

Crown Structure
& the Canopy Arthropod Biodiversity
of
100 Year Old and Old Growth
Tasmanian *Eucalyptus obliqua*

by

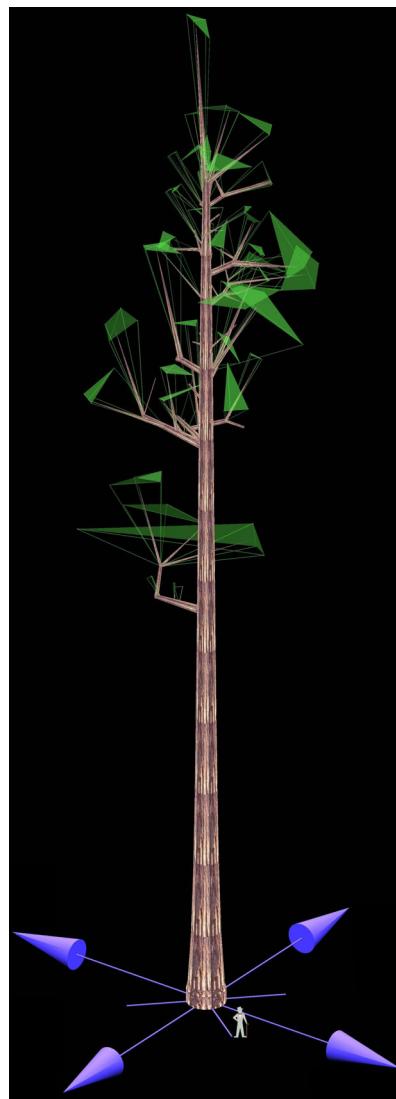
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Yoav Daniel Bar-Ness



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Abstract:

The crown structure and canopy arthropods of *Eucalyptus obliqua* were studied at the Warra Long Term Ecological Research Site in the wet sclerophyll forests of Southern Tasmania. Eight 100 year old and eight old-growth (between 300-500 years old) trees were studied in pairs. Despite their critical role in the economy and ecology of Tasmania, few studies have addressed the canopy arthropod biodiversity of these trees. The crown structure was mapped by recording a vector in spherical space for every branch. 3- dimensional computer models were generated to aid in illustrating the tree maps. Sticky traps, flight intercept traps, and funnel crawl traps were placed in the crown to sample mobile arthropods.

The age classes were quantifiably different in crown structure. 100 year old trees had young mature crowns of original branches. Old trees had either senescent original crowns or resprouted epicormic secondary crowns. Old trees expressed a greater variability in crown structure, and were more complex as measured by the amount of information required to display the computer image. Structural attributes such as hollows, dead tops, dead flanks, trunk fissures, burls, vascular epiphytes, snapped trunks, and litter collections were all present more often in the old trees than the 100 year old trees.

Old trees showed a more diverse community structure and the evidence suggested a more rich fauna in these trees. The age classes showed differences in composition that were often masked by environmental effects.

The structural descriptors were tested against the arthropod biodiversity variables to explore the influence of crown structure on canopy arthropod communities. In the context of the study trees, several rank correlations were identified. Old trees with a higher portion of their total wood volume in the trunk had a more diverse total arthropod fauna. Trees with less crown depth had a richer Diptera fauna. Trees with a narrower range of dead branch starting diameters had a more diverse sticky trap catch. Trees with a wider range of live branch starting diameters had a richer hangtrap catch. Old trees with greater mean upwards arc had a richer hangtrap catch. Trees with a lower mean branch height as % of total height had a richer hangtrap catch. No other study is known to have investigated the influence of crown structure on canopy arthropod biodiversity in a forest tree.



Geography & Environmental Studies

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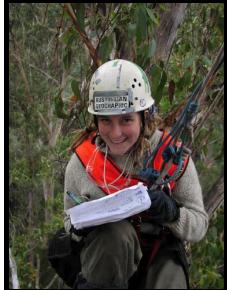
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COOPERATIVE RESEARCH CENTRE
FOR SUSTAINABLE PRODUCTION FORESTRY
Kate Harrison, Anna Hopkins, Caroline
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He was actively involved in the development of our own unique style of rigging.



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-Jerry Romanski offered constructive criticism and rigged tree 4



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-Ben Meadows Forestry Suppliers provided 2 60m ropes for the price of 1

-Malcolm Grant suggested several design ideas for funnel traps

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-Erin Buttermore kindly hosted Robert Junker

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-Peter Lillywhite provided access to microscopes & other resources at the Melbourne Museum

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“Ultimately, there would be only a single tree, incorporating all living things without exception...”
E.C. Pielou, *Biogeography*

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1) Introduction:

1.1 Biodiversity and forest structure

The conservation of biological diversity is an overriding concern in a world well supplied with urgent environmental issues (Hunter, 1999). Arthropods form a vast portion of the Earth's eukaryotic biodiversity (Erwin, 2004; Gaston & Spicer, 1998). Despite their critical importance, they are under-represented and under-valued by both the general public and the decision makers (Kim, 1993; New, 1999). The range of arthropod ecosystem services and ecological niches underpins the survival of humans on this planet, and actively working towards their conservation will benefit us greatly in the future (Beattie, 1994; Grove & Stork, 2000; Kim, 1993; New, 1999). Any loss of arthropod biological diversity in the forest canopy can impact humans in many ways, including monetarily, ecologically and spiritually (Beattie, 1994; Kim, 1993; New, 1999; Yen, 1993).

Arthropod biodiversity reaches its greatest levels in forest ecosystems (Erwin, 1995). Australian *Eucalyptus* forests harbour a globally significant number of species (Majer *et al.*, 1994). Like other animals in these ecosystems, their biodiversity is dependant on forest structure (Spies, 1998).

Forest management drastically alters both the structure and demographics of *Eucalyptus* forests (Floren *et al.*, 2001; Lindenmayer & McCarthy, 2002; Lindenmayer *et al.*, 2000a). Studies in other forest regions have addressed the impact of harvesting on the canopy arthropod community (Chey *et al.*, 1998; Floren & Linsenmair, 2001; Winchester & Ring, 1996).

Very little is known about the arthropod biodiversity or the habitat structures in ancient or mature *Eucalyptus* trees (Majer *et al.*, 1997). Forest management can only be considered sustainable if it maintains biodiversity (Lindenmayer, 1995). If old-growth trees are reservoirs of arthropod biodiversity, then the loss of these irreplaceable trees would be an unsustainable practice.

Alteration of Tasmanian forests: The wet sclerophyll *Eucalyptus* forests of Tasmania are ecologically and economically critical to the island (Dovers *et al.*, 1994; Whiteley, 1999; Williams & Brooker, 1997; Williams & Potts, 1996), and contain the tallest and largest flowering plants in the world (Hickey *et al.*, 2000; Kostoglou, 2000;

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Mifsud, 2003). *Eucalyptus* trees in wet sclerophyll forests grow and decay at high speeds, with an estimated lifespan of 400-500 years. (Alcorn *et al.*, 2001; Gibbons & Lindenmayer, 1996; Lindenmayer *et al.*, 2000a)

Forest management in Tasmania is based on an 80-100 year rotation of clearfelling, burning, and replanting of wet *Eucalyptus* forests (Figure 1.1). It is a politically sensitive issue and the source of a limitless quantity of public debate and spite (Forestry Tasmania, 2003; Green, 2003).



Figure 1.1. Clearfelling alters the structure of *Eucalyptus* forests.

Forest management impacts arthropod biodiversity: A critical element of this controversy is the impact of forest management on the native fauna. Studies on the arthropods associated with *E. obliqua* forests play an important role in assessing this impact. Arthropods biodiversity is linked to structures (Spies, 1998). Like all arthropod biodiversity research, these must deal with an overwhelming number of animals and the lack of comprehensive taxonomic knowledge. Targeted studies investigating the impact of land management on these animals can offer solutions to mitigate the loss of biodiversity (Bashford *et al.*, 2001; Brown *et al.*, 2001; Grove, 2003; Michaels & McQuillan, 1995).

Under current forest harvest regimes, older trees are removed from the Tasmanian *Eucalyptus* forest landscape, and replaced with young trees destined for

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harvesting before formation of old-growth characteristics. The tree population, and subsequently the forest environment, will change dramatically (Lindenmayer *et al.*, 2000a). Research comparing different tree ages offers insight into the results of changing the forest tree demographics (Harrison *et al.*, 2003; Yee *et al.*, 2001).

Forest biodiversity is managed through structures: Management of arboreal biodiversity requires knowledge of arboreal habitats. Despite humans' great ability to destroy natural forest structures, our ability to generate them is very limited. To properly manage forest structural attributes to conserve biodiversity, more knowledge is needed on their occurrence and formation.

A critical component of that knowledge is information on how and where structures form, and consequently how to best plan for their conservation (Ball *et al.*, 1999; Gibbons & Lindenmayer, 1996; Hallett *et al.*, 2001; Lindenmayer, 1995). Using natural disturbance regimes as a model for forest management can most effectively conserve these structures (Franklin *et al.*, 2002).

Modern forest management aspires to mimic natural disturbances (Franklin *et al.*, 2002; Hickey & Wilkinson, 1999; Lindenmayer & McCarthy, 2002). In *Eucalyptus* forests, the major disturbance factor is fire. In practice, the proximate goal is to protect biodiversity from the adverse effects of harvest by preserving specific, identifiable forest structures that would survive a fire. The ultimate goal is to foster similar dynamics such as regrowth and decay in the disturbed forest (Grove *et al.*, 2002). Measures to conserve features of forest stands such as standing dead trees, large old trees, and coarse woody debris are considered part of a "new forestry" and have been adopted with varying degrees of success (Franklin, 1989). In Tasmania, the Silvicultural Systems Trial has been testing these measures (Hickey *et al.*, 2001).

Targeted preservation of structure is the best approach: Taking a conservative approach to conserving unknown arthropod biodiversity (Bickel & Tasker, 2004) would require the preservation of all forest structures. This is incompatible with modern forestry. Research on the use and formation of habitat structures can maximize the value of the efforts being made by the industry for wildlife conservation.

Forest managers protect biodiversity by retaining trees: The most effective method of conserving forest structures is to not destroy them. Forest managers have

the mandate of preserving native animal biodiversity to be factored into planning for the primary requirement of extracting forest products for economic value (Norton & May, 1994; Orr & Gerrard, 1998). One method to achieve this goal is the retention of old, living trees in clusters or singly (Neyland *et al.*, 1999).

Legal requirements to manage forests for endangered species in Australia and the United States have prompted research into their habitat requirements. For example, large, older trees are required for the survival of animals such as the red-cockaded woodpecker (Hanula *et al.*, 2000), marbled murrelets (USFS, 2004), and Leadbetter's possums (Lindenmayer *et al.*, 1990). The conservation of ancient oak trees required by saproxylic beetles had been addressed in Sweden (Ranius, 2000). Because these trees take so long to develop, preservation of forest trees in harvested areas is the basic tool of foresters in biodiversity conservation (Franklin, 1989; Lindenmayer *et al.*, 1993). Replacement is not an option in the scale of a human lifetime.

Retained tree selection guided by knowledge of habitat use and formation: The selection of retained trees requires knowledge of which attributes contribute to animal biodiversity. When these attributes are not readily visible, assessing the likelihood of their presence is critical (Whitford, 2002). Retained trees in *Eucalyptus* forestry are usually old trees with visible hollows. By examining trees felled for harvest, Koch (2004) has been studying marsupial occupancy of the tree hollow habitat in *E. obliqua*. Using similar techniques Harrison *et al.* (2003) have been studying the beetle communities in these trees and their association with fungus.

Lindenmayer *et al.* (1993) and Gibbons & Lindenmayer (2002) discuss factors in hollow formation and their application to retaining trees in the landscape. Gibbons & Lindenmayer (2002) estimate that 303 Australian native vertebrate species utilize hollows in live or dead trees, and that each one of these animals has its own requirements as to what makes a suitable hollow. Larger animals require larger hollows only found in larger, older trees (Mackowski, 1984). Forest birds for example, may seek out exceptionally large trees of a particular species (Hansell, 2000), and forest marsupials may seek out trees with a secondary epicormic crowns (Mackowski, 1984). However, management of tree hollows for vertebrate fauna is one element of a complex problem. Other habitats exist besides hollows, and myriad other organisms exist besides vertebrates. In addition, these vertebrate animals may only be

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present at a specific tree because of the availability of arthropods as food (Abbott & Van Heurck, 1985; Hanula & Franzreb, 1998; Recher *et al.*, 1996; Scarff *et al.*, 1998).

Knowledge of habitat utilisation aids management of habitats: Creation or fostering of animal habitat is an option when evidence exists for its effectiveness. A very familiar example is the common artificial birdhouse. Gibbons & Lindenmayer (2002) and Mackowski (1984) discuss the use of artificial nest boxes in creating marsupial habitat in the absence of tree hollows. The killing of trees can be a simple way to generate standing dead wood habitat in managed landscapes where it is in short supply (Hallett *et al.*, 2001; Moorman *et al.*, 1999). Killing branches within a tree crown may create similar habitat in microcosm. The same knowledge that guides tree retention can be applied to habitat creation.

Keystone structures support biodiversity: Forest structure is the template for the picture of biodiversity (Spies, 1998). Tews *et al.* (2004) introduce the concept of **keystone structures**. These structures are a resource, or combination of resources required by certain taxa to exist in a region, and the removal or lack of these resources will result in their extirpation. The trees in the forest are prominent keystone structures.

A keystone structure may be an aggregate of other keystone structures. It may be abundant or scarce. It may seem irrelevant to humans..

Different animals may require contradictory or mutually exclusive structures. A tree with many branches may be better than a tree with few branches to some animals. In Victorian *Eucalyptus* forests, for example, understorey *Acacia* trees and old decayed eucalypts have been identified as a keystone structures for marsupials (Lindenmayer, 1995).

However, location of these structures may be critically important as well. McCune *et al.* (2000) investigate the microhabitats of arboreal bryophytes and report that similar structures in different locations within the tree are distinct habitats. The same *Acacia* trees from the Victorian forests can be irrelevant to the animals if in the wrong context, such as steep slopes (Lindenmayer, 1995).

Not all trees have all keystone structures: Trees in the forest may be keystone structures in that they contain, or have the potential to form, specific structures. Trees at different life stages, and even pieces of the tree at different stages,

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can potentially fulfil different requirements for different animals (Mackowski, 1984; Whitford, 2002). For example, leaves are more likely to be found on a given tree than burls. Fruit is a temporary resource (Andersen & New, 1987).

Some keystone features are age linked: For example, several marsupial and bird species require hollows formed in old trees (Abbott & Whitford, 2001; Ambrose, 1981; Gibbons, 1994; Hanula *et al.*, 2000; Haseler & Taylor, 1993; Lindenmayer *et al.*, 1997). While some elements of a tree may be similar to those in other trees (e.g. foliage), the presence of a hollow increases the biodiversity value of the tree and the forest stand. Conversely, the loss of these features by natural or human disturbance can destroy animal biodiversity (Franklin *et al.*, 2002).

