Brook, Beth Mary (2001) ***The effect of Coccotrypes fallax (Coleoptera; Scolytidae) on the recruitment of Rhizophora stylosa (Family Rhizophoraceae) in North Queensland mangroves.*** **PhD Thesis, James Cook University.**

The effect of *Coccotrypes fallax* (Coleoptera; Scolytidae)
on the recruitment of
***Rhizophora stylosa* (Family Rhizophoraceae)**
in North Queensland Mangroves

Thesis submitted by

Beth Mary Brook B.Sc (Wits)

in January 2001

for the degree of Doctor of Philosophy
in the School of Biological Sciences
James Cook University

STATEMENT OF ACCESS

I, the undersigned, the author of this thesis, understand that James Cook University will make it available for use within the University Library and, by microfilm or other means, allow access to users in other approved libraries.

All users consulting this thesis will have to sign the following statement:

> **In consulting this thesis, I agree not to copy or closely paraphrase it in whole or in part without the written consent of the author; and to make proper public written acknowledgment for any assistance which I have obtained from it.**

Beyond this, I do not wish to place any restriction on access to this thesis.

	10-11-01
Signature	**Date**

STATEMENT OF SOURCES

DECLARATION

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education.

Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

Signature

10 - 11 - 01

Date

ACKNOWLEDGEMENTS

This study would not have been possible without the support of many people. I wish to thank the following individuals;

My original supervisor ***Ushi Kaly*** who headed me in the direction of a problem on which I have thoroughly enjoyed working and who supported and guided me in the initial stages of my research.

Jamie Seymour helped me finish writing up through copious use of his red pen.

David Cumming (beloved son) who was the only one I could get to work with me in the mud, mosquitoes and heat of the mangroves when I had hundreds of propagules to collect for experiments.

Debra Cumming (beloved daughter) who supported me when I needed it most and helped prepare me for the final write up.

Barbara Paulus who proof read chapters for me (any errors are mine).

Cathy Fowler and other members of the library staff who gave invaluable help with resources.

Rod Armstrong (computer support) who helped me through all those times the computer played up.

ADB and ***MRB***, without you it just wouldn't have happened.

To everyone else who was prepared to listen to me talk about my boring beetles and whose questions helped clarify my thoughts, many **many** thanks. It was fun.

Abstract

The host specificity of *Coccotrypes fallax* (Coleoptera; scolytidae) infesting propagules of the mangrove tribe of Family Rhizophoraceae was investigated. Collections within the mangrove forest in three locations in North-east Australia of propagules of *Bruguiera gymnorrhiza*, *B. exaristata*, *B. parviflora*, *Ceriops australis*, *C. tagal*, *Rhizophora apiculata* and *R. stylosa* were made and examined for scolytid infestation. It was found that *C. fallax* infest *Rhizophora* spp to a much higher level than *Bruguiera* or *Ceriops* spp.

Seasonal and yearly variations in the level of infestation of *R. stylosa* propagules at each location were measured on transects within the locations. Numbers of propagules on the forest floor varied seasonally. Initially the number of propagules infested by *C. fallax* was small, peaking at densities of up to 2.8 infested propagules per square metre by late April. Regression of time on ground against level of infestation showed that propagules became infested after falling from the tree. Levels of infestation of propagules that remained on the site reached 100 % at some locations.

The effect of infestation on the recruitment of propagules and survival of seedlings was investigated. Damage caused by the feeding scolytid larvae was easily visible on dissection of the propagule and took the form of an irregular tunnel (feeding chamber) within the hypocotyl. The effect of infestation was assessed by recording number of surviving seedlings in October and correlating this with the infestation level within the site in the preceding March. A negative log linear relationship, between level of infestation and number of seedlings, was found. Plant out trials confirmed that infested propagules did recruit, but did not survive as seedlings.

The effect of temperature on the survival of the scolytids and their host propagules was investigated through immersion of infested propagules in hot water at 40^0, 45^0 and 50^0 C for temperature periods of 5, 10, 15 and 20 minutes. Heat treated propagules were planted out in the field to assess effect of heat treatment on recruitment of propagules and subsequent survival of the seedlings. *C. fallax* are killed by exposure of host propagules to temperatures of 45^0 C for periods of ten minutes or more. Propagule recruitment and seedling survival were not significantly affected by the heat treatment.

The internal temperature of propagules exposed to direct sunlight was measured and temperatures of up to 55^0 C were recorded. Mortality rates of scolytids in propagules exposed to sunlight were significantly higher than in controls placed in adjoining shade. Collections of propagules from locations with high levels of insolation had no active infestation.

The host specificity of *C. fallax*, the level of infestation recorded in various locations and the effect of infestation on survival of *Rhizophora* seedlings suggest that *C. fallax* infestation on *Rhizophora* spp is a possible factor in succession within the *Rhizophora* zone. Host specific predation by *C. fallax* affects only *Rhizophora*. *Ceriops* and *Bruguiera* seedlings were not affected.

