 10.1093/treephys/17.3.195.
- Kamal, J.K., Gandhi, D., Herms, A., 2010. North American arthropods at risk due to widespread *Fraxinus* mortality caused by the Alien Emerald ash borer. Bol Invasions 12:1839–1846. doi: 10.1007/s10530-009-9594-1.
- Kliejunas, J.T., Burdsall, J.R., DeNitto, G.A., Egliti, A., Haugen, D.A., Harverty, M.I., Micales, J.A., Tkacz, B.M., Powell M.R., 2003. Pest risk assessment of the importation into the United States of unprocessed logs and chips of eighteen Eucalypt Species from Australia. Gen. Tech. Rep. FPL-GTR-137. Madison, WI: U.S. Department of Agriculture, Forest Service, Forest Products Laboratory.
- Kramer, P.J., 1969. Plant & Soil Water Relationships: A Modern Synthesis. McGraw-Hill Company, New York.

- Lahbib, M., Jamâa, B., Dhahri, S., Villemant, C., 2009. First Record of *Avetianella longoi*, an Egg Parasitoid of *Phoracantha semipunctata* in Tunisia. *Tunisian Journal of Plant Protection* 4(2), 229-234.
- Långström, B., Solheim, H., Hellqvist, C., Krokene, P., 2001. Host resistance in defoliated pine: effects of single and mass inoculations using bark beetle-associated blue-stain fungi. *Agricultural and Forest Entomology* 3, 211-216.
- Lawson, S.A., 2003. Susceptibility of eucalypt species to attack by longicorn beetles (*Phoracantha spp.*) in Queensland. *Hardwoods Queensland Report no 10*, Queensland: Queensland Government, Department of Primary Industries, 2003.
- Leuzinger, S., Zotz, G., Ashhoff, R., Körner, C., 2005. Responses of deciduous forest trees to severe drought in Central Europe. *Tree Physiology* 25, 641–650. <http://treephys.oxfordjournals.org>.
- Leite, G.L.D., Alves, S.M., Paulo, A.F.N., Lopes, S do N., Ferreira, P.S.F., Zanuncio, C.S., 2011. Identification of the wood-borer and the factors affecting its attack on *Caryocar brasiliense* trees in the Brazilian Savanna. *Maringá* 33(4), 589-596. doi: 10.4025/actasciagron.v33i4.8629.
- Lieutier, F., 2004. Host resistance to bark beetles and its variations. Chapter 9. In: Lieutier, F., Day, K.R., Battisti, A., Grégoire, J-C., Evans, H.F., (Eds.), *Bark and Wood Boring Insects in Living Trees in Europe a Synthesis*. Kluwer Academic Publishers. Dordrecht The Netherlands, pp.135-180.

- Liley, D., 2005. Ring-barking of Scots pine *Pinus sylvestris* trees to create standing deadwood on heathland at Great Ovens, Dorset, England. *Conservation Evidence* 2, 123-124.
- Linsley, E.G., 1959. Ecology of Cerambycidae. *Annual Review of Entomology* 4, 99–138.
- Loewenstein, N.J., Pallardy, S.G., 1998. Drought tolerance, xylem sap, abscisic acid and stomatal conductance during soil drying: a comparison of canopy trees of three temperate deciduous angiosperms. *Tree Physiology* 18, 431-439. <http://treephys.oxfordjournals.org/>.
- Logarzo, G., Gandolfo, D. Cordo, H., 2002. Biology of *Apagomerella versicolor* (Boheman) (Coleoptera: Cerambycidae) in Argentina, a candidate for biological control of cocklebur (*Xanthium* spp.). *Biological Control* 25, 22-29. 1049-9644/02/\$.
- Lundquist, J.E., Beatty, J.S., 2002. A method for characterizing and mimicking forest canopy gaps caused by different disturbances. *Forest Science* 48, 582-594.
- Luzzi, M.A., Wilkinson, R.C., Tarjan, A.C., 1984. Transmission of the pinewood nematode, *Bursaphelenchus xylophilus*, to slash pine trees and log bolts by a cerambycid beetle, *Monochamus titillaor*, in Florida. *Journal of Nematology* 16(1), 37-40.
- MacLeod, A., Evans, H.F., Baker, R.H., 2003. The establishment potential of *Anoplophora glabripennis* in Europe *Nachrichtenbl.Deut, Pflanzenschutzd.* 55,83-84.
- Maher, D., McCaw, L., Yates., 2010. Vulnerability of Forests in South-West Western Australia to Timber Harvesting Under the Influence of Climate Change. SFM Technical Report No 5, Perth: DEC.