Elements such as flowers, leaf litter, fruit, pollen, shedding bark, and fallen branches are all structures within a tree that change as the tree grows, ages, and dies. Some structures, such as charcoal on tree trunks, are created during disturbances that may change the abundance of several other structures. The same fire that left charcoal on the tree trunks may have destroyed all of the nonvascular epiphytes. Research on the chance formation of these structures over time and their relation to disturbance regimes can aid prediction of their presence in the landscape (Lertzman *et al.*, 1996; Lindenmayer *et al.*, 1990; Mackowski, 1984; McCarthy & Lindenmayer, 1998; Mushinsky & Gibson, 1991; Nilsson *et al.*, 2002; Pausas *et al.*, 1997).

Management of structures: The perfect forest management plan would optimally conserve cryptic taxa by conserving all types of structures (Bickel & Tasker, 2004). This also means preserving the chance rhythms of disturbance that may stochastically generate these structures.

The presence of a structure does not necessarily mean it is a keystone structure. However, a conservative approach to management would assume, and plan accordingly, that all of these elements are utilized and required at some stage by some animal. Human knowledge of forest invertebrate biodiversity is very poor in regards to the number of species in the forest, let alone the ecological requirements of these unknown animals (Basset *et al.*, 2003; Erwin, 1995; Grove & Stork, 2000; Stork *et al.*, 1997).

Research on structures in *Eucalyptus* forests, such as large, old living and dead trees, and coarse woody debris, has emphasized that forest industry land managers

must plan for the loss and recruitment of these features throughout the landscape over time (Grove *et al.*, 2002; Lindenmayer *et al.*, 1997). This requires detailed knowledge of the abundance, formation, and loss of these structures in relation to the planned forest harvest regime. Unfortunately, most studies of long term sustainability of old-growth structures in *Eucalyptus* forests harvested by total clearing predict that these goals are not being met (Gibbons, 1994; Gibbons & Lindenmayer, 1996; Kirkpatrick, 1994; Lindenmayer *et al.*, 2000b). Little is known about the canopy arthropods of old *Eucalyptus* trees, and consequently little is known about the impact of forest management on them.

1.2 Research questions

Gaps in the knowledge:, three major research questions were identified and engaged. The overarching goals are to aid forest managers in conservation of arboreal animal biodiversity, and to fill some of the gaps in human knowledge of these ecosystems

1) What are the structural differences between 100 year old and old-growth *E. obliqua*, and how can they be measured and displayed?

Eight trees in each age class were mapped and compared. Spatial measurements of every branch within the tree crown were collected and summarized. The presence of structural features, such as hollows and vascular epiphytes, was noted. Computer visual models of each tree were generated to illustrate the shape of each tree.

2) How is the canopy arthropod biodiversity different in 100 year old and old-growth *E. obliqua*?

Three types of traps were set in the crowns of the study trees and the collected arthropods analysed for differences in abundance, richness, diversity, community structure, and distinctness.

3) In what ways does crown structure influence arthropod biodiversity in *E. obliqua*?

The arthropod biodiversity responses to tree structural descriptors was explored. Several correlations between structural predictors and arthropod responses of composition, abundance, richness, and diversity are identified and explored. These are presented as promising avenues of future investigation.

1.3 Limitations of the present study

The effort involved in accessing the study trees limited all aspects of fieldwork. Days lost to windy conditions had to be made up later in the season. Without the assistance of several enthusiastic field helpers, studying sixteen trees would have been impossible.

The study trees were biased towards safe climbing trees. Most of the trees in the study site were deemed too dangerous for climbing.

Mapping of branches required careful consideration of resolution. It was impossible to map every leaf and branch on trees reaching 75 metres in height, so a precise method of scaling back the mapping resolution was required. However detailed any tree map may be, the structural measures of gross branch morphology that seemed important to a human climber may actually be irrelevant to some arthropods.

Like all arthropod biodiversity studies, time and resources limited trap placement and processing. For some arthropod taxa, taxonomic identification was aided by local experts (please see section 7.2). Consequently other taxa were not sorted to the same degree. Fieldwork was only done in summer, therefore missing out on seasonal differences in fauna.

E. obliqua also grows in dry sclerophyllous forests. It is present in a wide range of environments in Tasmania and mainland Australia. The wet sclerophyll forest site in the study has a strong Gondwana rainforest floristic element, and contains representatives of some of the tallest and biggest trees in Australia. The environmental conditions at the study location are significantly different from other *E. obliqua* localities. It may therefore not adequately represent *Eucalyptus* in other circumstances.

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In this section, the study aims are defined. These aims were designed to answer the research questions and to maximize the value of the time and effort spent in the *Eucalyptus* trees. A review of the relevant literature is presented. Previous crown structural mapping research is cited, and current models of crown development in *Eucalyptus* are presented. Next, a brief review of trends in canopy arthropod research is followed by a more detailed treatment of what is known about *Eucalyptus* trunk and canopy arthropods. Finally, the literature on the link between tree crown structure and arthropod biodiversity is discussed.

2.1 Addressing the research questions

2.1.1 Study Design

Comparison of neighbouring old and young trees: By studying trees of different ages, a picture can be formed of their structural development through time (Van Pelt & Nadkarni, 2004). Tasmanian *Eucalyptus* forests are difficult to age by ring counts and high intra-cohort variability can mask differences in age (Alcorn *et al.*, 2001). Therefore, the study site was selected where cohorts of *Eucalyptus* were sufficiently distinguishable by size. Comparison of two ages illuminates only two stages of the 450 year lifespan of *E. obliqua* (Hickey *et al.*, 1998), but allows for control of spatial confounds (Burgman & Williams, 1995; Richardson *et al.*, 1999).

Schowalter (1995), Schowalter & Ganio (1998), and Jukes *et al.* (2002) compared the canopy arthropods of different tree species simultaneously with forest age, and reported that most variation in forest arthropod communities was linked to the tree species sampled. To control the confounding effects of tree species and site, nearby old and young study trees of a single species were paired, controlling for site-specific effects (Burgman & Williams, 1995; Richardson *et al.*, 1999).

Habitats are studied in situ in live trees: Study of the arboreal environment within a tree is best done by accessing the trees (Nadkarni, 1995). Several habitats in mature *Eucalyptus* trees cannot be studied after the tree has been felled. Characteristics, such as the distinctive arrangement of branches in the crown, are modified greatly as the tree lands. Animals living in the airspace of the tree are likely

to have flown away. Modern canopy access techniques allow observations and measurements of undisturbed tree crowns *in situ* (Moffett & Lowman, 1995).

2.1.2 Study Aims and Applicability

Few researchers have climbed *Eucalyptus* trees for study purposes (Hickey *et al.*, 2000; Larson, 2004; Lowman *et al.*, 1987; Mifsud, 2003; Ohmart *et al.*, 1983b; Palzer, 1983; Van Pelt *et al.*, 2004). The present project was therefore exploratory in nature. The project aims were developed to address the research problems. The aims are divided into structural “mapping” aims, and arthropod “trapping” aims. Not all aims were built around hypothetical tests. Embedded in the study aims are eight hypothesized quantifiable differences between the age classes. In the presentation of this thesis, the mapping aims will be addressed first, followed by the trapping aims, and then an exploration of their correlation.

Throughout the rest of this document, the 100 year old *E. obliqua* are referred to as “100yr” trees, and the old-growth *E. obliqua* are referred to as “old trees.”

The ten study aims are:

- 1.** Mapping Aim 1: Quantitatively assess the differences in crown structure and size between 100yr and old *E. obliqua*
- 2.** Mapping Aim 2: Investigate the presence of structural features in the crowns of 100yr and old *E. obliqua*
- 3.** Mapping Aim 3: Modify the conifer mapping technique of Van Pelt *et al.* (2004b) for *Eucalyptus* trees
- 4.** Mapping Aim 4: Develop a technique for displaying crown structure of forest trees using computer models based on 3-dimensional spherical coordinates
- 5.** Mapping Aim 5: Expand Jacob’s (1955) theories of intra-branch competition in Eucalyptus saplings to mature and old-growth *E. obliqua*
- 6.** Mapping Aim 6: Generate a predictor data set to explore the influence of crown structure on canopy arthropods

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7. Trapping Aim 1: Determine what differences exist in arthropod biodiversity between 100 year old and old growth *Eucalyptus obliqua*
8. Trapping Aim 2: Contribute to the knowledge of *Eucalyptus* canopy arthropods
9. Trapping Aim 3: Develop robust, inexpensive trap designs suitable for transport to and use in *E. obliqua*
10. Trapping Aim 4: Generate a response data set to explore the influence of crown structure on canopy arthropods

These aims are described in greater detail:

Mapping Aim 1: Quantitatively assess the differences in crown structure and size between 100yr and old *E. obliqua*: Identifying age-related changes in crown structure can aid in understanding the growth of these trees, and aid in assessing what forest structures are lost with harvested old-growth trees.

- **Hypothesis 1)** Old *E. obliqua* are quantifiably and objectively distinct from 100yr trees, i.e. old trees are not scaled-up versions of 100yr trees.
- **Hypothesis 2)** Old *E. obliqua* have a more variable crown structure than 100yr *E. obliqua*.

Mapping Aim 2: Investigate the presence of structural features in the crowns of 100yr and old *E. obliqua*. The opportunity to observe and record these features *in situ* allows for discussion of their formation and location. A photographic record can aid future researchers in selecting arboreal habitats to investigate.

- **Hypothesis 3)** Structural features such as epiphytes, hollows, dead tops, snapped trunks and burls are more commonly present in old *E. obliqua* than 100yr *E. obliqua*.

Mapping Aim 3: Modify the conifer mapping technique of Van Pelt *et al.* (2004b) for *Eucalyptus* trees. The mapping methods used in the present project are derived from techniques of Van Pelt *et al.* (2004b). Their methods were developed in coniferous trees. *Eucalyptus* has a distinct growth pattern which required

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modifications to their technique. Researchers wishing to map *Eucalyptus* or other trees in a similar fashion can utilize these adopted changes if appropriate.

Mapping Aim 4: Develop a technique for displaying crown structure of forest trees using computer models based on 3-dimensional spherical coordinates. The rendering of the study trees using 3-dimensional computer models allows for illustration of crown dynamics and offers a faithful visual representation of the collected data.

- **Hypothesis 4)** Old *E. obliqua* will have a greater complexity than 100yr trees, as measured in surrogate by the amount of information required to describe them.

Mapping Aim 5: Expand Jacob's (1955) theories of intra-branch competition in *Eucalyptus* saplings to mature and old-growth *E. obliqua*. The crown structure of *E. obliqua* is a product of competitive interactions between individual branch units (Halle, 1995). Jacobs (1955) introduced the concept for saplings, but did not extend it to older trees. Applying the principles of intra-branch competition to mature and old-growth *E. obliqua* can clarify differences in crown structural measurements.

Mapping Aim 6: Generate a predictor data set to explore the influence of crown structure on canopy arthropods. When combined with measures of arthropod biodiversity, structural attributes of *Eucalyptus* trees can be identified that are important in determining the abundance, richness, diversity, and composition of canopy arthropods.

Trapping Aim 1: Determine what differences exist in arthropod biodiversity between 100 year old and old growth *Eucalyptus obliqua*. The loss of old, senescent *Eucalyptus* trees and the spread of regrowth forests has been identified as a threat to conservation of marsupial biodiversity (Lindenmayer *et al.*, 1999). It is unknown if arthropod communities are similarly at risk. While the literature suggests that old-growth trees have a more diverse arthropod fauna than younger trees (Martikainen *et al.*, 2000; Schowalter, 1995), this has not been addressed in *Eucalyptus* trees.

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- **Hypothesis 5)** Old-growth *E. obliqua* trees have a more abundant arthropod fauna than 100 year old trees, i.e more individual arthropod animals.
- **Hypothesis 6)** Old-growth *E. obliqua* trees have a richer arthropod fauna than 100 year old trees, i.e. more recognizable types of arthropods.
- **Hypothesis 7)** Old-growth *E. obliqua* trees have a more diverse arthropod fauna than 100 year old trees, i.e. a greater quantitative index implying both a richer community and more even abundances between morphospecies.
- **Hypothesis 8)** Old-growth *E. obliqua* trees have a distinct arthropod fauna from 100 year old trees, i.e. the taxonomic composition of animals differs.

Trapping Aim 2: Contribute to the knowledge of *Eucalyptus* canopy

arthropods. There is a gap in the knowledge of the arthropod biodiversity in wet sclerophyllous *Eucalyptus* trees (Majer *et al.*, 1997). Because *Eucalyptus* is the dominant forest tree in Australia (Lindenmayer *et al.*, 1997), and because arthropods are a critical part of the global ecosystem (Kim, 1993), it is important to study their presence and diversity. Listing, photographing, and curation of collected specimens will add to the resources available for arthropod biodiversity research.

Trapping Aim 3: Develop robust, inexpensive trap designs suitable for transport to and use in *E. obliqua*. Because of the effort involved in accessing the crowns of tall forest trees, passive traps allow greater flexibility in placement schedules than active collecting methods. Traps are needed that are durable and inexpensive. Recycled bottles and compact disk cases were found to fulfil both of these requirements.

Trapping Aim 4: Generate a response data set to explore the influence of crown structure on canopy arthropods. In tandem with Mapping Aim 6, the results from the arthropod trapping can be paired with the structural data. The combination of detailed structural measurements and the arthropod biodiversity results allows for exploration into their correlation. It is assumed that crown structure predicts arthropod biodiversity, rather than the other way around (Spies, 1998; Tews *et al.*, 2004).

Arthropods responses of abundance, richness, diversity, and composition can be related to structural variables for each tree.

2.2 Background Research

2.2.1 Crown Structure and development

Vertical structure: The structural qualities of individual tree crowns and forest canopies is often referred to as vertical structure, whereas the landscape pattern is referred to as habitat heterogeneity (Brokaw & Lent, 1999; Tews *et al.*, 2004; Tscharntke & Brandl, 2004). In the present study, only vertical structure is addressed. Vertical structure includes all of the aerial portions of the forest (Brokaw & Lent, 1999). The vertical structure of a forest location can be a determining factor in the climate and light on the forest floor (Holbrook & Lund, 1995; Nunez, 1985; Parker, 1995; Van Pelt & Franklin, 2000). The forest industry is based on utilizing the trunk component of vertical structure.

Tree crowns as opposed to forest canopies: The terms “crown” and “canopy” have different meanings and are frequently confused (Moffett, 2000). An individual tree has a crown, while forests have a canopy composed of combined crowns (Moffett, 2000; Parker, 1995). The distinction can blur (Nadkarni *et al.*, 2004). Conifers with reiterated trunks can be viewed as an aerial collection of smaller crowns forming a canopy (Sillett & Van Pelt, 2000). In savannah ecosystems, or *Eucalyptus* woodlands, tree crowns form “islands in the sky” that usually do not overlap (Dean *et al.*, 1999; Dial *et al.*, 2004; Hnatiuk *et al.*, 2003; Kruger & McGavin, 1997). Herbs, shrubs and grasslands may be considered canopies by smaller animals (Nadkarni *et al.*, 2004; Parmenter & MacMahon, 1984). Furthermore, the subject of interest may be the gaps, or airspace between tree crowns (Dial *et al.*, 2004; Van Pelt & Franklin, 2000). In the context of the present study, the unit of interest is the individual tree crown. In the wet sclerophyll forests, mature *Eucalyptus* crowns form an emergent island over the closed canopy of the rainforest below.