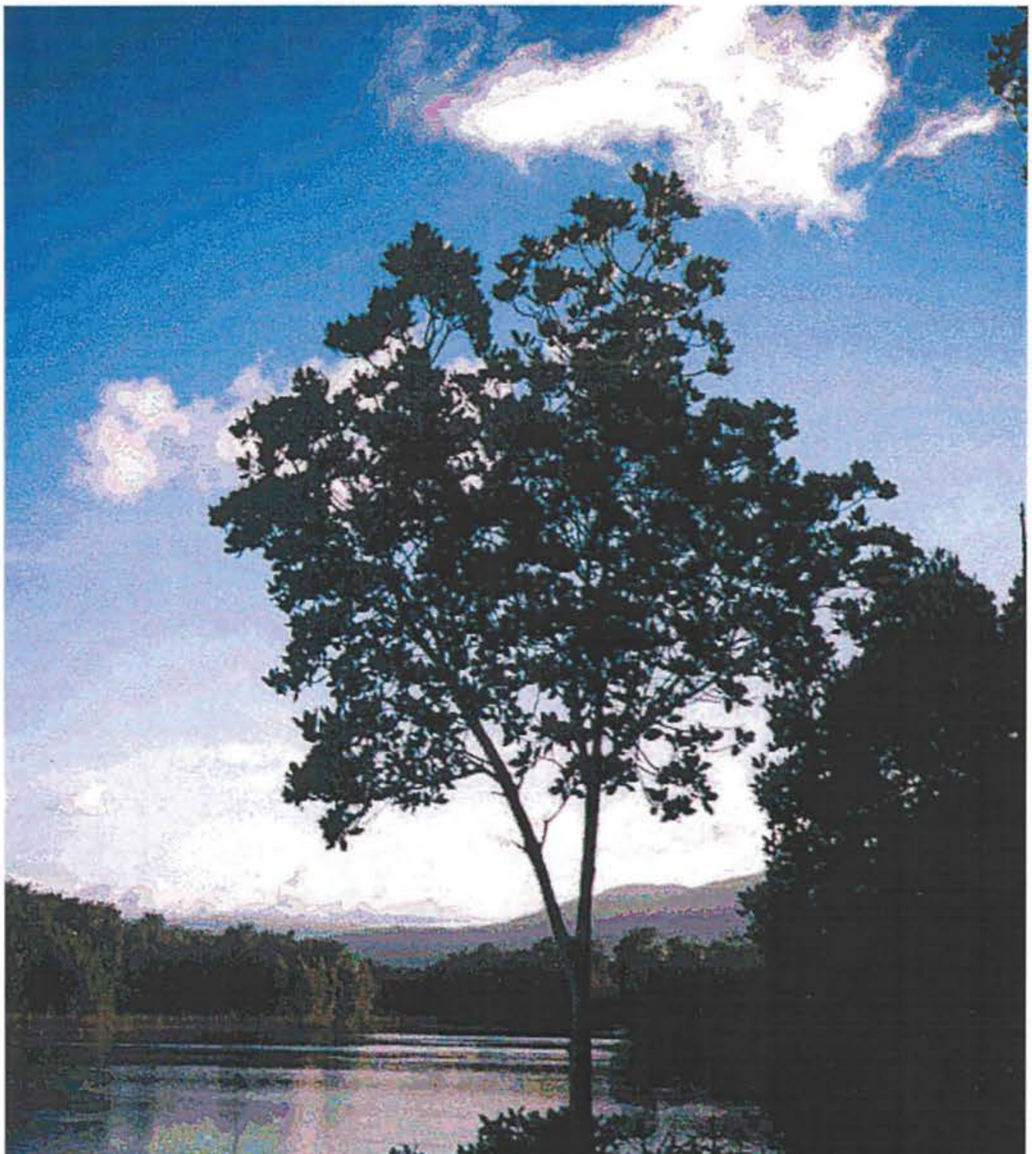
C. fallax infestation is not a factor in colonisation by *Rhizophora* of exposed substrate. Sunlight has the potential to quarantine propagules from the effects of any predation. This research demonstrates the importance of investigating both biotic and abiotic factors as well as their interactions in looking at factors affecting community structure.

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1

INTRODUCTION



1.1 Introduction

Forests are dynamic communities in which natural disturbances are recognised as powerful ecological forces (Platt and Strong 1989). Treefalls in forests create gaps that increase light levels and change other characteristics of the environment (Platt and Strong 1989). Colonisation of treefall canopy gaps and their formation play an important role in the dynamics of many forest ecosystems (Denslow 1987). Competition between species, the role of herbivores (which may have density dependant distance interactions within a gap) as well as gap size and orientation, propagule availability and chance may all play a role in determining community structure (see Chapter 2).

Community structure in mangroves is traditionally seen as zoned, with a range of hypotheses to explain the perceived zonation (Chapter 2). Although the existing hypotheses all explain some aspects of zonation, none deal with the importance of light gaps on the characteristics of the environment. These changed environmental conditions have the potential to affect both recruiting seedlings and the composition of the suite of predators that prey on them. Light gaps have the potential to provide refuges from predators that, under the canopy, reduce the ability of the seeds to become established and the seedlings to survive.

Recent research in mangrove forests has addressed the potential for predation on seedlings to affect forest structure. Smith (1987c) looked at the difference in predation levels of propagules both in gaps and under the canopy and found the level of predation by grapsid crabs had the potential to affect forest structure in *Avicennia* spp.

1.2 Elements of Mangrove forests and common zonation patterns.

The Family Rhizophoraceae is one of the larger mangrove families with respect to number of species and is represented in Australia by three genera, *Rhizophora*, *Bruguiera* and *Ceriops*. The mangrove Rhizophoraceae are unusual in that all reproduction is by means of propagules not seeds (Tomlinson 1994). Propagules are the result of continuous growth of the embryo. In Rhizophoraceae the hypocotyl growth extends well beyond the seed before falling from the tree. Other mangrove species exhibit some form of propagule production, but it is in the Rhizophoraceae that it has been most fully developed (Tomlinson 1994). As the propagule is the unit of reproductive dispersal, predation on propagules is equivalent to seed predation in terrestrial forests.

Of the three genera in the mangrove Rhizophoraceae found in this North-east Australia, *Rhizophora* is usually described as 'a pioneer species'. *Bruguiera* is frequently described as a member of the 'climax community' although both are often found growing together. *Ceriops* is also frequently found in association with both *Bruguiera* and/or *Rhizophora*. *Rhizophora* are found from the highest to the lowest portions of the intertidal, they are however frequently replaced by *B. gymnorrhiza* or *B. parviflora* in mid to high intertidal areas (Elsol and Saenger 1983).