- Majer, J.D., Abbott, I., 1989. Invertebrates of the jarrah forest. Chapter 8. In: Dell, B., Havel, J.J., Malazcuk, N., (Eds.). *The Jarrah Forest a Complex Mediterranean Ecosystem*. Chapter 4. Kluwer Academic Publishers, Dordrecht. pp. 111-122.
- Manion, P.D., 1981. *Tree Decline Concepts*. Prentice-Hall, Inc. Englewood Cliffs, N.J.
- Marshall, T.J., 1959. *Relations Between Water and Soil*. Technical Communication No. 50, Commonwealth Bureau of Soils. Harpenden. England.
- Marshall, J.M., Storer, A.J., Fraser, I., Mastro, V.C., 2010. Efficacy of trap and lure types for detection of *Agrilus*. *Journal of Applied Entomology* 134, 296–302. doi: 10.1111/j.1439-0418.2009.01455.x.
- Martin, G.B., Bogdanove, A.J., Sessa, G., 2003. Understanding the function of plant disease resistance proteins. *Annual Review of Plant Biology* 54, 23–61. doi: 10.1146/annurev.arplant.54.031902.135035.
- Martini, A.M.Z., Maës dos Santos, F.A., Prado, P.I., and Jardim, J.G., 2007. Community structure of vascular plants in treefall gaps and fire-disturbed habitats in the Atlantic rainforest, southern Bahia, Brazil. *Revista Brasil Bot* 30(2), 303-313.
- Martínez-Vilalta, J., Piñol, A.J., 2002a. Drought-induced mortality and hydraulic architecture in pine populations of the NE Iberian Peninsula. *Forest Ecology and Management* 161: 247-256.

- Martínez-Vilalta, J., Piñol, A.J., 2002b. The hydraulic architecture of *Pinaceae*—a review *Plant Ecology* 171(1):3-13. doi:10.1023/B:VEGE.0000029378.87169.b1.
- Matthews, E.G. 1997. A guide to the genera of Beetles of South Australia. Part 7 Polyphaga: Chrysomeloidea: Cerambycidae. Special Educational Bulletin Series No 10. South Australian Museum. Adelaide Print Centre Adelaide.
- Matusick, G., Ruthrof, K., Brouwers, N., Dell, B., Hardy, G. accepted. Sudden forest canopy collapse corresponding with extreme drought and heat in a mediterranean-type forest in southwestern Australia. *European Journal of Forest Research*.
- McArthur, W.M., Churchward, H.M., Hick, P.T., 1977. Landform and Soils of the Murray River Catchment Area of Western Australia. Division of Land Resources Management. Land Resources Management Series no. 3; 1-23. CSIRO, Australia
- McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G., Yezzer, E.A., 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist* 178, 719–739.
- McMillin, J.D., DeGomez, T.E., 2008. Arizona Fivespined Ips, *Ips lecontei* Swaine, in the Southwestern United States Forest Insect & Disease Leaflet no 116, U.S. Department of Agriculture Forest Service.