Quantification of plant structure: Two major approaches to quantification of plant physical structure exist. Descriptive empirical **mapping** of a crown structure,

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used in this study, is distinct from **modelling** hypothetical tree architecture (Godin, 2000).

Halle (1995) defined the architectural unit as an individual plant's unique expression of an architectural model dictated by its genotype. Events in the life of a forest tree can dictate the exact form of the architectural unit, such as:

1. decay (Ball *et al.*, 1999; Manion, 1981; May & Simpson, 1997; Palzer, 1983; Parks & Shaw, 1996; Wardlaw & Neilsen, 1999; White & Kile, 1994; Whitford, 2002),
2. insect herbivory (Landsberg, 1990; Lowman *et al.*, 1987; Lowman & Heatwole, 1987; Mopper *et al.*, 1991),
3. competition from other plants(Aiba & Kohyama, 1997; Anten & Hirose, 2001; Dial *et al.*, 2004), and
4. fire (Franklin *et al.*, 2002; Jacobs, 1955).

Even the loss of one bud at a branching point can change the future shape of the plant (Hadlington & Johnston, 1988; Halle, 1995). For example, the foliage scorching of *E. obliqua* saplings can completely kill the dominant treetop and create an entirely new shape, with several smaller branches vying for apical leadership (Wilkinson & Jennins, 1993). This familiar “candelabra” shaped pattern of reiterated branches is one of the more obvious outcomes of individual tree life experiences, and can be witnessed in ancient forest trees such as *Sequoia sempervirens* (Sillett & Van Pelt, 2000) and *Thuja plicata* (Van Pelt, 2002). The stochastic event responsible for the pattern, and the tree's growth responses to it, are the focus of modelling, whereas those mapping the tree focus on the observed results of these factors.

Although the actual distinction between these two approaches is flexible, the scientific literature suggests that studies of plant architecture using the modelling approach appear in genotypic, predictive and mechanistic studies (Attiwill, 1962; Ball *et al.*, 1999; Coder, 2000; Godin *et al.*, 2004; Hanan & Room, 1997; Maguire *et al.*, 1998; Parker, 1995). By contrast, descriptive mapping lends itself towards phenotypic, experimental and biogeographic analysis (Clement & Shaw, 1999; Ishii *et al.*, 2004; Sillett, 1999; Sillett & Rambo, 2000; Van Pelt & Nadkarni, 2004).

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Previous plant mapping research: The subjects of descriptive plant mapping studies can be divided into four types:

1. Features of plants
2. Individual plants
3. Similar plants
4. Different plants

Examples of these include:

1) Features of plants: The subject of interest is the physical location of a component within the plant. Mackowski (1984) dissected two *E. pilularis* and reported on their position and formation. Whitford (2002) concentrated on tree hollows in West Australian *E. marginata* and *Corymbia calophylla*. Peeters (2002) examined leaf structural features and their impact on herbivore communities.

2) Individual plants: No comparisons are made within the framework of a study design. When trees are studied individually, they are usually of exceptional size or age. The popular literature has several qualitative portraits of individual trees (Lewington & Parker, 1999; Mortimer & Mortimer, 2003; Pakenham, 1996), but these are rarely linked to any quantifiable measurements beyond height, girth, and crown spread. The crown of a *Sequoia sempervirens* tree with a complex network of secondary trunks was described and illustrated by Sillett & Van Pelt (2000). The crown of a giant *Sequoiadendron giganteum* was described by Sillett *et al.* (2000a). The largest and tallest representatives of Western North American species have been measured and illustrated by Van Pelt (2002).

3) Similar plants: Several similar plants are used as representatives of a larger group. Ishii & Wilson (2001) measured the branching architecture of six old *Pseudotsuga menziesii* and report on the processes of branch death and epicormic resprouting in these trees. Takenaka *et al.* (1998) used a simple angular and distance measuring devices to quantify and illustrate several Japanese forest shrubs, and to quantify the light capture of each plant. Clement & Shaw (1999) quantified the crown shape and branching characteristics of *P. menziesii* and its influence on epiphyte biomass. They discuss the importance of limb size and vertical height. Sillett (1999) measured the crown shape of old-growth *Sequoia sempervirens* and detailed

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epiphyte habitats at a branch scale. Sillett & Bailey (2003) compared crown-level structural variables with the biomass of epiphytic fern in *Picea sitchensis*.

4) Different plants: The structure of plants representing multiple groups is compared. They are not necessarily from different species. The present study is a comparison of different ages of trees. Schmid & Bazzaz (1994) compared the leaf mortality and height growth of the perennial flowering plants *Aster lanceolatus* and *Solidago canadensis* throughout a single growing season. Van Pelt & Nadkarni (2004) and Ishii & McDowell (2001) measured the branching architecture of *P. menziesii* of different ages to investigate trends in crown development. Clement *et al.* (2001) studied the crown structure and foliage arthropods of the Chilean conifer *Fitzroya cupressoides*. They compared trees ~500 years old with those ~2000 years old, and discussed the differences in crown structure, epiphytes, and arthropod communities.

2.2.2 Growth and developmental of *Eucalyptus*

Fifty years ago, M.R. Jacobs summarized a career's worth of knowledge of *Eucalyptus* trees in a single book. The Growth Habits of the Eucalypts (1955) begins with a discussion on the dynamics of buds, and moves up the spatial scale to leaves, branches, crowns, and silvicultural stands. The concepts are illustrated in clear and appealing line drawings. Jacobs' (1955) interest extended primarily to silviculturally useful specimens, in contrast to the modern scientific interest in the growth and structure of old-growth trees (Ishii & Wilson, 2001; Van Pelt & Nadkarni, 2004). Decadent, gnarled old trees that were considered "useless veterans" (Jacobs 1955, figure 137) are now considered to be an invaluable and effectively irreplaceable resource for wildlife (Lindenmayer *et al.*, 1997; Mackowski, 1984). In the context of the current study, Jacobs' (1955) treatments of *Eucalyptus* crown and branch development are utilized.

Eucalyptus crowns: (Jacobs, 1955) distinguished four crown stages, or "types", in *Eucalyptus* (Figure 2.1) These are:

- A. Vigorous young trees, which develop into
- B. Early mature trees, which develop into either
- C. Trees with fire-induced epicormic crowns or

D. Mature trees of high quality

All 100 year old trees in the present research possessed early mature crowns. Old trees had either an epicormic crown or a mature, high quality crown. If a crown fire had burnt through the crown, most original branches were lost and epicormic branches sprouted. If a fire had not burnt the crown, original branches were lost slowly to crown senescence, and epicormic branches sprouted to replace them.

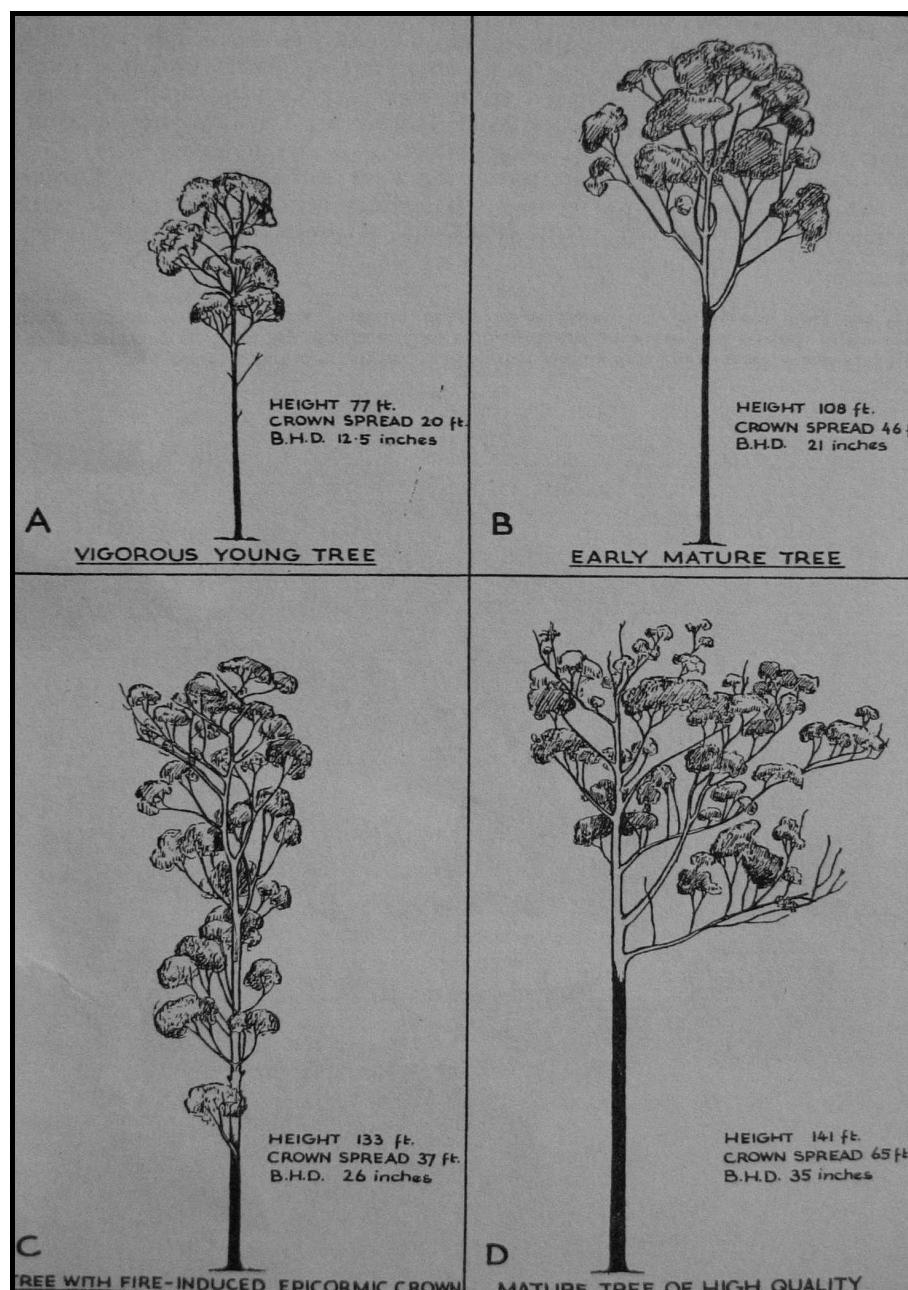


Figure 2.1: Crown types in Eucalyptus. Clockwise from upper left, A, B, D, C. Figure 58 in Jacobs (1955)

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Eucalyptus branch dynamics: Jacobs (1955) illustrated a progression of ages downwards through four years of branches in the crown of a *Eucalyptus* sapling (Figure 2.2). The youngest branches are uppermost in the crown. These branches are held upright, and descend to a horizontal attitude over time. The lowest branches, older than four years, are moribund and will be dropped as the tree ages. Competition between branches was discussed only in regards to the terminal branch. This model was not extended to old-growth *Eucalyptus*.

Curtin (1970) addressed the crown shape and branch allometry of even-aged *E. obliqua* between 10 and 93 years old. This range of ages may be less than one quarter of the lifespan of *E. obliqua* at Warra LTER (Hickey *et al.*, 1998). He discussed the “non-plasticity” of branch sizes. It is, however, unclear if the dynamics as illustrated by Curtin (1970) and Jacobs (1955) hold true for *Eucalyptus* older than 100 years of age.

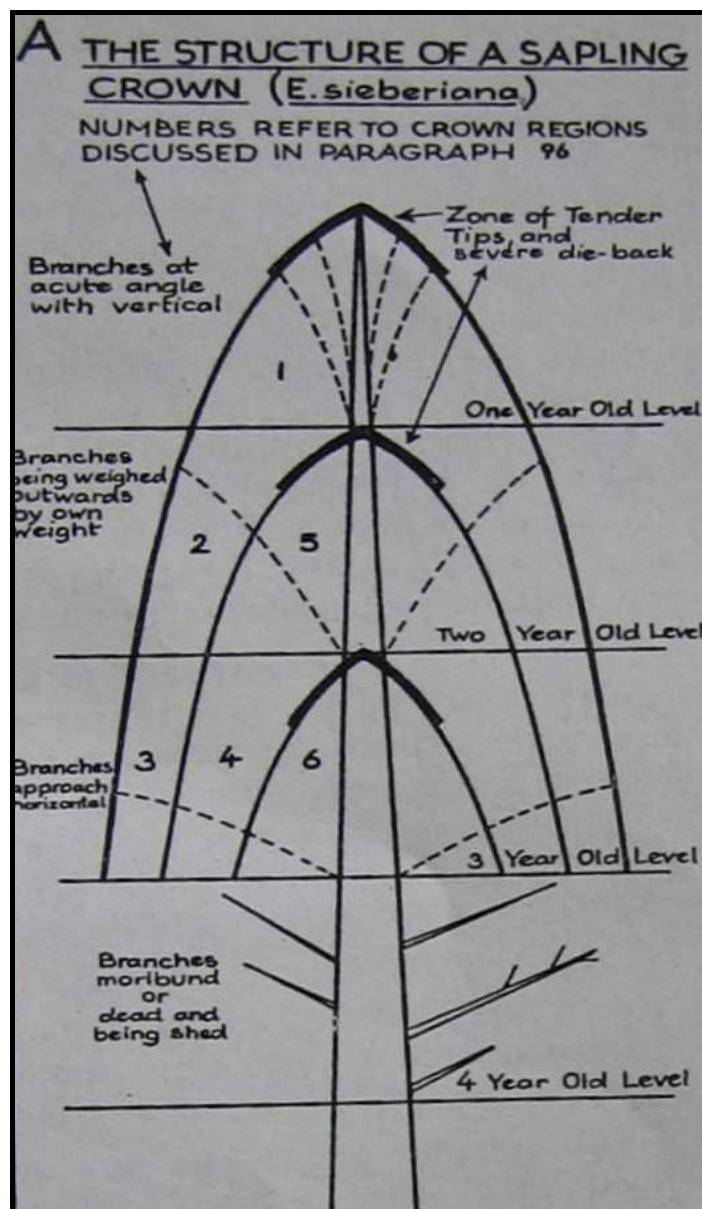


Figure 2.2: Intra-crown competition of branch cohorts in *E. sieberana* sapling crown. The youngest branches are the most vertical, the oldest live branches are more horizontal, and the oldest live branches are lowest in the crown. Figure 55b from Jacobs (1955)

The competition of branches within the crown of young and old-growth forest trees is addressed by Ishii & McDowell (2001). Following Halle's (1995) description of branches as competing individuals, they treated branches as microcosms of whole trees (Figure 2.3). They present a model of *Pseudotsuga menziesii* development in which branch competition is compared to stand dynamics (Franklin *et al.*, 2002). Lower original branches are older branches. Branch cohorts of decreasing altitude and increasing age show similar dynamics to the development of forest stands (Halle, 1995). The young upper crown of old trees resembles the young upper crown of younger trees, but the older lower crown shows its age in lower

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branch density and higher numbers of dead branches (Ishii & Wilson, 2001). Ishii and McDowell (2001) likened the death of branches in the lower crown of *P. menziesii* to the mortality of trees in a forest stand, and the sprouting of epicormic buds to the recruitment of young trees.