1.3 The potential of C. fallax to affect forest structure.

A small scolytid, *Coccotrypes fallax* (Coleoptera, Scolytidae) bores into mangrove propagules and reproduces within the hypocotyl (San Valentin 1986). The damage caused by this infestation may affect the survival of the seedling. There are several elements that must be demonstrated to support the hypothesis that predation by scolytids has the potential to affect community structure. Firstly it would be necessary to show that predation by *C. fallax* is host specific and that *Rhizophora* propagules are infested at a higher rate than either *Bruguiera* or *Ceriops*. It would also be necessary to demonstrate that infestation by scolytids affects recruitment of seedlings and at infestation levels of *C. fallax* which occur in mangroves.

If these elements can be demonstrated, then it would help explain observations in the literature which report *Bruguiera* spp replacing *Rhizophora* (Tomlinson 1994; Hutchings and Saenger 1987; Lugo 1980) and descriptions of *Rhizophora* forests with no *Rhizophora* saplings, very few seedlings with *Bruguiera* and *Ceriops* saplings and seedlings dominating the understorey (Smith 1987b). These elements are demonstrated in Chapters 4 and 5.

1.4 The importance of light gaps as refuges for Rhizophora

The effect of infestation on *Rhizophora* survival in the long term obviously does not threaten the survival of the species. *Rhizophora* spp are represented in tropical mangrove forests around the world (Tomlinson 1994). Similarly whereas *C. fallax* are found infesting propagules in the Indo West Pacific Mangroves, *C. Rhizophorae* are found infesting propagules in the Atlantic East Pacific Mangroves (Rau and Murphy 1990). It may thus be inferred that strategies for coexistence have been developed by predator and prey.

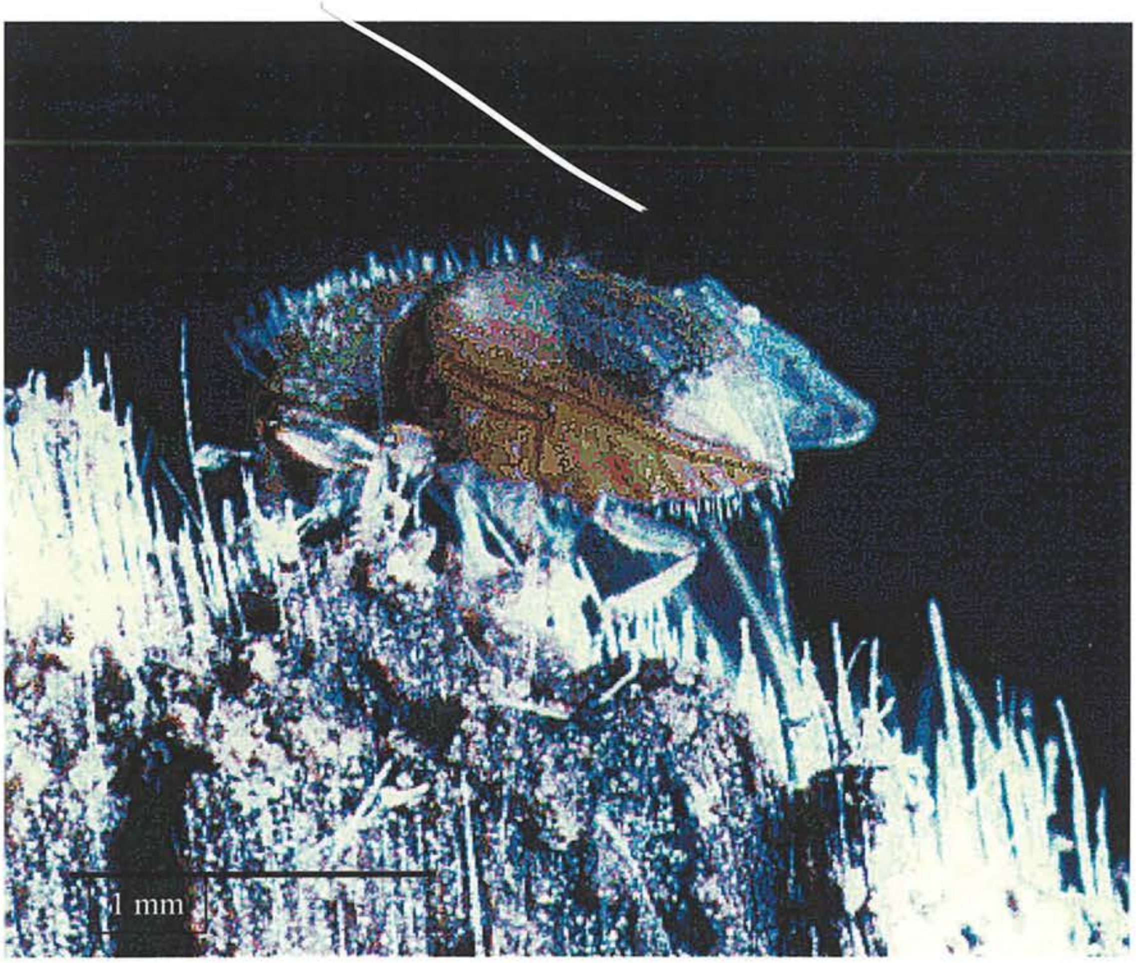
If recruitment of *Rhizophora* propagules in the *Rhizophora* zone is affected by scolytid infestation to the extent that *Rhizophora* are not represented in the sapling cohort, it implies the existence of refuges where predation does not affect recruitment and survival of seedlings. *Rhizophora* has many of the features of a pioneer species, capable of colonising gaps. It is frequently found lining river banks and colonising accreting mud flats. Colonising of mud flats may be attributable to reduced predation related to distance and density effects as proposed by Connell (1971) and Janzen (1970) independently. Distance and density effects would be more difficult to justify on riverbanks and in light gaps immediately adjacent to *Rhizophora* forests. It appeared that a second factor might work alongside any distance/density effect, one that quarantined the propagules from infestation and provided a refuge where *Rhizophora* propagules could recruit free from scolytid infestation. Connell (1975) defines refuges as areas where one or more environmental conditions exceed the tolerance limits of the predator but not the prey. One such environmental factor identified was temperature. Direct sunlight (high levels of insolation) was observed to increase the temperature of propagules on the substrate.