- Merchant, A., Tausz, M., Arndt, S.K., Adams, M.A., 2006. Cyclitols and carbohydrates in leaves and roots of 13 Eucalyptus species suggest contrasting physiological responses to water deficit. *Plant Cell Environ* 29(11), 2017-29.
- Mitchell, K., 2007. Quantitative Analysis by the Point-Centered Quarter Method. arXiv:1010.3303v1 [q-bio.QM] 16 Oct 2010, pp. 1-34.
- Morelli, M.E., Sanchez, A., 2002. The immature stages of *Phoracantha recurva* Newman, 1842 and *Phoracantha semipunctata* Fabricius, 1775 (Coleoptera, Cerambycidae) and a key to larvae of these species. *Brazil Journal Biology* 62(4B), 853-860.
- Mueller, R.C., Scudder, C.M., Porter, M.E., Gehring, C.A.T., Whitham, T.G. 2005. Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts, *Journal of Ecology*. 93(6), 1085-1093. doi: 10.1111/j.1365-2745.2005.01042.x.
- Muilenburg, V.L., Goggin, F.L., Hebert, S.L., Jia L., Stephen F.M., 2008. Ant predation on red oak borer confirmed by field observation and molecular gut-content analysis. *Agricultural and Forest Entomology*. 10, 1-9. www.uark.edu/~fstephen/new/ROB/Muilenburg.et.al.2008-proof.pdf.
- Muzika, R.M., Liebhold, A.M., and Twery, M.J., 2000. Dynamics of two lined chesnut borer. *Agricultural and forest entomology* 2, 283-289.
- Paine, T.D., Millar, J.G., 2002. Insect pests of eucalypts in California-implications of managing invasive species. *Bulletin of Entomological Research*. 92, 147-151. doi: 10.1079/BER2002151.

- Paine T. D., 2006. Rules regulating herbivore populations. In: Paine, T.D, (Ed.). Invasive forest insects, introduced forest trees, and altered ecosystems 15-51. Dordrecht, The Netherlands: Springer.
- Paine, T.D., Dreistadt, S.H., Davis, A., Millar, J.G. 2009. Pest Notes Publication 7425 University of California State wide Integrated Pest Management Program Agriculture and Natural Resources September.
- Pekin, B.K., Boer, M.M., Macfarlane, C., Grierson, P.F., 2009. Impacts of increased fire frequency and aridity on eucalypt forest structure, biomass and composition in southwest Australia Forest Ecology and Management. 258, 2136–2142. doi: 10.1016/j.foreco.2009.08.013.
- Pittock, A.B., (2009). Climate Change: The science Impacts and Solutions. 2nd ed. Collingwood VIC: CSIRO Publishing Pook, E.W., 1980. Drought and dieback of eucalyptus in dry sclerohyll forest and woodlands of the southern tablelands, New South Wales. In: Old, K.M., Kile, G.A, Ohmart, C.P. (Eds.), Eucalyptus Dieback in Forests and Woodlands. CSIRO Australia.
- Podger, F.D., 1972. *Phytophthora cinnamomi*, a cause of lethal disease in indigenous plant communities in Western Australia. Phytopathology 62, 972-981.
- Poot, P., Veneklaas, E.J., 2012. Species distribution and crown decline are associated with contrasting water relations in four common sympatric eucalypt species in southwestern Australia. Plant Soil. doi: 10.1007/s11104-012-1452-8.

- Powell, R., 1991. Leaf and Branch-trees and tall shrubs of Perth. Department of Conservation and Land Management.
- Powell, H., 2000. The influence of prey density on post-fire habitat use of the Black-backed Woodpecker. MSc. Thesis. The University of Montana.
- Ridge, R.W., Bell, D.T., Colquhoun, I.J., Kuo, J., Loneragen, W.A., 1984. Comparative studies in selected species of *Eucalyptus* used in rehabilitation of the Northern Jarrah Forest, Western Australia. II Wood and Leaf Anatomy. *Australian Journal of Botany* 375-386.
- Riggins, J.J., Galligan, L.D., Stephen, F.M., 2009. Rise and fall of the red oak borer (Coleoptera: Cerambycidae) in the Ozark Mountains of Arkansas, USA. *Florida Entomologist* 92(3), 426-33.
- Robinson, R.M, Jensen, G.D, Morrison D.J. 2004. Necrophylactic periderm formation in the roots of western larch and Douglas fir trees infected with *Armillaria ostoyae*. I. The response to abiotic wounding in noninfected roots. *Forest Pathology* 34, 105–118.
- Rouault, G., Candau, J.N, Lieutier, F., Nageleisen, LM., Martin JC., Warzee. N., 2006. Effects of drought and heat on forest insect populations in relation to the 2003 drought in Western Europe. *Annals of Forest Science* 63(6), 613-624. doi: 10.1051/forest:2006044.
- Sala, A., Tenhunen, J.D., 1993. Site-specific water relations and stomatal response of *Quercus ilex* in a Mediterranean watershed. *Tree Physiology* 14, 601-617. <http://treephys.oxfordjournals.org/>.