The concepts introduced by Jacobs (1955) for *Eucalyptus* saplings, by Halle (1995) for rainforest trees, and by Ishii & McDowell (2001) for *P. menziesii* development are applied in the present study to aid in understanding the crown structure of 100yr old and old-growth *E. obliqua*.

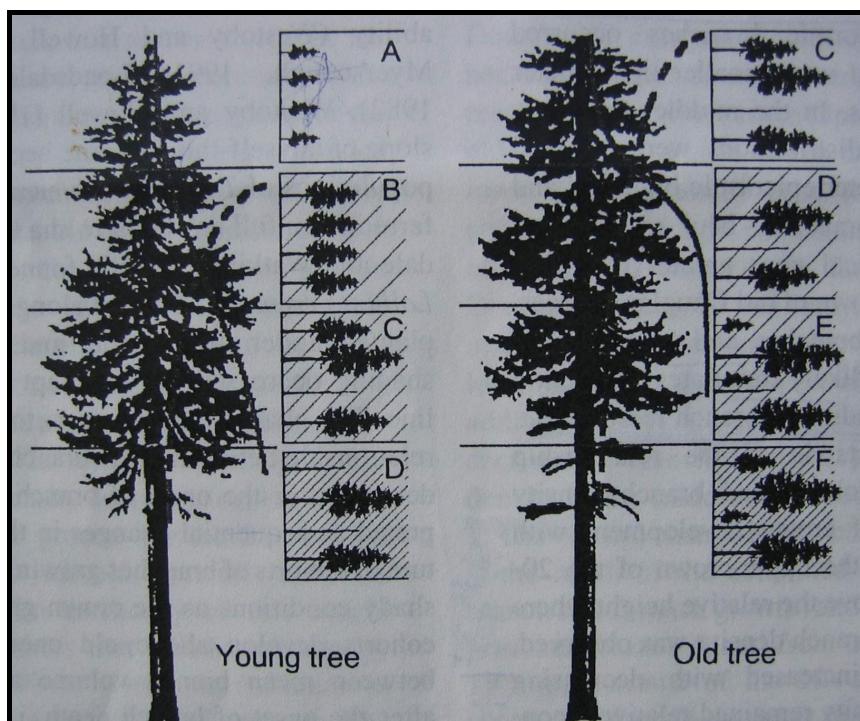


Figure 2.3: Conceptual model of crown development comparing branch cohorts to stand development.
From Ishii & McDowell (2001)

Empirical crown structural mapping of Eucalyptus crowns: Current research on *Eucalyptus* crowns has generally moved away from Jacobs' (1955) focus on tree ontogeny. The forest industry continually refines its models of forest stand growth, but published literature on *Eucalyptus* crown structure at a tree scale is less common. Recent studies have addressed light dynamics, disease responses, and the measurement of exceptional specimens of the genus.

Kelly *et al.* (2004) quantified light levels and leaf numbers in a sapling *E. regnans*. They applied computer technology to assign 3-dimensional coordinates to every branching point on the young trees.

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Rather than measure the position and size of branches, another approach to quantification of structure is the mass of tree elements. Lowman *et al.* (1987a) measured the aerial and subterranean biomass of two *E. nova-anglica* trees, one of which was suffering from rural *Eucalyptus* dieback syndrome. They quantify the loss of root biomass and increase in wood-borer damage in the dieback tree.

Published literature showing the crown structure of individual trees is rare for *Eucalyptus*. Exceptionally tall *Eucalyptus* trees have measured in one dimension in efforts to find the tallest living specimen (Hickey *et al.*, 2000; Kostoglou, 2000; Mifsud, 2003). Van Pelt *et al.* (2004b) detailed a method of quantifying forest structure at branch-scale and stand-scale, and compare tree crown attributes of old-growth *E. regnans* and *P. menziesii*. They link a hand-drawn profile illustration of an old-growth wet sclerophyll *Eucalyptus* forest stand to 3-dimensional computer profiles of a forest tree. Mackowski (1984) presents a detailed hand-drawn rendering of two *E. pilularis* trees to depict the location of hollows.

2.2.3 Canopy Arthropods

The study of treetop arthropods: Sampling canopy arthropods from trees is inherently difficult (Basset *et al.*, 2003c). Animals must be either brought down into reach, or the researcher must be brought up to them (Mitchell, 1982; Nadkarni, 1995). Despite these difficulties, canopy arthropods are the subject of a growing interest (Basset *et al.*, 2003b; Stork *et al.*, 1997).

Current concentrations in canopy arthropod research include:

- The total number of species in the world forest canopy, e.g. (Erwin, 2004)
- the host specificity of insects in trees, e.g. (Kitching *et al.*, 2003; Odegaard, 2000),
- the function of arthropods as herbivores, e.g. (Basset, 2001; Landsberg & Cork, 1997; Lowman, 1995; Lowman & Rinker, 2004; Rinker *et al.*, 2001; Wotherspoon, 1998)
- the effects of forest management, e.g. (Chey *et al.*, 1998; Chung *et al.*, 2000; Floren & Linsenmair, 2001, 2003)

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- vertical stratification, e.g. (Basset *et al.*, 2003a; Le Corff & Marquis, 1999; Shaw, 2004)

New techniques have been developed in the last thirty years to collect arthropods living in regions out of reach. Most important among these are chemical knockdown (Basset *et al.*, 1997; Erwin, 1995; Majer & Recher, 1988; Stork & Hammond, 1997), canopy cranes (Basset *et al.*, 2003c; Davis, 2001; Odegaard, 2000), and rope access techniques (Dial & Tobin, 1994; Moffett & Lowman, 1995; Perry, 1978). While a thriving field of study, the difficulties in access and the vast numbers of animals present a difficult challenge. It is apparent that much remains to be learned (Basset *et al.*, 2003b, c; Stork *et al.*, 1997).

Chemical knockdown, or canopy fogging by insecticide mist, is considered to be less biased in that it collects several animal taxa, but the ability to link animals to the habitat they were collected from is limited (Majer *et al.*, 1990; Richardson *et al.*, 1999; Stork *et al.*, 2001). As an active collecting technique, chemical knockdown vulnerable to temporal and climatic (such as wind) conditions that can render it useless (Majer *et al.*, 1996).

Canopy cranes are used in several research sites around the world. While offering safe and comfortable access to all parts of the outer tree crown, cranes are prohibitively expensive to build, operate, and maintain, and are fixed in a single location (Basset *et al.*, 2003c; Moffett & Lowman, 1995; Wind River Canopy Crane Research Facility, 2002).

Rope techniques offer the most inexpensive and portable method of direct access to the canopy. The initial investment of equipment and training allows study of canopy arthropods in their habitat by direct observation, active collecting or passive trapping methods. Drawbacks to the methods include risks associated with working at heights, and difficulties in movement away from sturdy branches (Nadkarni, 1995; Smith & Padgett, 1996). However, to sample and measure canopy biodiversity directly, rope techniques allow exact placement of traps and the ability to observe habitats *in situ*.

2.2.4 Comparing ages of trees

It is an ecological truism that old, complex forest trees sustain an animal biodiversity both richer and distinct than that of younger, simpler trees. In Australian

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Eucalyptus forests, and other forests of the world, several studies support this claim for vertebrates animals (Gibbons, 1994; Jackson, 2000; Lindenmayer *et al.*, 2000; Lindenmayer *et al.*, 1991; Mackowski, 1984; McCarthy & Lindenmayer, 1998; Pausas *et al.*, 1997; Spies, 1998). While it is perhaps a logical next step to conclude the same is true for invertebrates, less evidence is available.

Studies comparing the arthropod biodiversity of different forest ages (Floren & Linsenmair, 2001; Schowalter, 1995) are not designed to compare different ages of individual trees of the same species. Studying different sites may confound results even when comparing trees of the same species.

Published evidence of age-related arthropod differences: Differences in arthropod biodiversity associated with plant age have been identified in several plant types around the world. These investigations have generally found a richer fauna in older plants, forests, or structural elements. It is sometimes unclear if this is due to differences in size- older plants are usually larger than younger plants. A confounding element in comparing results is the measure of scale, i.e. did the researcher choose to standardize arthropod results by some measure of scale. This confound is discussed in detail in section 7.6.

Within a single plant, Waltz & Whitham (1997) studied juvenile ramets vegetatively propagating clonally from the base of mature adult *Populus* trees. The fauna of the adult was both different and richer than that of the juvenile foliage. Between plants, Banerjee (1981) found more herbivore species in older individuals of plantation tea (*Camellia sinensis*).

Working from a canopy crane, Basset (2001) reported a greater abundance and richness of phytophages collected per unit of leaf area in mature specimens of Panamanian tree *Pourouma bicolor* than in saplings. Differences in herbivore composition were attributed to the greater resource of young foliage, microclimate differences, increased toughness of leaves in mature trees, and the presence of enemy-free space. Ants were far more abundant on saplings, suggesting a different trophic web in the crowns of *P. bicolor* at different ages. At the same site, Barrios (2003) compared the herbivores on mature and sapling *Castilla elastica* and found a greater richness and diversity in the mature specimens.

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Thunes *et al.* (2003) found a greater richness of arthropods collected by canopy fogging in older Norwegian *Pinus*, but not when quantitatively controlling for their greater volume.

Clement *et al.* (2001) studied the foliage of *Fitzroya cupressoides* (Cupressaceae), the giant alerce of Chile, and found more psocids and aphids, but fewer cercopids and staphylinids in the larger, older trees (>2,000 years old) than the smaller, younger (~500 years old) trees.

Schowalter (1995) studied age effects on *Pseudotsuga menziesii* forests in Oregon, USA, and found a higher diversity and abundance of predators and detritivores in older forests. In Finland, Martikainen *et al.* (2000) found a richer beetle fauna in old-growth *Picea* forests than in younger regrowth forests.

Applicability to biodiversity conservation: The management implications of these results to conserving biodiversity are related to the changing demographics of forested landscapes. *Pinus*, *Picea* and *Pseudotsuga* are important forest resources that are harvested today. Like *Eucalyptus* forests, harvested old trees in their native environment are not replaceable within the time scale of a human life.

In Tasmania, other concurrent projects at Warra LTER (described below) are comparing the biodiversity associated with 100 year old *E. obliqua* with that of large old growth trees. Harrison *et al.* (2004) is investigating the invertebrate and fungal biodiversity of interior habitats in *E. obliqua* by dissecting felled trees, and preliminary results show a distinct and richer beetle fauna in old trees. Yee *et al.* (2001) have found a distinct fauna between small and large naturally fallen logs. These projects, as well as the canopy fogging by Grove *et al.* (2002) were all performed within a 10km radius at Warra LTER (Bashford *et al.*, 2001).

2.2.5 *Eucalyptus* Canopy arthropods

Knowledge of Eucalyptus canopy arthropod biodiversity: When the co-dominance between *Acacia* and *Eucalyptus* of the entire Australian continent is considered, very little is known about the arthropod biodiversity associated with their crowns (Majer *et al.*, 1997; Williams & Brooker, 1997). A chart outlining the

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scientific literature addressing the canopy, foliage, and trunk arthropod biodiversity of adult *Eucalyptus* in Australia is presented as Table 2.1.

Most research on *Eucalyptus* canopy arthropods has addressed three broadly overlapping themes:

- 1) herbivore and foliage arthropods (Abbott *et al.*, 1992; Abbott & Wills, 2001; Elliot *et al.*, 2002; Fensham, 1994; Fox & Morrow, 1983; Landsberg & Cork, 1997; Lowman *et al.*, 1987),
- 2) comparisons between species or subgenera (Morrow, 1977a, b; Ohmart *et al.*, 1983a, b; Woinarski & Cullen, 1984; Wotherspoon, 1998), or
- 3) biodiversity assessments of the *Eucalyptus* forest canopy in Western Australia, New South Wales, and Tasmania (Elliot *et al.*, 2002; Grove *et al.*, 2002a; Majer *et al.*, 1994; Majer *et al.*, 2000; Recher *et al.*, 1996b; Recher *et al.*, 1993).

Some of the significant findings of these studies are quantitative evidence that:

- 1) arthropod biodiversity in *Eucalyptus* forest canopy may be richer than in other temperate forest ecosystems (Majer *et al.*, 1994),
- 2) the arthropods associated with *Eucalyptus* differ throughout the seasons (Bell, 1985; Lowman & Heatwole, 1992; Recher *et al.*, 1996b),
- 3) herbivory is an important factor in the ecosystem (Landsberg & Cork, 1997; Ohmart, 1984; Ohmart & Edwards, 1991),
- 4) arthropods respond to drought (Bell, 1985),
- 5) some arthropods respond to fire (Radho-Toly *et al.*, 2001; Steinbauer *et al.*, 1998),
- 6) arthropod and bird communities are interlinked (Abbott & Heurck, 1985b; Evelegh *et al.*, 2001; Recher *et al.*, 1996a),

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- 7) there are differences in communities associated with different subgenera (Burdon & Chilvers, 1974a; Morrow, 1977a; Ohmart *et al.*, 1983a; Wotherspoon, 1998), and
- 8) communities vary with altitude (Burdon & Chilvers, 1974b), geographic region (Burgman & Williams, 1995; Majer *et al.*, 1990; Richardson *et al.*, 1999) and within the tree (Majer *et al.*, 1990).

The present research fits into the third theme of biodiversity assessment. Very little research has been done on the biodiversity of *Eucalyptus* without limiting the scope to phytophagous of foliage insects.

There are three outstanding gaps in the knowledge: Very little is known about old-growth trees (Bashford *et al.*, 2001; Majer *et al.*, 1997), the effect of tree age on the arthropod community (Abbott & Whitford, 2001), or the habitats utilized by arthropods in the crowns of mature trees. These three subjects are critically important to forest management in Australia. The clearfelling and replanting of native forests is reducing the number of very old tree with young trees (Lindenmayer *et al.*, 1990). Planned forestry rotations will not allow sufficient time for the regeneration of this resource (Lindenmayer, 1995). It is unknown if old-growth *Eucalyptus* are as important as reservoirs for arthropod biodiversity as they are for vertebrates (Gibbons & Lindenmayer, 2002). Consequently, little is known about the impacts of forest harvesting on *Eucalyptus* canopy arthropods.