There are several elements which must be demonstrated to support the hypothesis that light gaps, and specifically the higher temperature experienced in propagules present in the gap-have the potential to quarantine propagules from scolytid infestation. First it must be shown that infesting scolytids are less tolerant of elevated temperatures than the host propagules and secondly that the internal temperature of propagules on the substrate in a light gap exceed the levels at which scolytid mortality occurs. Finally, exposure of infested propagules on the substrate in a light gap should result in death of the infesting scolytid. These elements are investigated in Chapter 6.

These two aspects of the predator- prey relationship between *C. fallax* and *R. stylosa* are both essential in understanding some of the complex factors which govern forest structure in mangroves and may explain some of the apparent contradictions in mangrove zonation studies.

CHAPTER 2

FACTORS AFFECTING FOREST STRUCTURE IN MANGROVES



2.1 Special features of Mangrove forests

Mangroves are a taxonomically diverse group of plants that possess a wide range of morphological, anatomical and physiological adaptations. These characteristics give them the ability to survive and perpetuate along sheltered tropical coastlines in saline environments under tidal influence (Snedaker 1982). These adaptations include extensive above ground root development in a variety of shapes and forms, salt exclusion and excretion mechanisms and viviparous propagules which are dispersed by water (Warming 1925; Davis 1940; Saenger 1982). Vivipary, the germination of the seed while still on the tree so that the unit of dispersal is a propagule rather than a seed, is well developed in mangroves. Although mangroves share a common ability to exist as halophytes in a common environment, they frequently form rather predictable mono-specific zones parallel to shorelines, tidal channels and estuaries (Davis 1940; Macnae 1967; Saenger and Robson 1977).

Australia has approximately 11500 km of mangrove forest, with the largest forested areas in the tropics (Galloway 1982). The high rainfall and/or extensive fresh water run off associated with the wet tropics of northeast Australia also contributes to luxuriant mangrove development. For successful mangrove establishment, a suitable substrate and protection from strong wave action is necessary. Mangroves generally require soft marine muds, silts and clays to become established. The most extensive mangrove development is found in low energy, high silt areas (Dowling and McDonald 1982).

2.1.1 Forest structure in mangroves

Forest structure can be discussed in a number of ways. Species diversity (based on the number of species making up the forest), zonation within the forest and associations between species is reported extensively in the literature on mangroves. Titles on these topics make up a significant proportion of the bibliographies compiled by Frith (1977) and Rollet (1981). In different zones within a forest however, a particular species may exist in one of a variety of structural forms. For example, *Avicennia* spp vary in height and may appear as a shrub on exposed salt flats while the same species is present as a tree on the river bank (Tomlinson 1994). The structure of a particular forest could therefore be described in terms of community characteristics, for example as tall open forest, closed forests, woodland etc comprised of a number of species (Dowling and McDonald 1982; Specht 1970).

Forest structure can also be described in terms of the geomorphological features of the habitat (Thom 1975). The combination of the geophysical and geomorphic components of the environmental setting give five generalised environmental settings for mangrove colonisation and development. River discharge of fresh water and sediment leads to the rapid deposition of terrigenous sands silts and clays producing two settings, river dominated and tide dominated. In those areas where higher wave energy reworks the sediment delivered by rivers, wave dominated barrier lagoon results. A composite setting occurs where both river and wave dominate. The fifth generalised setting occurs within drowned bedrock valley (Thom 1975). Within these groups, community change and zonation patterns respond to sea level change (Thom 1975).

In discussing mangrove zonation, it is important to be aware of these different approaches. In this thesis, however, the focus is on those factors that affect species composition of zones within a mangrove forest. Discussion on factors affecting zonation is confounded by the fact than in one region, a 'highly diverse' mangrove forest may consist of four species, representing all the species found in that region. Whereas in another region of the world a highly diverse forest may have up to thirty-two species present (Duke 1992).

2.1.2 Mangrove Floristics and biogeography

Floristics

Mangrove forests are a dominant feature of tropical forests and are best developed where there is an extensive suitable intertidal zone, an abundant supply of fine grained sediments and high rainfall or freshwater run-off (Walsh 1974). The word mangrove has been used to describe trees and shrubs growing in the marine intertidal zone (Tomlinson 1994; Duke 1992). This broad definition has led to the need to arbitrarily determine the floristic limits of the group of plants to be included when discussing mangroves. Tomlinson (1994) set limits between three groups; major elements, minor elements and mangrove associates. The species included as major elements possess **all or most** of the following features.

They occur only in the intertidal zone and do not extend into terrestrial communities.

They play a major role in the structure of the community and are known to form pure stands.

They have morphological specialisations that adapt them to their environment. These specialisations include aerial roots associated with gas exchange and vivipary of the embryo.

They have a physiological mechanism for salt exclusion, which enables them to grow in seawater that results in visible salt excretion in some species.

They are separated from their relatives at least at the generic level and often at subfamily level (Tomlinson 1994).

On this basis Tomlinson (1994) includes a total of 9 genera (34 species) in his list of major elements of the mangrove (Table 2-1).

Table 2-1 Genera of mangroves on a cosmopolitan basis comprising major elements of mangrove. Taken from Tomlinson (1994).