- Sama, G., Buse, J., Orbach, E., Friedman, A.L.L., Rittner, O., Chikatunov, V., 2010. A new catalogue of the Cerambycidae (Coleoptera) of Israel with notes on their distribution and host plants. *Mun. Entomological Zoology* 5(1), 1-51.
- Sanchez-Martinez, G.N., Moreno-Rico, O., Siqueiros-Delgado, M.E., 2010. *Crioprosopus magnificus* LeConte (Coleoptera: Buprestidae) in Aguascalientes, Mexico: biological observations and geographical distribution. *Coleopterists Bulletin* 64(4), 319-328. doi: 10.1649/0010-065X-64.4.319.
- Schepper, V.D., Steppe, K., 2011. Tree girdling responses simulated by a water and carbon transport model *Annals of Botany* 108: 1147–1154. doi: 10.1093/aob/mcr068.
- Scott, P.M., Burgess, T.I., Barber, P.A., Shearer, B.L., Stukely, M.J.C., Hardy, G.E.St.J. Jung, T., 2009. *Phytophthora multivora* sp. nov., a new species recovered from declining *Eucalyptus*, *Banksia*, *Agonis* and other plant species in Western Australia. *Persoonia* 22, 1–13. doi: 10.3767/003158509X415450.
- Scriven, G.T., Reeves, E.L., Luck, R.F., 1986. Beetle from Australia threatens Eucalyptus. *Californian Agriculture* 40, 4-6.
- Shearer, B.L., Tippett, J.T., 1989. Jarrah Dieback: The dynamics and management of *Phytophthora cinnamomi* in the Jarrah (*Eucalyptus marginata*) forest of South-western Australia. Research bulletin No3. CALM. Como Western Australia.
- Shigo, A.L., Marks, H.G., 1977. Compartmentalisation of decay in trees. Bulletin No. 405. Washington DC: Forest Service US Department of Agriculture.

- Siemann, E., Weisser, W.W., 2004. Testing the role of insects for ecosystem functioning. In: Weisser, W.W., Siemann, E., (Eds.). *Insects and Ecosystem Function*. Ecological Studies Series. Springer-Verlag. pp. 383-401.
- Simonin, K., Kolb, T.E., Montes-Helu, M., Koch, G.W., 2007. The influence of thinning on components of stand water balance in a ponderosa pine forest stand during and after extreme drought. *Agricultural and Forest Meteorology* 143, 266–276. doi: 10.1016/j.agrformet.2007.01.003.
- Slatyer, R.O., 1967. *Plant-Water Relations*. Academic Press, London.
- Smith, I.N., McIntosh, P., Ansell, T.J., Reasons, C.J.C., McInnes, K., 2000. Southwest western Australian winter rainfall and its association with Indian Ocean climate variability. *International Journal Climatology* 20, 1913–1930.
- Smith, R., 2003. Preliminary assessment of rainfall and groundwater trends in areas of wandoo. *Salinity and Land Use Impacts Series No. slui 27*. Resource Science Division, Water and Rivers Commission.
- Specht, R.L., Roe, E.M., and Boughton, V.H., 1974. Conservation of major plant communities in Australia and Papua New Guinea. *Australian Journal of Botany Supplementary Series No. 7*, 667 pp.
- Stanaway, M.A., Zalucki, M.P., Gillespie, P.S., Rodriguez, C.M., 2001. Pest risk assessment of insects in sea cargo containers. *Australian Journal of Entomology* 40, 180 – 192.