Research on Eucalyptus trunk and canopy arthropods: In addition to the foliage, the surface and airspace within the tree crown are inhabited by arthropods. The invertebrate biodiversity associated with the trunks of live, standing *Eucalyptus* trees has been studied on Western Australia (hereafter "WA") by Majer *et al.* (2003) using flight intercept and funnel traps, by Bickel & Tasker (2004) in NSW using sticky traps, by Scarff *et al.* (1998) in WA by hand-collecting, and by Harrison *et al.* (2004) on recently fallen *E. obliqua* using emergence traps on pieces of bark. Larson (2004) climbed *E. grandis* in subtropical rainforest and trapped flying insects with flight intercept and sticky traps.

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Table 2.1 (following pages) Citations in the scientific literature on native Eucalyptus trunk and canopy biodiversity

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Start Date	Primary Author	Location	Time	Eucalyptus species sampled	Method	Primary Authors affiliation or contact	Compartments		Citations
							General Taxonomic Order: "Broad Economic categories"	Between Euc. Species; Within Euc. Species; Other plants	
1982	Abbott	32° 51'11" S 107° 27' E Yarragul 4°, Western Australia	Oct 1982	marginalia, calophylla	Sweep net on foliage up to 44 meters	CALM Dept of Conservation and Land Management, Western Australia	Between Euc. Species; Within Euc. Species	Abbott, I. & Heurck, P.v. (1983b) Tree species preferences of foraging birds in jarrah forest in Western Australia. <i>Australian Wildlife Research</i> , 12 .	
1985	Abbott	34° 05'11" S 116° 10' E Murchison 30° Sep 1985, Jan 1988 Island of Manjimup, Western Australia	Sep 1985, Jan 1988	marginalia	Eucalypt clipping	Morphospecies, Fauna; Freeding group: CALM Dept of Conservation and Land Management, Western Australia	Between Euc. Species; Within Euc. Species	Abbott, I., Burridge, T., Williams, M., & Heurck, P.v. (1992) Arthropod fauna of jarrah (<i>Eucalyptus marginata</i>) foliage in Mediterranean Forests of Western Australia: spatial and temporal variation in abundance, biomass, guild structure and species composition. <i>Australian Journal of Ecology</i> , 17 .	
1990	Abbott	-33° 21' S -116° 09' E Colle, Southwestern Western Australia	Sep 1990	marginalia, calophylla	Branch clipping	Morphospecies; guilds	Between Euc. Species; Within Euc. Species	Abbott, I., Willis, A., Burridge, T., & Heurck, P.v. (2000) Arthropod fauna of crowns of jarrah (<i>Eucalyptus marginata</i>) and marri (<i>Correa pulchella</i>) in mediterranean-climate forests: a preliminary regional-scale comparison. <i>Australian Forestry</i> , 63 .	
1978	Bell	30° 32'15" S 127° 12' E Northern Wales Tablelands, New South Wales	Sep 1978- Aug 1981	Studied as one	Branch clipping	Larvae, beetles, ants, scale insects, hemiptera, isopoda, spiders, and orthoptera.	Spatial fire local; Between Euc. Temporal/Seasonal	Bell, H.L. (1985) Seasonal variation and the effects of drought on the abundance of arthropods in savanna woodland on the Northern Tablelands of New South Wales. <i>Australian Journal of Ecology</i> , 10 .	
1997	Birkel	Caris and Wernham, Northern Tablelands, New South Wales	1997-1998	Unidentified eucalypt species	Sticks/transects on trunk at ground level	Sticks/transects on trunk at ground level	Between Euc. Species	Buckel, D. & Tasker, F.M. (2004) Tree trunk invertebrates in Australian forests: constraining unknown species and complex processes. In: <i>Conservation of Australia's Forests, fauna</i> (ed D. Lunney), pp. 888-898. Royal Zoological Society of NSW, Mosman, New South Wales, Australia.	
1971	Burdon	26° 53'14" S 141° 02' E Bindabul Range Australian Capital Territory	Dec 1971-Oct 1972	robusta, diversifolia, delegatiana, pauciflora, ramosissima, diastylis, tenuissima	Stem and leaf searching	Insect leaf parasites only, Entom Dept. Australian National University, Canberra	Spatial fire local; Between Euc. Species; Within Euc. Species	Burdon, J.J. & Chifford, G.A. (1974) Fungal and insect parasites contributing to niche differentiation in mixed species stands of eucalypt saplings. <i>Australian Journal of Botany</i> , 22 .	
1973	Elliot	41° 19'51" S 142° 32' E Toorloo 34° 51'10" S 147° 32' E East Coast Tasmania	1975-1987	americana, dalzielii, deflexa, glauca, obliqua, ornata, pauciflora, tenuissima	Sweep netting, beating hand collecting, light trapping	Morphospecies	Spatial fire local, Between Euc. Species; Within Euc. Species; Other plant species	Burdon, J.J., Radford, R., Lecren, S.I., & Neild, M.G. (2002) Edge/Forest Diversity in Dry Eucalypt Forests in Eastern Tasmania. <i>Papers and Proceedings of the Royal Society of Tasmania</i> , 136 , 17-32.	
1997	Engelbrecht	-31° 50' S 111° 40' E Swanston Apr 1997-May 1998 Coral Coast, Western Australia	Apr 1997-May 1998	calophylla	Foliage beating from ground	All taxa to order, samples > 1 mm in morphospace	Temporal/Seasonal, Within Euc. Species; Other plant species; Experimental	Engelbrecht, N., Maier, J., & Recher, H. (2001) The effects of reducing bird predation on canopy arthropods of eucalypt (<i>Eucalyptus calophylla</i>) saplings on the Swan Coastal Plain, Western Australia. <i>Journal of the Royal Society of Western Australia</i> , 84 , 15-21.	
1987	Fensham	11° 54' S 130° 41' E Maheno Island, Northern Territory	Sep 1987-Jun 1988	corymbifera, manitensis, tereticornis	Leaf searching foliage beating, sweep sampling	Phytophagous insects only, morphospace	Temporal/Seasonal, Between Euc. Species; Within Euc. Species; Other plant species	Fensham, R.J. (1994) Phytophagous insect-woody sprout interactions in tropical eucalypt forest II. Insect community structure. <i>Australian Journal of Ecology</i> , 19 .	
2002	Grove	42° 3' S 146° 36' E Warrnambool, Victoria, Tasmania	early 2002	obliqua	Chemical knockdown	Order: beetles to morphospace	Temporal/Seasonal, Within Euc. Species; Other plant species	Fensham, R., Taylor, R., Dressen, M., Duran, N., & Richardson, A. (2001) Research on invertebrate assemblages at the Warrnambool Site. <i>Taspress</i> , 13 , 109-118.	
1986	Maier	-32° 5'11" S 116° 04' E Dryandra State Forest, Western Australia, Australia/Kangaroo, Australia/Kangaroo, Australia/West	Mar-Oct 1986	wandoa, accedens, calophylla, marginata	Chemical knockdown; branch clipping	Dept. of Environmental Biology, Curtin Univ of Technology, Bentley, Western Australia	Spatial continental; Spatial within tree, temporal/seasonal. Collecting methods: Between Euc. Species; Within Euc. Species	Grove, S., Basslin, F., Lillywhite, P., & Maurithead, A. (2002) Sampling the high life: Canopy fogging in Tasmanian wet <i>Eucalyptus obliqua</i> forest. In: <i>Int. International Canopy Conference poster</i> . June 2002, Cairns, Queensland.	
1987	Maier	32° 53'10" S 121° 21' E Shelly Bay, River South West (East) 32° 52'04" S 116° 07' E Kalgoolie, Western Australia (West)	Feb 1987-Jan 1988, Apr 1987-Nov 1989	crebra, mollissima, marginata, calophylla	Chemical knockdown;	Morphospecies	Spatial continental; Spatial within tree, temporal/seasonal. Collecting methods: Between Euc. Species; Within Euc. Species	Maier, J.D., Recher, H.F., Penman, V., & Ashton, N. (1990) Spatial variation of invertebrate abundance within the canopies of Australian eucalypt forests. <i>Studies in Avian Biology</i> , 13 , 65-72.	
1986	Maier							Maier, J.D., Recher, H.F., & Posse, A. (1994) Comparison of arthropod species richness in eastern and western Australian eucalypts: a contribution to the species number debate. <i>Memories of the Queensland Museum</i> , 36 , 121-131.	
1987	Recher							Recher, H.F., Maier, J.D., & Gansch, S. (1996) Eucalyptus arthropods and birds: On the relation between foliar nutrients and species richness in Australia. <i>Australian Journal of Ecology</i> , 41 .	
1996	Recher							Recher, H.F., Maier, J.D., & Gansch, S. (1996) Seasonality of canopy invertebrate communities in eucalypt forests of eastern and western Australia. <i>Australian Journal of Ecology</i> , 41 .	

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Starting Year	Primary Author	Lectin	Time	Eucalyptus Species sampled	Method	General Environment	Primary Authors Affiliation or Context	Comparisons	Critiques
1993	Majer	31° 09' 11.7" S 117° 05' E Anney Reserve, Western Australia	Sep 1992-Nov 1993	wandoos, millefiora	Chemical knockdown, branch shaking	Order	Dept of Environmental Biology, Curtin Univ of Technology, Bentley, Western Australia	Spatial continental, Spatial fire	Majer, J.D., Recher, H., & Keats, N. (2000). Canopy arthropod faunas in fragmented agricultural landscapes: In <i>Temperate eucalypt woodlands in Australia: biology, conservation, management and restoration</i> . Surrey Beatty & Sons Pty Ltd., Chipping Norton Australia.
1998	Majer	31° 10' 11.7" S 117° 14' E Namberring Reserve, Western Australia 31° 11' S 117° 23' E Wyndham, Australia	Oct 1998-Oct 1999	wandoos, acrodens, calophylla, marginata	Bush fauna trap & flight intercept panel targeted at trunk, traps placed at ground level	Order	Dept of Environmental Biology, Curtin Univ of Technology, Bentley, Western Australia	Temporal/Seasonal, Collecting methods, Between Euc. species, Within Euc. species	Majer, J.D., Recher, H.F., Graham, R., & Gupta, R. (2003). Trunk invertebrate faunas of Western Australian forests and woodlands influence tree species and season. <i>Austral Ecology</i> , 28 .
1973	Morrison	31° 17' 51.4" S 115° 45' E Dams' Ob. Mt. Kasminna New South Wales	Oct 1973-Mar 1974	petiolaria, stelliflora, paucijuga	Foliage stripping, sweep netting	Phytophagous Coleoptera, Hemiptera and Orthoptera only, morphospecies	Dept of Ecology, University of Minnesota, St. Paul, Minnesota, USA	Temporal/Seasonal, Between Euc. species, Within Euc. species	Majer, J.D., Reiner, H., Hercock, B., & Poole, A. (2002). The canopy, bark, soil and litter invertebrate fauna of the Darling Plateau and adjacent woodland near Perth, Western Australia, with reference to the diversity of forest and woodland invertebrates. <i>Pacific Conservation Biology</i> , 7 , 229-239.
1981	Ohmart	35° 26' 141° 30' E Bumbilla Range, Australian Capital Territory	Dec 1981-Apr 1982	deglupta, paucijuga, drakei	Branch clipping	Spider counts, Phytophagous insects only, morphospecies	CSIRO Forest Research, Canberra, Australia	Spatial fire local, Spatial within tree, Between Euc. species, Within Euc. species	Morrison, P. (1977a). The significance of phytophagous insects in the <i>Eucalyptus</i> forests of Australia. In <i>Arthropods in Forest Ecosystems</i> (ed. W. Maitson) pp. 19-29. Springer-Verlag, New York.
1999	Radio-Tidy	31° 56' 21.5" S 115° 30' E Kalgan Park, Perth, Western Australia	May 1999	margarita, gomphocarpa, cladocalyx (introduced), capillaris, longifolia, erythrocoryne, pilgermannii	Chemical knockdown	Order	Dept of Environmental Biology, Curtin Univ of Technology, Bentley, Western Australia	Spatial fire local, Between Euc. species, Within Euc. species	Ohmart, C.P., Stewart, I.G., & Thomas, J.R. (1983a). Phytophagous insect communities in the canopies of three <i>Eucalyptus</i> forest types in south-eastern Australia. <i>Australian Journal of Ecology</i> , 8 .
1987	Recher	31° 35' E 117° 45' S Killeberri, Wheat Belt Western Australia	Sep 1987		Chemical knockdown	Order	Dept of Environmental Biology, Curtin Univ of Technology, Bentley, Western Australia	Temporal/Seasonal, Between Euc. species, Within Euc. species	Radio-Tidy, S., Majer, J.D., & Yates, C. (2001). Impact of fire on leaf nutrients, arthropod fauna and herbivory of native and exotic eucalypts in Kings Park, Perth, Western Australia. <i>Austral Ecology</i> , 26 , 500-506.
1979	Weiszaki	16 sites across state of Victoria	May 1979-Jun 1982	31 species, listed in final column > 2	Branch clipping	Invertebrates larger than 3mm. Divided into 13 categories, mostly order + family	Dept of Zoology, Monash University, Victoria, Australia	Spatial continental, Spatial fire	Recher, H.F., Major, J.D., Gowing, G., & Scott, N.L. (1993). Canopy invertebrate communities in woodland: a comparison of morning and afternoon samples by chemical knock-down. <i>Magpie Research Centre Journal</i> , 11 .
1995	Wetherpoon	42° 52' 30" S 147° 16' 48" E Mt. Wellington, SW of Hobart, Tasmania	Nov 1995-Mar 1996	globoflua, viminalis, oblonga, pulchella	Branch clipping	Phytophagous insects only, morphospecies, Feeding group	Dept of Geography and Environmental Studies, Univ. of Tasmania, Hobart, Tasmania	Between Euc. species, Within Euc. species	Major, J.D., Recher, H.F., & Scott, N.L. (1993). Patterns of invertebrates on foliage in forests of south-eastern Australia. <i>Australian Journal of Ecology</i> , 9 .
1979	Yen	35° 42' S 141° 57' E Lake Abbeys, The Big Desert, Victoria	Sep 1979-Dec 1983	domosa, secunda, querzata	Foliage beating	Family, Feeding Group	Museum of Victoria, Melbourne, Victoria	Spatial fire local, Between Euc. species, Within Euc. species	Wetherpoon, K.P. (1998). Patterns of phytophagous insect herbivory and abundance on juvenile regrowth of <i>Eucalyptus</i> subgenera occurring in southeastern Tasmania. <i>Australian Journal of Ecology</i> , 23 , 430-442.
									Yen, A. (1988). Overstorey invertebrates in the Big Desert, Victoria. In <i>Mediterranean Landscapes in Australia: Native Ecosystems and their management</i> (eds J. Noble & R. Bradstock), pp. 285-299. CSIRO, Melbourne.