Family	Genus	No. of mangrove species	Aerial roots	Vivipary	Level of taxonomic isolation and status
Avicenniaceae	*Avicennia*	8	++	+	Monogeneric family related to Verbenaceae
Combretaceae	*Laguncularia*	1	+	-	Tribe Lagunculariae (+ *Macropteranthes* nonmangrove)
	Lumnitzera	2	+	-	
Palmae	*Nypa*	1	-	+	Isolated group (subfamily?) within the family
Rhizophoraceae	*Bruguiera*	6	++	+	Collectively form a natural tribe, Rhizophoreae, within the family.
	Ceriops	2	++	+	
	Kandelia	1	-	+	
	Rhizophora	8	++	+	
Sonneratiaceae	*Sonneratia*	5	++	-	One of two genera in the family (*Duabanga* nonmangrove)
Total	9	34			

In summary the closest relatives of the mangrove taxa forming the major elements of mangrove are; families, subfamilies, tribes, or genera.

Note. ++ means well present or well developed; + means present; - means absent.

In this grouping of mangroves by Tomlinson (1994), minor elements are distinguished by their inability to form a conspicuous element of the vegetation. This means they rarely form pure communities and may occupy peripheral habitats. In comparison the major elements form zones for example, the *Rhizophora* zone in the lower intertidal. Tomlinson includes a further 11 genera (20 species) in this second grouping (Table 2-2).

Table 2-2 Genera of mangroves on a cosmopolitan basis comprising minor elements of mangrove. Taken from Tomlinson (1994).

Family	Genus	No. of mangrove species	Aerial roots	Vivipary	Level of taxonomic isolation and status
Bombacaceae	*Camptostemon*	2	+	-	Genus isolated within family
Euphorbiaceae	*Excoecaria*	1 (-2)	-	-	Genus includes about 35 nonmangrove taxa
Lythraceae	*Pemphis*	1	-	-	Genus distinct within family, one species nonmangrove.
Meliaceae	*Xylocarpus*	2	+ +	-	One species non-mangrove; forms with *Carapa* tribe Xylocarpeae
Myrsinaceae	*Aegiceras*	2	-	+	Genus isolated within family.
Myrtaceae	*Osbornia*	1	-	-	Genus isolated in the family.
Pellicieraceae	*Pelliciera*	1	-	+	Monotypic family related to and sometimes included within Theaceae
Plumbaginaceae	*Aegialitis*	2	-	+	Isolated genus, sometimes segregated as family Aegialitidaceae
Pteridaceae	*Acrostichum*	3	-	-	
Rubiaceae	*Scyphiphora*	1	-	-	
Sterculiaceae	*Heritiera*	3	-	-	
Total	11	20			

Note. + + means well present or well developed; + means present; - means absent.

Duke (1992) does not distinguish between these major and minor elements and includes in his discussion twenty families from two plant divisions namely Polydiophyta (ferns) and Magnoliophyta (also known as angiosperms). Of these twenty families only two are exclusively mangrove and there are no orders or higher ranks with all mangrove taxa. Mangroves therefore, are not a genetic entity but an ecological one (Duke 1992). Family *Rhizophora* is often referred to as the 'true mangrove' family, but it has only 4 of its 16 genera inhabiting mangroves. Generally the families with mangrove representation are pantropical in distribution and are commonly represented in tropical rainforests. Two orders, the Myrtales and Rhizophorales dominate the mangroves. Together they comprise 25 % of all mangrove families and 50 % of all mangrove species.

Biogeography

Distribution of mangroves can be discussed on at least four important scales, their global distribution, their coastal range, their location within an estuary and/or their position on the intertidal range (Duke 1992). On a global scale, mangroves are found in tropical regions, with major deviations matching the presence of warm and cold oceanic currents. Limits to mangrove distribution generally match the winter 20°C isotherm (Duke 1992) being found further south on east coasts with warm currents than on the western continental margins which have cold currents pushing up from the poles).

Dispersal of mangrove species along coastlines is by means of floating seeds and propagules. These seeds and propagules of some genera have the ability to remain viable for many months (Rabinowitz 1978a). Global dispersal is apparently constrained by both wide bodies of water and landmasses blocking the equatorial flow of tropical waters (Duke 1995). Presently, there are four major barriers influencing the pantropical dispersal of most organisms found in warm coastal regions (Briggs 1974). These are the continental land masses of Africa and Euro-Asia, the North and South American continents, the North and South Atlantic Oceans and the Eastern Pacific Ocean (Briggs 1974). The landmasses extend into latitudes where mangroves can not successfully recruit and reproduce, thus preventing the movement of mangrove species between geographical regions. The oceans act as effective barriers when seeds and propagules carried by currents lose viability before reaching suitable land on which to settle and grow.

The relative effectiveness of these barriers differs throughout geological history and varies with the dispersal-establishment ability and evolution of each taxon (Ricklefs and Latham 1993; Duke 1992). During recent geological time (Cenozoic), the African Euro-Asian continents and the Pacific Ocean appear to have been reasonably effective in preventing movement of mangroves. Thus mangrove species are divided into two global hemispheres, the Atlantic East Pacific (AEP), usually referred to as the New World mangroves, and the Indo West Pacific (IWP) or Old World mangroves (Duke 1992).

The area of mangroves in these two regions is more or less equivalent, however the AEP has fewer species and fewer additional genera (Ricklefs and Latham 1993; Duke 1992). World wide, the mangrove flora consists of 69 recognised mangrove species, belonging to some 20 families (Duke 1992). The Australasian (New Guinea, New Caledonia, Australia and New Zealand) and neighbouring Indo-Malaysian regions, both within the IWP have approximately five times the species richness of all other regions (Duke 1992; Tomlinson 1994). Forty five taxa of mangrove plants are found in an area covering southern New Guinea and north-eastern Australia, representing the greatest concentration of mangrove species in Australasia (Duke 1992).

The continental distribution of mangroves is affected by both latitude and rainfall (Duke 1992). There is a decline in species numbers with increasing latitude, many species being restricted to the tropics. Species richness is also higher in those areas with increased rainfall, specifically where the number of months in which precipitation exceeds evaporation by one third (Duke 1992). This occurs across the north and northeastern coastlines of Australia and it is in these areas that the greatest species richness occurs. Community characteristics and species lists for mangrove vegetation in Northern Australia, Queensland, Western Australia and the Southern and Western Australian Coastline illustrate this distribution pattern (Wells 1982; Dowling and McDonald 1982; Kenneally 1982; Bridgewater).