- Stone, C. 2001. Reducing the impact of insect herbivory in eucalypt plantations through management of extrinsic influences on tree vigour. *Austral Ecology* 26, 482–488.
- Stoneman, G.L., Schofield, N.J., 1989. Silviculture for water production in jarrah forest of Western Australia – an evaluation. *Forest Ecology and Management* 27, 273-293.
- Thomsen, I.M., Harding, S., 2010. Fungal symbionts of siricid woodwasps: isolation techniques and identification. *Forest Pathology* pp. 1-13. doi: 10.1111/j.1439-0329.2010.00677.x.
- Timms, L.L., Smith, S.M., Groot, P., 2006. Patterns in the within-tree distribution of the emerald ash borer *Agrilus planipennis* (Fairmaire) in young, green-ash plantations of south-western Ontario, Canada. *Agricultural and Forest Entomology* 8, 313–321.
- Tippett, J.T., Hill, T.C., Shearer, B.L., 1985. Resistance of *Eucalyptus* spp. to Invasion by *Phytophthora cinnamomi*. *Australian Journal of Botany* 33, 409-18.
- Took, F.G.C., 1935. The *Phoracantha* beetle. Insects injurious to forest and shade trees. Bulletin. Department of Agriculture South Africa. Reprint no. 79, 5pp.
- Turtola, S., Manninen, A-M., Rikala, R., Kainulainen, P., 2003 Drought stress alter the concentration of wood terpenoids in Scots Pine and Norway Spruce seedlings. *Journal of Chemical Ecology* 29(9), 1981-95.

- Vaz, M., Pereira, J.S., Gazarini, L.C., David, T.S., David, J.S., Rodrigues, A., Maroco, J., Chaves, M.M., 2010. Drought-induced photosynthetic inhibition and autumn recovery in two Mediterranean oak species (*Quercus ilex* and *Quercus suber*). *Tree Physiology* 30, 946–956. doi: 10.1093/treephys/tpq044.
- Wang, Q., 1995. A Taxonomic Revision of the Australian Genus *Phoracantha* Newman (Coleoptera: Cerambycidae). *Invertebrate Taxonomy* 9, 865-958.
- Weaving, S., 1999. Peel-Harvey Catchment: Natural resource atlas. Spatial resource information group, Department of Agriculture and Food, Western Australia.
- Weisser, W.W., Siemann, E., (Eds.). 2004. *Insects and Ecosystem Function Series: Ecological Studies*, Vol. 173: pp. 413.
- Williams, K., Mitchell, D., 2002. Jarrah Forest 1 (JF1 – Northern Jarrah Forest subregion). In: *A Biodiversity Audit of Western Australia's 53 Biogeographical Subregions in 2002*. Department of Conservation and Land Management. pp. 369-381.
- Wills, R.T., Keighery, G.J., 1994. Ecological impact of plant disease on plant communities. *Journal of the Royal society of Western Australia* 77, 127-131.
- Wingfield, M., Hurley, B., 2003. Forest insect pests. Saapi tree farming guidelines chapter 14 pp 101-119.

- Worrall, J.J., Egeland, L., Eager, T., Mask, R.A., Johnson, E.W., Kemp, P.A., Shepperd, W.D., 2008. Rapid mortality of *Populus tremuloides* in southwestern Colorado, USA. *Forest Ecology and Management* 255, 686–696. doi: 10.1016/j.foreco.2007.09.071.
- van Wyk, M., Pegg, G., Lawson, S., Wingfield, M.J., 2007. *Ceratocystis atrox* sp. nov. associated with *Phoracantha acanthocera* infestations on *Eucalyptus grandis* in Australia. *Australasian Plant Pathology* 36, 407–414. doi: 10.1071/AP07042.
- Yesertener, C., 2010. Hydrogeochemical assessment of the Superficial aquifer Perth metropolitan area. Department of Water Hydrogeological record series Report no. HG37.
- Zolubas, P., Negrón, J., Mmison, A.S., 2009. Modelling Spruce Bark Beetle Infestation Probability. *Baltic Forestry* 15(1), 23-27.