Table 2.1 (previous pages) Citations in the scientific literature on native Eucalyptus trunk and canopy biodiversity

Trunk and canopy biodiversity research in *Eucalyptus* has generally focused on the “active” collecting rather than “passive” trapping. Only two published trunk studies have used trapping techniques (Bickel, 2003; Majer *et al.*, 2003). Bagging, beating, or sweep-netting foliage has been used to compare differences in the invertebrate fauna between tree species (Abbott *et al.*, 1992; Abbott & Wills, 2001; Evelegh *et al.*, 2001; Majer *et al.*, 1996; Majer & Recher, 1988; Morrow, 1977a; Ohmart *et al.*, 1983b; Yen, 1989) and to test ecological effects such as fire, predation or drought (Bell, 1985; Evelegh *et al.*, 2001; Radho-Toly *et al.*, 2001; Yen, 1989). Wotherspoon (1998) reported on the phytophagous foliage insects of *E. obliqua* in comparison to other *Eucalyptus* species.

Canopy fogging, or insecticide knockdown, has been performed on *Eucalyptus* in W.A. and New South Wales by Recher *et al.* (1996b) and Majer *et al.* (1990). In Tasmania, canopy fogging collections have been taken from mature specimens of *E. obliqua* within 5 km of the trees studied by the present research (Bashford *et al.*, 2001; Grove *et al.*, 2002a). Yen & Lillywhite (1990) performed a preliminary fogging project in Tasmanian rainforest plants, which are often found growing near or with *Eucalyptus* (Kirkpatrick & Backhouse, 1981).

The foliage and trunk biodiversity of the southwestern WA dry sclerophyll trees, *E. marginata* and *Corymbia callophylla* have been researched by several different projects and techniques, mostly in comparison to different *Eucalyptus* species (Abbott *et al.*, 2000; Majer *et al.*, 1990; Majer *et al.*, 2003; Radho-Toly *et al.*, 2001). No comparable body of research exists for *Eucalyptus* in the rest of the continent.

In sclerophyllous forests throughout the world, fire regularly disturbs the ecological community (Pielou, 1979). Radho-Toly *et al.* (2001) investigated the responses to fire of arthropods on native and exotic *Eucalyptus* in W.A. They linked a higher abundance on burnt trees to higher nutrient levels in the leaves. Steinbauer *et al.* (1998) examined the preference of a Hemipteran pest to fire coppiced *Eucalyptus* trunks over intact stems.

2.2.6 Previous research on the link between structure and arthropod biodiversity

Branches in crown are analogous to trees in forest: Halle (1995) considers branches of a tree as independent pieces sprouting from similar pieces. Ishii and McDowell (2001) analysed the branch distribution within a *Pseudotsuga* crown as corresponding to trees in a forest stand. In a forest management setting, older, mixed-age forests containing dead trees are considered to be more desirable than younger single-cohort plantations for biodiversity conservation (Seymour & Hunter, 1999). A parallel situation may exist within the crown of individual trees, with those trees containing dead branches fostering more biodiversity than a simpler tree (Paviour-Smith & Elbourn, 1993). Standing dead trees (McComb & Lindenmayer, 1999) and dead branches (Schiegg, 2001) may be comparable, similar habitats.

This analogy can be taken further: shed branches may be like falling trees, branches in poor health like dying trees, old healthy branches like older trees, and epicormic resprouts like seedlings. Sillett & Van Pelt (2000b) found the outstanding number of reiterated secondary trunks in a *Sequoia* crown to be best described as a “forest canopy” of its own. The relationships between forest structures and forest biodiversity may therefore apply at the finer scale of the tree crown.

Surrogate measures of complexity: Habitat complexity is often presented as a predictor of biodiversity (Tews *et al.*, 2004), but is often inadequately defined (Loehle, 2004). Quantification of the crown structure and the presence of distinct structural attributes can be surrogate measures of geometric, physical complexity (Loehle, 2004). (Anand & Orloci, 1996) comment that complex things require more effort to describe than simple things. In the context of the current structure, the amount of information need to describe different trees is quantifiably measured (in surrogate) by the computer file sizes of 3-d virtual illustrations.

The abundance or presence of a certain feature, or attribute, in a landscape may be considered to add complexity to it. For example, the abundance of trees, and the presence of volcanos, islands, mountains, and valleys on one island might make it more appealing to the geologist and the biologist than an island with none of these features. Similarly, the crown of a tree with abundant branches, epiphytes, litter collection, and shards of broken wood may be considered to be more complex than a

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tree with few branches and none of these features. For the purposes of this study, complexity is measured in surrogate by characteristics of branch architecture, and the presence of structural features.

Linking structure to biodiversity: Lawton (1983) highlights five key components of plant architecture that determine insect diversity: size, growth form, seasonal development, variety of above-ground elements, and persistence of individual components. In this study, the size, growth form, and variety of elements is quantified.

In the framework of the current study, the effects of age and crown structure may be indistinguishable. Like all organisms, *Eucalyptus* follows a distinct ontogeny (Jacobs, 1955). Different structural attributes may develop together as the tree ages. Research on their influence may be confounded at a tree level by their interaction.

Lawton (1983) presents two approaches to explaining the higher diversity detected in larger, more complex plant types. First, more complex plants have more areas to be colonized by insects. Second, more complex plants offer larger numbers and types of spatial situations and resources. The former can be addressed by looking at tree size and shape through its crown structure, and the latter can be addressed by looking at the presence or absence of different features.

Lawton's (1983) approach 1 – Complex trees offer more area for arthropods: Strong *et al.* (1984) present a comparison of broad growth forms and show a descending trend in phytophagous insect diversity from trees through shrubs, perennial herbs, annual herbs, and monocotyledons. They describe these growth forms as a descending trend of architectural complexity.

A further refinement of the concept could be used to compare different forms of the same species, or even within the same trees. Fowler (1985) investigated the phytophage fauna on *Betula* seedlings, shrubs, and trees. His study found little significant difference in composition and richness between the three, except for a winter sampling period in which seedlings had the poorest fauna. He postulates that the proximity of the three size classes to each other could foster recruitment of the fauna from the trees to the smaller classes, and that a lack of overwintering sites on seedlings could be responsible for difference in winter.

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Experiments on plant structure and its effect on spider communities has shown that structural complexity supports spider abundance (Rypstra *et al.*, 1999). Sundberg & Gunnarsson (1994) and Gunnarsson (1990) investigated the relationship of spider abundance to foliage needle structure *Picea* branches. Densely needled branches contained more spiders, and experimental removal of needles resulted in a decrease in numbers.

Similarly, Halaj *et al.* (2000) experimentally modified the foliage habitats of *Pseudotsuga* by removing needles, removing branches, and tying branches together. They found several differences in predator and prey relationships, and conclude that the habitat structure within the tree may influence the animal food web in a “bottom-up,” fashion, in which changes in prey affect the predators.

Structures at a scale finer than the leaf may influence arthropod composition. Peeters (2002) examines the presence of specific leaf attributes and their relationship with the function feeding group community. Plants with leaf defences such as spines or thickened cuticles had lower levels of herbivores.

Research in conifers of Western North America has identified several relationships between crown structure and epiphyte biodiversity. McCune *et al.* (2000) examine the lichen biodiversity in several arboreal microhabitats. Clement & Shaw (1999) and Sillett (1999) report on the effect of branch-level descriptor variables such as branch size and crown depth on arboreal resources such as epiphytes and soil collections. Arthropod communities utilize these resources, and subsequently are affected by the tree structure (Nadkarni & Longino, 1990; Prinzing, 1997).

Larger trees have more habitat area: A larger tree may represent a larger “island” to arthropods (MacArthur & Wilson, 1967). Southwood & Kennedy (1983) compare the geographic range of trees to the size of an island. The title under which they publish their theory is “Trees as islands.” An alternative analogy views individual trees as islands. An appropriate title for this view would be “A tree as an island.”

A basic principle of island biogeography is that larger islands support more species (MacArthur & Wilson, 1967). In the present study, the old trees were significantly larger than the 100yr trees in several measures. Height, crown volume, total foliage, surface area, and wood volume were significantly greater in the old

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trees. If these measures are analogous to the 2-dimensional land area of an island, then richness should therefore be greater in the old trees. Other possible measures of size include the abundance of fruits (Andersen & New, 1987) or volume of dead wood (Schiegg, 2001). The choice of a measure of scale is discussed in detail in the canopy arthropods methods section.

The relationship between the size of an island and the number of species of a taxa is presented by MacArthur & Wilson (1967) as

$$\# \text{ of species} = C * \text{Area}^Z$$

where

C is a constant which varies between taxa,

Z is a constant which varies with habitat heterogeneity from the theoretical expected value of 0.27 for a population with a lognormal distribution, and

Area is a two-dimensional measure of habitat size.

Other measures of size could substitute for island land area. For trees, it may be crown volume, foliage mass or surface area. As discussed above, none of these measures are satisfactory.

An important observation is that usually $Z < 1$. If $Z = 1$, then species richness would scale linearly with size. In the context of trees, a tree twice as big as another (with no differences other than size) would therefore have twice the number of species within it. The definition of “twice as big” is problematic and dependent on the organisms of interest. An appropriate measure of scale is difficult to choose (see section 7.6). Abundance might (but not necessarily) scale linearly with the available quantity of the appropriate habitat, but because $Z < 1$, species richness increases more slowly than area.

Lawton's (1983) approach 2 – Complex trees have a variety of spatial situations and resources: Carey (1996) writes that, for arboreal mammals, “all attributes of canopies could have biological importance.” The same statement applies to arboreal arthropods.

The invertebrate biodiversity associated with several different arboreal habitats has been investigated in several studies. Majer *et al.* (1997) review the literature on habitats within *Eucalyptus* forests. When an animal community is found

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to be associated with a certain feature, it can be assumed that the loss of that feature would affect that community. These include, but are not limited to:

1. foliage and live branches ((Abbott *et al.*, 2000; Basset, 2001; Clement *et al.*, 2001; Lowman *et al.*, 1993; Peeters, 2002; Schowalter, 1995; Winchester, 1997; Woinarski & Cullen, 1984; Wotherspoon, 1998))
2. dead wood (Hanula & Franzreb, 1998; Paviour-Smith & Elbourn, 1993; Ranius, 2000; Ranius & Hedin, 2000; Schiegg, 2001)
3. hollows in the trunk and branches (Harrison *et al.*, 2004; Ranius & Wilander, 2000)
4. flowers, fruit and cones (Abbott & Heurck, 1985a; Andersen & New, 1987; Jaffe *et al.*, 2003; Kirmse *et al.*, 2003; Majer *et al.*, 1997; Roubik *et al.*, 2003; Shea, 1989; Turgeon *et al.*, 1994)
5. bark and branch surfaces (Bickel & Tasker, 2004; Buchs, 1990; Hanula & Franzreb, 1998; Heterick *et al.*, 2001; Majer *et al.*, 2003; Moeed & Meads, 1983; Nicolai, 1986; Nicolai, 1995; Proctor *et al.*, 2002)
6. fungal hyphae and fruiting bodies, which may actually owe its presence in the tree to a saprophytic animal (Harrison *et al.*, 2004; Komonen 2001; Sippola, 2001)
7. individual leaf structural features (Lill & Marquis, 2004; Peeters, 2002; Shaw & Walter, 2003; Walter & O'Dowd, 1995)
8. suspended soils (Nadkarni & Longino, 1990; Paoletti *et al.*, 1991)
9. vascular epiphytes (Benzing, 1983; Coxson & Nadkarni, 1995)
10. non-vascular epiphytes (Prinzing & Wirtz, 1997; Rhoades, 1995)
11. vines (Odegaard, 2000)
12. charcoal on tree trunks (McQuillan, personal communication)
13. water-filled tree hollows, or phytotolmata ((Kitching & Callaghan, 1982))
14. leaves bound by caterpillar-silk (Lill & Marquis, 2004)

Other features with the potential to foster animal biodiversity include sap flows, cambium wounds, cracked wood, suspended bark ribbons, branch fusions, and rubbing points between branches.

Bickel & Tasker (2004) argue for consideration of unknown fauna in land management. The presence of structural attributes in a tree suggests the potential to

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harbour more animal diversity than their absence would. Cryptic ecological associations, chance probability, and the time scale involved in the formation of these structural attributes are factors to be considered in forest management.

Age of elements: The age of elements within a tree may alter its role for animals in the arboreal ecosystem. Furthermore, structures within a tree may grow, shrink, or stay the same size as the tree ages. Branches sprout, grow and die in a microcosm of the entire tree (Attiwill, 1962; Jacobs, 1955; Lowman, 1992). Dead branches in a tree, like dead trees on the forest floor, change as they age. As logs and coarse woody debris age, they are utilized by different animal communities (Grove *et al.*, 2002b; Irmler *et al.*, 1996; Yee *et al.*, 2001).

Young leaves in a tree are chemically and physically distinct from old leaves (Landsberg, 1990). Studies by Lowman (1985) and Peeters (2002) found higher abundances of herbivores on softer, greener young foliage than harder, lignified mature foliage. Waltz & Whitham (1997) compared resprout suckers and mature foliage within *Populus* trees, and found significantly more insect species on mature foliage. They relate their findings to a larger scale view, and comment on the influence of developmental heterogeneity in single trees may contribute to the biodiversity in a stand of trees. Within a tree crown, the presence of both younger and older foliage together may foster animal diversity.

Tree trunks in older *Eucalyptus* trees are often decayed and harbour fungal hyphae, whereas younger tree trunks may not (Barry *et al.*, 2000; Harrison *et al.*, 2004; Wardlaw & Neilsen, 1999). Fungal biodiversity is interlinked with animal biodiversity (Komonen 2001).

Hollows develop and grow over time, and are suitable for different animals at different stages (Gibbons & Lindenmayer, 2002; Mackowski, 1984). Fungal hyphae can develop fruiting bodies (May & Simpson, 1997). Water filled tree-hollows can dry out or overflow (Kitching & Callaghan, 1982). Buds can flower, fruit, and disperse (Andersen & New, 1987). The tree can be burnt (Radho-Toly *et al.*, 2001). Jukes *et al.* (2002) found an increase in saproxylic beetles in older British *Pinus* plantations. *Pinus* may carry more dead wood in its crown as it ages, and similarly, older branches in trees may contain more dead branchlets.

2.3 Synthesis of previous research

Crown structural mapping addresses the empirical shape of individual trees.

Mapping measures the actual expression of the trees innate architectural model (Section 2.2.1). *Eucalyptus* crown structure has been studied from various aspects. Jacobs (1955) addressed stages of crown development and senescence; a theoretical branch competition framework utilising his stages and the analogy of branches to trees presented by Ishii & McDowell (2001) is presented.

Empirical mapping of Eucalyptus trees has been done at the level of biomass (Lowman *et al.* 1987a), leaf position (Kelly *et al.* 2004), tree height (Mifsud, 2003), hollow locations (Mackowski 1984), and the branch structural level (Van Pelt *et al.* 2004b).

Canopy arthropods have been studied by several methods, but few studies have compared the arthropod fauna associated with different aged forests or trees. *Eucalyptus* canopy arthropods have been studied in respects to herbivores, faunal composition differences between species, and biodiversity assessments comparing eastern and Western Australia.