Mangrove propagules are dispersed by water, and distribution within regions does not appear to be limited by propagule availability (Duke 1995). Long distance dispersal properties of mangrove propagules is well documented (Gunn and Dennis 1973; Rabinowitz 1978a). For example, viable *Rhizophora mangle* propagules are frequently found on the beaches of South Texas having originated in mangrove populations several hundred kilometres to the south in Mexico. These propagules may recruit as seedlings, but do not survive the first winter, suggesting that the distribution limit is associated with environmental factors, not lack of propagules (Sherrod and McMillan 1985; Sherrod *et al* 1986).

Mangrove habitat within a region can be described with respect to estuarine location and intertidal position. Generally, within an estuary, salinity will be greater in the downstream region than in the upstream region, with fresh water found above the upper limits of tidal influence. In the intertidal region the position can be broken into low, mid and high intertidal (Duke 1992). Distribution of mangrove species within these different habitats is patchy, with zones evident to the casual observer.

2.1.3 Zonation patterns in mangroves

A great deal of effort over many years has been devoted to describing and rationalising zonation and succession in mangrove forests around the world (Bunt and Williams 1981b; Tomlinson 1994). Species zonation patterns have been described over many years for just about every country with mangroves (see Chapman 1976, Hutchings and Saenger 1987 for lists) many describing zonation patterns as typical to the region. This led to the paradigm that zonation was a classical feature of mangrove forests and was present in almost all forests worldwide. Not all researches reported this classical view of mangrove zonation (Bunt and Williams 1981b; Hutchings and Saenger 1987).

The work of Macnae (1966) and Jones (1971), on zonation in mangroves in North East Queensland remain standard works of reference, but they were based on relatively limited field experience. Macnae (1966) recognised the following ordering of shore parallel zones as characteristic of North Eastern Australia. (1) a landward fringe, (2) landward *Avicennia*, (3) *Ceriops* thickets, (4) *Bruguiera* forests (5) *Rhizophora* forests (6) seaward fringe (*Avicennia* and/or *Sonneratia*). While this frequently occurs in mangrove vegetation along open coasts, it is far less common in riverine environments (Bunt and Williams 1981b).

Bunt and Williams (1981b) carried out extensive surveys in 21 locations in tropical Australian mangroves, recording species associations from 1391 sites along 142 transects. They used classificatory techniques to define 29 association groups within the 35 species, showing that a uni-dimensional approach to the sequences of vegetational association groups is inadequate. Early 'classical' zonation patterns were all given along a typical transect at right angles to the waters edge (Macnae 1968; Saenger *et al* 1977). Despite this lack of consistency in zonation patterns, along the coast of North East Australia, there are situations where virtually all the species may be found in pure stands, even though some may be restricted in area (Bunt and Williams 1981a)

Generalisations within regions can be made, with some species occupying the lower intertidal range, others in the mid intertidal, and a third group in the upper intertidal. Unfortunately for efforts to interpret the distribution patterns, double distributions occur, for example *Avicennia marina* is reported in both the lowest and highest intertidal zone (Macnae 1967; Bunt *et al* 1982b; Smith 1992). *Rhizophora* spp are also reported to occur in all three zones, often missing from the mid intertidal (Macnae 1967; Bunt *et al* 1991; Bunt *et al* 1982b). Still other regions report no observable zonation within their mangroves. Bunt and Williams; (Bunt *et al* 1991; Williams *et al* 1991; Bunt 1996) developed methods of sequencing species and graphically illustrating the associations using minimum spanning trees. Bunt (1996) applied a simple numeric procedure to define species sequential ordering across the intertidal surfaces. He found considerable diversity in zonal pattern. This was attributed to differing response of individual species to the character and pattern of environmental controls.

Mangrove zonation is thus not as straightforward as was once thought. There is no single consistent 'typical' pattern of mangrove zonation, rather regions and individual locations have distinctive zones. Close examination of these zones indicates that advanced techniques are required in order to accurately illustrate and describe the distribution and associations of species within the zones. Just as advances have been made in recording and illustrating complex zonation patterns, so advances have been made in understanding the factors influencing zonation.

2.2 Hypotheses on the factors influencing local zonation patterns.

Several hypotheses have been advanced to explain the zonation patterns observed in some mangroves. Typical zonation patterns from the Indo-Pacific show *Aegicéras*, *Avicennia* and *Sonneratia* occupying the lowest intertidal zones, various species of

Rhizophora and *Bruguiera* in the mid-intertidal area and *Heritiera*, *Xylocarpus* and numerous other species in the higher intertidal regions. These hypotheses include: -
plant succession due to land building properties of mangroves (Davis 1940)
response to geomorphological factors (Thom 1975; Woodroffe 1992)
response to physio-chemical gradients across the intertidal zone (Macnae 1968)
differential dispersal of propagules (Rabinowitz 1978a)
inter-specific competition (Clarke and Hannon 1971)
differential predation on propagules across the intertidal zone (Smith 1987b).

2.2.1 Succession

Curtis (1888) in Davis (1940) suggested that mangroves contribute to land building. Davis (1940) working in Florida built on this land building role, suggesting that the sequence was as follows. Sea grasses colonise bare sub-tidal areas, trapping sediments to the point where *R. mangle* could colonise the area and trap more sediment. As the land built up, *R. mangle* would be replaced by *A. germinans*, which in turn would give way to a terrestrial forest climax association.

This view, that zonation in mangroves represents a succession sequence from pioneer colonisers to mature climax forest, is a popular and often invoked mechanism (Snedaker 1982). Evidence from other accreting systems supports this mechanism (Bird 1972). However the theory only applies to actively accreting systems. Where the sediment budget is in deficit, erosion rather than accretion will occur (Watson 1928; Egler 1950). Not all mangroves grow in actively accreting systems; sea level rise, land sinking and erosion when sediment is carried away all alter the area affected by tides as well as inundation levels, frequency and duration of immersion. In these situations, land building and succession do not occur as described by Davis (Egler 1950) and other mechanisms must be used to explain the observed zonation.