The link between structure and arthropod biodiversity is discussed in reference to the analogy of branches in a tree as trees in a forest. Structural complexity, tree size, habitat presence, and the age of tree elements are all proposed as factors determining arthropod composition and biodiversity in trees.

3) Study Design and Site

The primary objectives of the research were to compare the differences in crown structure and canopy arthropod biodiversity of 100 year old and old growth wet sclerophyll *Eucalyptus obliqua* trees. The study site and design were selected to most effectively approach this objective.

The Warra Long Term Ecological Research Site (hereafter “LTER”) was chosen to utilize and integrate with the body of previous scientific research performed there (Alcorn *et al.*, 2001; Allen, 2001; Beaulieu, 2004; Brown *et al.*, 2001; Coops, 2001; Hickey *et al.*, 2001). In a multi-aged forest, old-growth trees and 100 year old trees were selected in nearby pairs. The age classes were coexisting and readily distinguishable by basal girth (Alcorn *et al.*, 2001). A confounding intermediate age class was not present. Selecting in pairs controlled for any potential environmental differences in fauna within the study area (Kirkpatrick, 2004; Richardson *et al.*, 1999; Schowalter, 1995).

3.1 Study Subject and Site

3.1.1 Tasmanian wet sclerophyll forests:

The wet sclerophyll forests of Tasmania are largely dominated by *E. obliqua*, *E. regnans*, *E. delegatensis*, and *E. globulus* (Forest_Resources, 1979). These are the tallest and most massive angiospermous forests on Earth (Hickey *et al.*, 2000; Kostoglou, 2000; Mifsud, 2003; Van Pelt *et al.*, 2004), and are second in height only to the coniferous forests of western North America (Van Pelt, 2002). Age cohorts of *Eucalyptus* originate from fire events (Ashton, 2000; Gill, 1997; Jacobs, 1955). Fires of insufficient intensity to cause complete mortality generate a cohort of *Eucalypts* seedlings (Lindenmayer *et al.*, 2000). Successive fires will therefore create multiple aged forests. In the absence of regular fires, high fuel loads in the wet sclerophyll forests can enable uncontrollable conflagrations, a fact well noted by residents of forested areas of Hobart (Gill, 1997; Marsden-Smedley & Slijepcevic, 2001).

In the absence of fire, temperate rainforest vegetation develops beneath the *Eucalyptus* canopy (Gilbert, 1959). The rainforest is floristically linked to the ancient supercontinent of Gondwanaland (White, 1986), and supports an herbivorous

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arthropod fauna distinct from that of the more recent *Eucalyptus* trees (McQuillan, 1993; Pielou, 1979; Yaxley, 2000).

Clearfelling, burning, and seeding of *Eucalyptus* forests is the most widely applied silvicultural method, although other methods are being trialled (Hickey *et al.*, 2001). The management of these forests for economic gain is the source of heated, ongoing controversy and is considered a matter of national significance (Beale, 2003; Forestry Tasmania, 2003; Green, 2003; Lindenmayer *et al.*, 1990).

3.1.2 *Eucalyptus obliqua*

E. obliqua is the type species for the *Eucalyptus* genus. The holotype was collected by Captain Cook's 1777 expedition to Bruny Island, 50 km east of the study site, and described by Charles-Louis L'Heritier de Brutelle in 1788 (Costermans, 1981).

E. obliqua is one of the tallest and largest trees flowering plant species in the world, after the closely related and co-existing *E. regnans*, and is the most widespread eucalypt in Tasmania (Figure 3.1) (Kirkpatrick & Backhouse, 1981; Williams & Potts, 1996). *E. obliqua* is known as "brown-top stringybark" in Tasmania, and as "messmate" in Victoria (Forest_Resources, 1979). It is more flexible in its environmental requirements than *E. regnans*, and will dominate it on less fertile sites (Ashton, 2000; Kirkpatrick, 2004).

It is a non-lignotuberous member of the Monocalyptus "ash" subgenus (Costermans, 1981). Characteristic flakes of flammable dead phloem cells cover the trunk and larger branches (Jacobs, 1955).

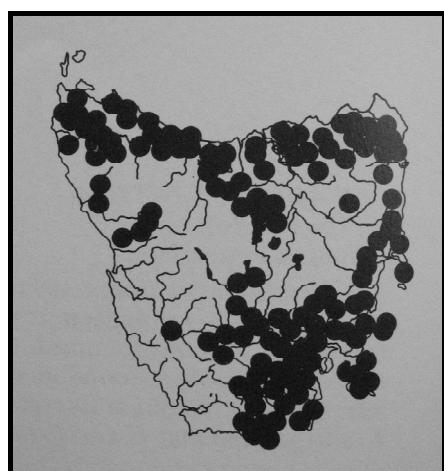


Figure 3.1: Distribution of *E. obliqua* in Tasmania, from Kirkpatrick & Backhouse (1981)

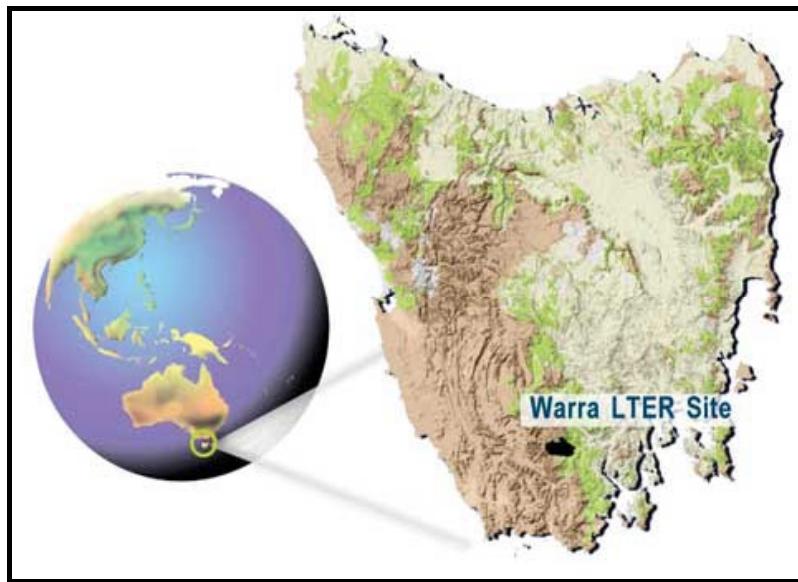


Figure 3.2 : Location of Warra LTER in southern Tasmania. Hobart is located beneath the “E” in “LTER”. Graphic from www.warra.com

3.1.3 Warra Long Term Ecological Research Site

Warra LTER is a 16,000 hectare site (Figure 3.2) straddling the border of the Southwest World Heritage Area 60 km southwest of Hobart (Brown *et al.*, 2001). It is primarily covered by virgin and managed *E. obliqua* forests, with additional areas of temperate rainforests and buttongrass moorland (Corbett & Balmer, 2001). The south and east boundaries follow the Huon and Weld rivers. At the confluence of the Huon and Picton rivers in the southeast corner, the Tahune Airwalk (offers tourists the opportunity to view *E. obliqua* trees from a canopy walkway (Figures 3.3, 3.4). Forestry Tasmania maintains a web site with information, metadata, and species lists from the LTER at <http://www.warra.com>.

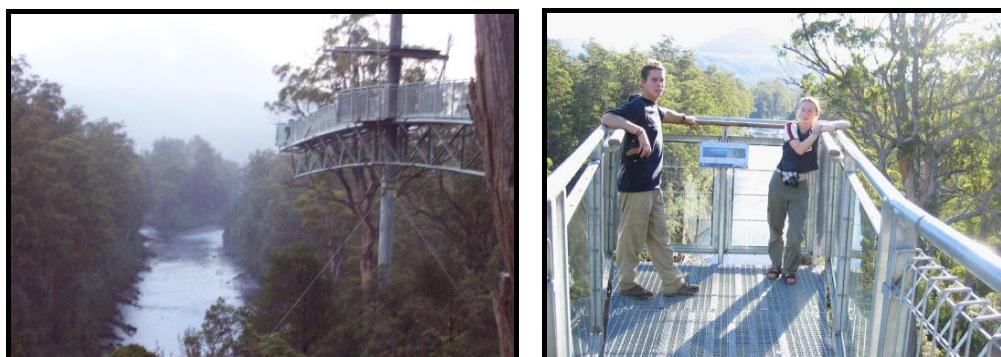


Figure 3.3(left): The Tahune Airwalk offers a canopy-level view of *E. obliqua* similar to the study trees.
Several illustrative photographs were taken from this platform.

Figure 3.4 (right): Robert Junker and Elaine Vale on the Tahune Airwalk.

3.1.4 West end of Manuka Road

Manuka Road runs upstream on the north banks of the Huon River and ends 10km west of the Airwalk (Figure 3.5). This site is the only road-accessible region of contiguous virgin forest in Warra. Several other studies have been conducted along Manuka Road, including investigations of: a) sustainable silvicultural methods (Hickey *et al.*, 2001; Neyland *et al.*, 1999) b) the association of beetles and fungus in *E. obliqua* (Harrison, 2004; Harrison *et al.*, 2004), c) chemical knockdown of arboreal arthropods (Bashford *et al.*, 2001; Grove *et al.*, 2002), and d) the arthropod biodiversity of fallen logs (Grove & Bashford, 2003; Yee *et al.*, 2001).

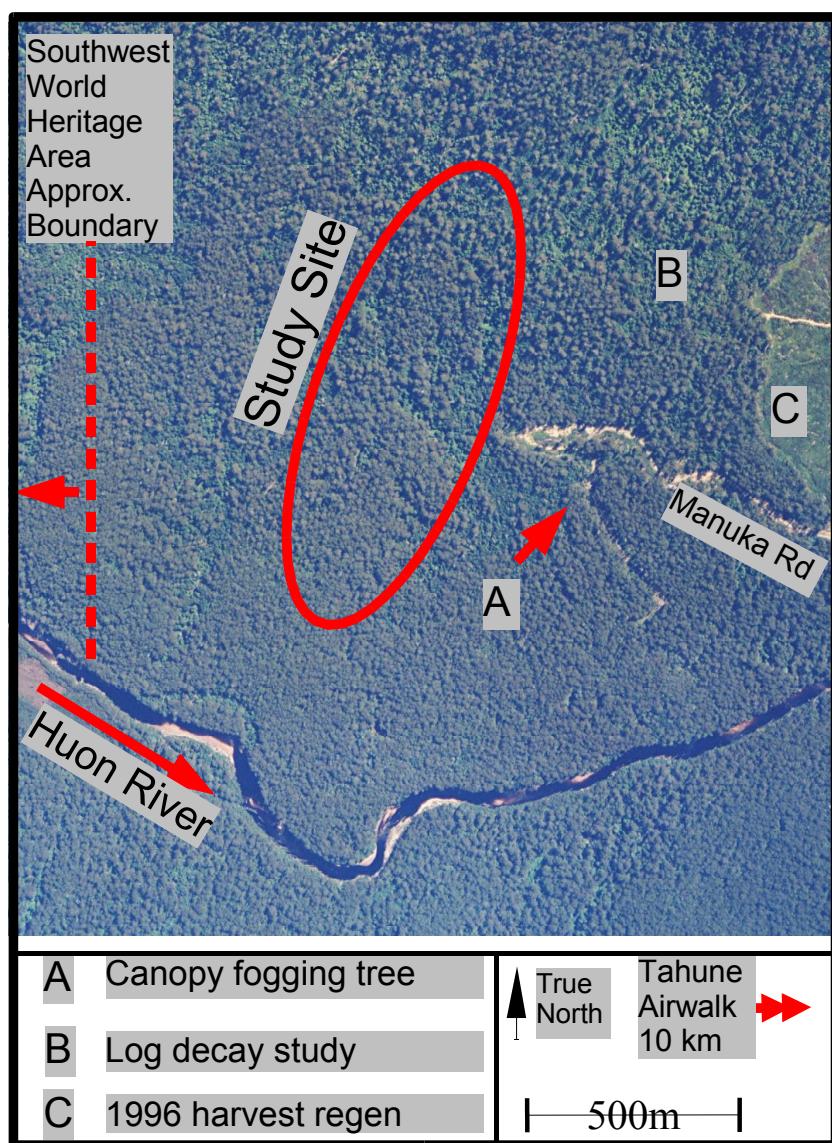


Figure 3.5: Aerial photograph of the west end of Manuka Road, Warra LTER, Tasmania. Aerial photograph supplied by Forestry Tasmania. Note the large crowns of old-growth trees in the northern section, and the finer grain of the younger trees in the southern section.

3.1.5 Topography and Geology

The trees used in the study were located within a 2 km² region immediately west of the road's western extent, on the southern slopes of Mt. Frederick Plateau. Study trees were between 100 and 300 m altitude. The Huon River flows eastward 1 km south at ~75 m altitude. The area is well drained, steep, and southern facing (250 m altitude gained in 1 km). All creeks drain southwards to the Huon River. All creeks were flowing throughout the year. The geology is composed of igneous Jurassic (~170 million years old) dolerite overlaying the Parmeener supergroup of Permian mudstone sediments (~300 million years) (Laffan, 2001). Pieces of mudstone with fossils of brachiopods and bryozoan *Fenestella* were visible where forest soil had been disturbed by landslide or uprooted trees (White, 1986). A small limestone outflow cave was found 1km west of the study site.

3.1.6 Vegetation

The uppermost forest stratum consists of very tall wet sclerophyllous *E. obliqua*, with *E. regnans* present in the northern section (Figures 3.7 and 3.8). *Eucalyptus* tree crowns do not overlap, forming an open canopy from 30-80 m in height.

Figure 3.7 (left): 100yr E. obliqua cohort as seen from Manuka road (MW)

Figure 3.8 (right): Old-growth E. regnans present in the northern section of the study site, with R. Junker descending.

Beneath the *Eucalyptus* trees, a middle stratum of rainforest trees 10-30 m tall forms a closed canopy (Figures 3.9 and 3.10). *Nothofagus cunninghamii*, *Atherosperma moschatum* and *Pomaderris apetala* were the most abundant trees, followed by *Acacia melanoxylon*, *Eucryphia lucida*, *Phyllocladus aspleniifolius*, and *Acacia dealbata*. Immediately beneath this stratum were *Dicksonia antarctica* treeferns 1-4 m tall. Patches of the study site were pure rainforest consisting of these trees without *Eucalyptus*. Fallen logs of large *Eucalyptus* and other smaller trees were abundant on the forest floor (Figure 3.11).

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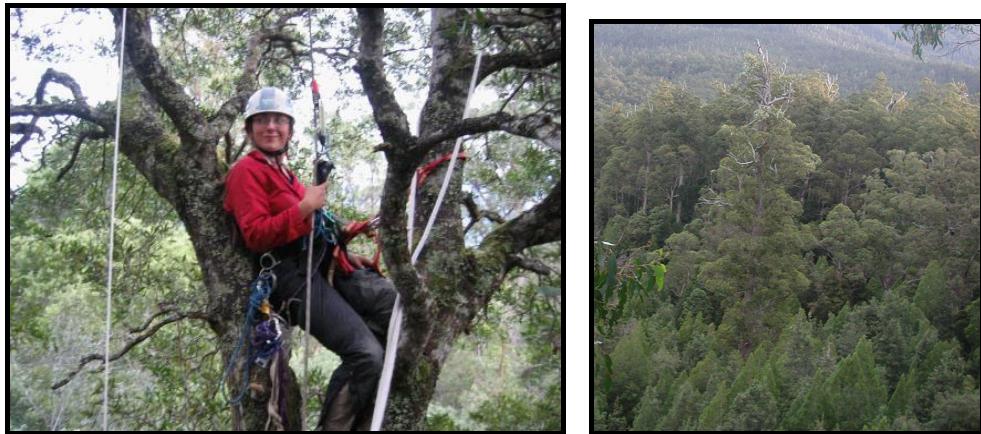


Figure 3.9 (left): *Acacia melanoxylon* was often encountered growing immediately below *E. obliqua*. M. Whitman shown examining epiphytic bryophytes

Figure 3.10 (right): The dead tops of old *E. obliqua* tower above the pointed crowns of *Atherosperma moschatum*. (MW)

Understorey vegetation included *Tasmannia lanceolata*, *Monotoca glauca*, *Acacia verticillata*, *Anodopetalum biglandulosum*, *Olearia argophylla*, *Cenarrhenes nitida*, *Anopterus glandulosus*, *Pimelea drupacea*, *Gahnia grandis*, *Urtica incisa*, *Polystichum proliferum*, *Hymenophyllum* spp. and numerous bryophytes (Figures 3.12, 3.13, 3.14) (Collier *et al.*, 1992; Corbett & Balmer, 2001; Costermans, 1981; Forest_Resources, 1979; Jarman & Kantvilas, 2001a, b; Kirkpatrick, 2004; Kirkpatrick & Backhouse, 1981).



Figure 3.11 (left): Burnt Eucalyptus stumps are frequently encountered as vertical shards. (MW)

Figure 3.12 (right): 100yr *E. obliqua* trunk and *Dicksonia antarctica*



Figure 3.13 (left): *Nothofagus cunninghamii* (left edge) and *Phyllocladus aspleniifolius* (right edge, dark foliage) near the base of tree 4

Figure 3.14 (right): *Dicksonia antarctica* near old tree 12, with Robert Junker on a fallen log

3.3 Study design

3.2.1 Age comparison

Trees originating from fires around 1898-1906 (“100yr”) were compared to veteran older neighbouring trees that survived that fire event (“old”.)

E. obliqua establishes after fire events (Kirkpatrick *et al.*, 1988). In Tasmania, the repetition of small-scale burning heterogeneity and the survivorship of individual trees creates multi-aged forests with cohorts originating from each fire event (Alcorn *et al.*, 2001). Older eucalypts were invariably rotten through the centre, masking dendrochronology through ring counts (Allen, 2001; Hickey *et al.*, 1998). No seedlings of *Eucalyptus* were ever seen in the forest. *Nothofagus* seedlings were common. In the absence of fire, the rainforest vegetation was regenerating and the sclerophyll vegetation was abiding for the next burn.

The age of the *E. obliqua* trees was inferred from the regional fire history compiled by Hickey *et al.* (1998). Old trees were inferred to range between 300 and 450 years of age, originating from a fire before recorded history (Figure 3.15). The 100yr trees germinated after fires in the period of 1898 to 1906 (Hickey *et al.*, 1998). The natural fire rotation has been determined to be 448 years long (Hickey *et al.*, 1998).

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Alcorn *et al.* (2001) warns of inferring wet sclerophyll *E. obliqua* age by diameter, but at this site size differences between the two age cohorts were sufficient for ready identification. Unlike other regions at Warra, the west end of Manuka road does not appear to have burnt in 1936 or at any other time since 1898-1906.

This survivorship of old trees contrasts with certain areas of *E. regnans* forest in Victoria, in which a single intense fire, followed by a long exclusion of fire, causes total mortality of a stand. This leads to even-aged stands of *Eucalyptus*, such as seen at Wallaby Creek, Victoria (Figure 3.16) (Ashton & Chinner, 1999; Mifsud, 2003).



Figure 3.15 (left): Matt Cracknell standing next to an old tree showing charcoal at its base. This indicates that the tree had survived a fire. Most old trees were observed with these markings

Figure 3.16 (right): Even-aged stand of *E. regnans* at Wallaby Creek, Victoria. Note the intra-cohort variation of stem diameters.

3.2.2 Tree selection methods

Eight pairs of *E. obliqua* trees were studied from August 2003 to April 2004 (Figures 3.17, 3.18, 3.19, 3.21). Each pair consisted of a 100yr old tree and an old tree. The two trees were always less than 50 m from each other, and all eight pairs were within a 2 km² region. Climber safety and tree health were the primary selection criteria. Because of the greater abundance of 100yr trees and the decayed nature of old *E. obliqua* (Jacobs, 1955), location of appropriate old trees guided selection of 100yr trees. By definition, the old trees had survived or avoided the fire events in the years 1898-1906 that gave rise to the 100yr cohort (Alcorn *et al.*, 2001; Allen, 2001;

Gill, 1997). The fire records compiled by Alcorn *et al.* (2001) found no evidence of fire in the location since then.



Figure 3.17 (left): The crown of 100yr tree 1

Figure 3.18 (right): The crown of old tree 8 (MW)

3.2.3 Study tree description

The old trees in the study were commercially overmature veterans (Figure 3.20) (Jacobs, 1955). They were no longer alive at the top and had lost most of their original branches, but still retained a number of original branches in addition to more recent epicormic growth. Many of the living branches in the old trees were not the original branches, but rather were mature epicormic shoots arising from the trunk or the basal portions of original branches (Figures 3.24, 3.25). These successful resprouts, especially when lower on the tree trunk, probably grew immediately after a fire that the tree survived. The old trees were very likely to have a hollow rotten centre (Gibbons & Lindenmayer, 2002). The branches on old trees were often decayed or hollow.

The 100yr trees possessed their original crowns with a live terminal shoot. They were vigorously growing upwards, but were often shaded by the old trees. The 100yr trees were always taller than the understorey trees (*Acacia melanoxylon*, *Nothofagus cunninghamii*, *Pomaderris apetala*, *Atherosperma moschatum*) standing nearby. Dominant trees possess an abundance of sturdy branches suitable for access.

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Subdominant trees generally had no suitable branches for climbing, and exhibited more kinks and irregularities in their trunk. All trees used in the study represented the dominant, least decayed members of their cohort.

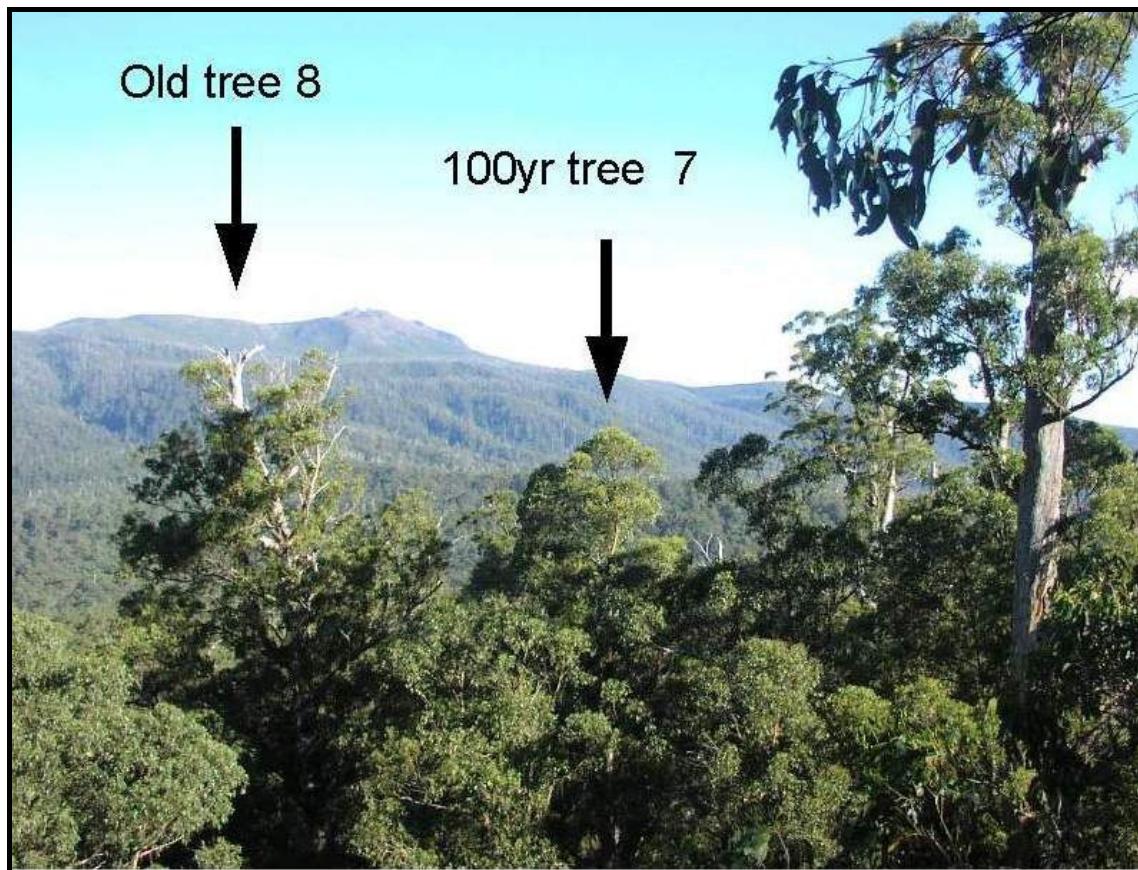


Figure 3.19: The study pair of 100yr tree 7 and old tree 8. Note the difference in crown shapes. Tree 7 is rounded and vigorous, whereas tree 8 is snag-topped and in decline. Mt. Picton is in the background across the Huon River, in the World Heritage Area. (MW)

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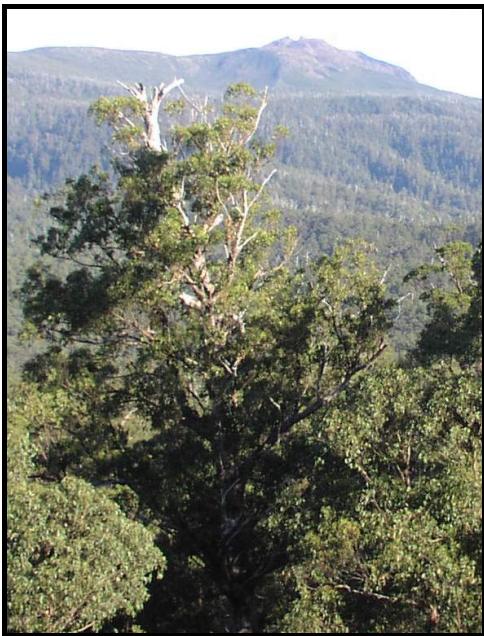


Figure 3.20 (left): Closer view of dead top of old tree 8 with an epicormic crown beneath. The "V" shape of the funnel drift fence is just visible on the trunk at the bottom of the photograph (MW)

Figure 3.21 (right): looking downwards from tree 1, both age cohorts are visible. An old tree is in the upper right corner, and the rest of the stems are 100yr trees. Note cave at base of old tree (R. Junker)

Judging by the lack of stringy bark in the upper crown of some study trees (especially old trees 3 and 4), it is possible that these are hybrids with *E. regnans* (Figures 3.22, 3.23) (Kirkpatrick & Backhouse, 1981; Williams & Potts, 1996).



Figure 3.22 (left): The upper trunk of old tree 4 is smooth barked. This may indicate hybridization with *E. regnans*. Sue Baker is shown descending.

Figure 3.23 (right): The smooth bark on the upper trunk of old tree 3 may indicate hybridization with *E. regnans*. Brendan Kayes is shown recording data



Figure 3.24 (left): Old *E. obliqua* with a secondary epicormic crown (MW)

Figure 3.25 (right): Old *E. obliqua* with snapped trunk, and a single large epicormic branch

3.2.4 Study tree identification

Each study tree was assigned a number (Table 3.1). With two exceptions, study pairs were made of consecutively numbered trees. The 100yr trees were given an odd number and the old trees given the even number immediately following. The first four trees were named in a pilot study and contradict this numbering scheme. Trees 1 and 2 are 100yr trees, and 3 and 4 are old trees. Renumbering these trees for clarity's sake was deemed to be too much of a risk to data integrity, and therefore the contradictory numbers were retained.

Study Pair	A	B	C	D	E	F	G	H
100yr Tree Number	1	2	5	7	9	11	13	15
Old Tree Number	3	4	6	8	10	12	14	16

Table 3.1: Tree identification numbers for each study pair

3.2.5 Rope techniques

Access to the trees was gained by launching a crossbow bolt trailed by fishing line over a sturdy branch. (Figures 3.26, 3.27, 3.28) A cord 2.5 mm in diameter was tied to the fishing line and the line reeled in (Mitchell, 1982). A climbing rope was then installed by tying it to the rigging cord installing a rope for climbing entry.

Caver-style Single Rope Techniques (SRT) were used to climb to the branch (Figures 3.29, 3.30). In SRT, a climber's weight is alternated between a pair of ratcheting ascenders or knots to move up the rope (Perry, 1978; Smith & Padgett, 1996; Warild, 2004)

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Figure 3.26 (left): Phillip Grosse using a compound bow for access to old tree 14

Figure 3.27 (right): Gene Miller using crossbow for access to old tree 4, the rightmost stem.



Figure 3.28 (left): Lucie Whitten using crossbow to access 100yr tree 11.

Figure 3.29 (right): Matt Cracknell ascending into tree 12 using SRT rope technique

Once in the crown, arborist doubled rope techniques were used to move upwards from the access branch until the highest safe point was reached (Figures 3.31, 3.32). In arborist rope technique, a rope is thrown over a branch, anchored to the climbers harness, and the standing end controlled by a ratcheting friction hitch knot

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(Figure 3.32)(Budworth, 1999; Dial & Tobin, 1994; Moffett & Lowman, 1995; Smith & Padgett, 1996).

The time required to access and rig each tree varied widely. For example, tree 1 was shot, climbed, and rigged in ~5 hours, whereas tree 14 took ~6 days of full-time work. Some time was wasted rigging trees that were considered, but not actually studied. Not all trees had easily targeted branches or slopes nearby to offer higher crossbow shots. Availability of field assistance and the proper equipment controlled whether rigging trees would be successful. Once in the tree, the time to reach the highest point varied with crown structure (branch anchor abundance), weather, field assistance, and myriad other concerns.



Figure 3.30 (left): Melissa Whitman ascending into old tree 8 using SRT rope technique

Figure 3.31 (right) Jerry Romanski secured with arborist rope techniques in old tree 4.

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Figure 3.32 (left): R Junker utilizing arborist rope techniques in *E. regnans* ~250 years old.

Figure 3.33 (right): Arborist doubled ropes: a schwabish friction knot and a barrel termination knot