The concept of succession need not however be linked to land building. Succession in terrestrial forests relates to modifications of the habitat, not sediment trapping. Mangrove zonation may arise through successional processes which have nothing to do with the supposed land building properties of mangroves (Hutchings and Saenger 1987; Lugo 1980). These processes include changes in inundation levels following sea level changes, sinking or elevation of the land as well as the replacement of pioneer species by those that form a climax community. Lugo *et al* (1990) provided a hypothetical maze of successional pathways for a relatively simple wetland community based on changes in hydrological factors. Johnstone (1983) found a climax in forests dominated by *Bruguiera gymnorhiza*. Similarly Putz and Chan (1986), on analysing over 60 years of forest composition and growth data from permanent plots in Malaysia, where no land building or sea level change occurred, found that species diversity increased over time, with *B. gymnorhiza* most abundant. *B. gymnorhiza* is one of the most shade tolerant of the mangrove species and this is in accordance with classical ecological succession (Putz and Chan 1986). Zonation in mangroves may thus be the result of succession without relying on land building as a necessary factor. In this case it is expected that those species with 'pioneer characteristics' are replaced by those with 'mature phase' characteristics for example, *Avicennia* spp with *Bruguiera* spp.

Tomlinson (1994) analysed the published work on pioneer and mature phase species and communities compared these with mangroves species and communities. He found that mangroves share a mix of attributes, having clearly pronounced characteristics of pioneer species in their reproductive biology, but of mature-phase species in some aspects of their community structure and vegetative growth. These characteristics do not explain all the observed species distribution patterns. In all of this work, no mention is made of the effect of predators as factors influencing the observed zonation in mangroves.

2.2.2 Response to geomorphological factors

It is now generally recognised that mangroves respond to geomorphological changes rather than causing them (Snedaker 1982; Woodroffe 1984). The 'land building' properties attributed to mangroves occur in naturally accreting systems and zonation changes respond to the changes in inundation level. In regions of erosion or no net accretion, no land building occurs (Woodroffe 1992). Mangrove development and zonation are historically bound to geomorphic processes through the particular soils and soil conditions that these processes have produced. Thom (1967; 1975) investigated vegetation in Mexico and Australia and related species assemblages, distributions and overall spatial organisation to factors such as depositional and erosional histories, subsidence, compaction, fresh water discharge and sea level rise. These studies do not, however, provide an insight into the mechanisms controlling zonation in mangroves.

2.2.3 Response to physio-chemical gradients across the intertidal zone

The hypothesis that physiological adaptations by different mangrove species to conditions in the intertidal range are an underlying cause of mangrove zonation patterns is a dominant theme in the literature. There are a number of physio-chemical gradients that exist across the intertidal zone. Many of these are maintained by tidal action and are correlated with inundation levels, both frequency and duration. The correlation of mangrove zonation patterns with surface hydrology and salinity has been extensively reviewed (Macnae 1967; Macnae 1968; Clarke and Hannon 1967; Clarke and Hannon 1969; Clarke and Hannon N.J. 1970; Clarke and Hannon 1971; Walsh 1974; Lugo and Snedaker 1974; Chapman 1976; Smith 1992). Good correlations may exist, but as both tidal inundation and salinity are confounded with many other physio-chemical gradients, correlation may not imply causation.

Frequency of tidal inundation is the most obvious parameter which varies across the intertidal zone and is frequently cited as a cause of zonation (Tomlinson 1994; Snedaker 1982; Martinez-Ramos *et al* 1989; Macnae 1967). High intertidal areas are inundated much less frequently than low intertidal regions. This tidal action in turn introduces two other gradients, soil pore water salinity and soil waterlogging (Giglioli 1965; Clarke and Hannon 1967). The soil pore water salinity gradient is affected by frequency of inundation; the salinity of the flooding tidal water, extent of rainfall, fresh water run-off and seepage as well as soil type profile and drainage.

At the lowest intertidal area, the pore water salinity approximates the salinity of the flooding water (35 $^0/_{00}$) and is less than 1$^0/_{00}$ at the upstream end of riverine mangrove systems (Bunt *et al* 1982a). In the high intertidal, the pattern of salinity variation is usually site specific, in arid regions, pore and surface water salinities in the high intertidal zone may exceed 90 $^0/_{00}$ (Wells 1982). Where a region has abundant rainfall, freshwater run-off and / or seepage, the high intertidal zone salinity may be less than that of the flooding water (Semeniuk 1983). Patterns of salinity are thus site specific.

Nutrients, such as nitrogen and phosphorus levels, oxidation-reduction potential, pH, pore water sulfide concentration and soil texture are other factors that vary across the intertidal zone (Watson 1928; ; Giglioli 1965; Boto and Wellington 1983; Carlson *et al* 1983; Boto and Wellington 1984; Nickerson and Thibodeau 1985; Mckee 1993). Frequency and duration of tidal immersion affects the extent to which the soil is waterlogged (hypoxic) (Ball 1988a). The roots of mangroves tend to be shallow, have numerous lenticels and extensive aerenchyma that increases the availability of oxygen to roots growing in oxygen deficient soil (Tomlinson 1994). In addition many species have aerial roots. These include stilt roots (eg. *R. stylosa*) knee roots (eg. *B. gymnorrhiza*) pneumatophores (eg. *A. marina*) and plank roots (eg *X. granatum*) (Tomlinson 1994). These roots are exposed to air at least during periods of low tidal inundation and facilitate the diffusion of oxygen from the atmosphere to sites of respiration in the roots (Scholander *et al* 1955). Mangrove forests are characterised by distinct species distribution relative to tidal inundation (see Ball 1988; Smith 1992 for reviews)

Tidal waters distribute both free and particulate bound nutrients. These inputs are greatest in frequently flooded areas of sediment deposition (Boto 1982; Valiela 1984). The degree of tidal inundation also affects the redox status of the sediments, and this in turn affects both the form and availability of inorganic nutrients (Boto and Wellington 1983; 1984). Each of these edaphic factors can be shown to be correlated with mangrove zonation. The task is to demonstrate that there is a causal relationship between any specific factor or combination of factors that results in the observed zonation.

Efforts to support this hypothesis include field observations, field experiments and laboratory and greenhouse experiments. Each of these is useful, but each has its limits. Field observations used for inferences are usually based on the distribution of the adults, yet the conditions under which seedlings recruit and grow may be much narrower than those in which adults may survive (Ball 1988a; Mckee 1993). Nor do field observations take into account the possibility that the conditions may have been modified by the community (Mckee 1993; Ridd and Sam 1996). In addition it is usually impossible to separate the effect of a single factor (eg soil texture) from other variables (eg salinity) as the entire range of physio-chemical parameters are rarely measured.

It has been demonstrated both in the field and experimentally, that species of salt tolerant plants do have definable tolerances and optima. These may help to explain the limits of landward and seaward distributions of various species, but these limits are usually so wide that they do not explain the distribution of species within the intertidal zone. There are two variations of the gradient hypothesis, the 'distinct preference' hypothesis, and the 'same-preference' hypothesis (Pimm 1978). Where each species has its own optimum along the gradient which controls where that species occurs (the 'distinct preference' hypothesis), zonation occurs. In the 'same preference' hypothesis, many species share the same optimum and other factors such as competition, seed dispersion or predation cause zonation (Ball 1988a).

Field experiments tend to suggest that factors other than the salinity gradient alone are responsible for observed zonation patterns. Rabinowitz (1978b) working in Panama planted seedlings of 4 species (*Rhizophora mangle, Avicennia germinans, Pelliciera rhizophorae, and Laguncularia racemosa*) in forests dominated by conspecific adults and forests dominated by each of the other species. She found that all four species could grow in any of the zones, in fact most species grew best away from the parent zone. This did not support the concept of physiological preference. Work on *A. bicolor* and *R. racemosa* in Costa Rica indicated that *A. bicolor* grew best in the lower intertidal which was dominated by *R. racemosa* (Jimenez and Sauter 1991). In Australia, four species *A. marina*, *B. gymnorrhiza*, *C. australis* and *R. stylosa,* in both high and low intertidal zones which differed in both frequency of inundation and salinity were studied (Smith 1987). All four species had their greatest survival in the high intertidal zone. Relative growth was greatest in the high intertidal for three species, for the fourth, *B. gymnorrhiza*, it was similar in both zones. In each of these studies the author(s) concluded that the study did not support the hypothesis that physiochemical adaptations explain the observed distributional pattern of the species.

Osborne (1988) examined the influence of high and low intertidal position and upstream vs. downstream salinities on the survival and growth of *Aegiceras corniculatum* seedlings. Salinity did not influence distribution, but frequency of tidal inundation did. McKee (McKee 1995b) evaluated the relative importance of factors affecting seedling establishment and survival on a mangrove-dominated island in Belize. Both of these studies supported the importance of these factors. Thus different field studies provide different answers as to the importance of physiological factors in mangrove zonation.

Laboratory studies that should give the best data with which to study the tolerance of mangroves to various physiological studies are often limited in relevance in that they examine a single potential causal agent without considering interactive effects. McMillan (1975) demonstrated the importance of this with a study on the interaction of salinity tolerances and soil texture. Seedlings grown in hypersaline conditions in sand failed to survive whereas seedlings grown in a sand clay mixture (90% sand, 10 % clay) had 100% survival in the same hypersaline conditions, although they showed some leaf discolouration. In a mixture composed of 75% sand and 25% clay in hypersaline conditions they reported 100% survival and no leaf discolouration (McMillan 1975). Single factor experiments, which shed light on the functioning of particular species under levels of a particular factor of interest, are unlikely to explain the complexity of mangrove zonation. Recent papers include studies in which combinations of factors are investigated. Smith (1987a) looked at the effects of light and intertidal position on seedling growth. He found that the results indicated that species zonation pattern cannot be explained by physiological adaptation alone, as the growth of *A. Marina, R. stylosa* and *B. gymnorrhiza* seedlings was greater in the high intertidal, whereas they reach maximum abundance in the lower intertidal. For example, *Ceriops tagal* grew best in the region where it is most abundant, but even there it was outperformed by the other three species used in the study.

McKee (1995a) looked at mangrove responses to light and nutrients. At high light and nutrient levels species response differed greatly. At lower light and nutrient levels species differences were greatly reduced. McKee (1995a) also analysed the relative amounts of secondary compounds, which may protect seedlings against herbivores, and found that these were significantly affected by light and nutrient availability.

2.2.4 Light gaps in mangroves

Gaps in terrestrial forests are the subject of numerous studies on gap regeneration (White and Pickett 1985) and some of these factors may be applicable in mangrove gap studies. There are however significant differences in the way in which gaps form in terrestrial and mangrove forests. Terrestrial forest gaps may result from the death of a tree protruding through the canopy, which brings down adjoining trees as it falls, fire, lightning strike to name the most common. Mangrove gaps occur most frequently as a result of lightning strike causing death of the tree while still standing. This results in formation of a light gap while the trees are still standing and this gives some protection to seedlings against wave borne debris (Duke 2001).

The processes by which mangrove gaps are filled also differ from those in terrestrial forests, with propagules transported in by water, lack of understorey with saplings, vivipary in mangroves resulting in the absence of a seed bank (a store of viable ungerminated seeds from previous seasons) etc (Saenger 1982; Tomlinson1994). In addition, many mangrove seedlings are shade intolerant, growing very slowly in shade conditions (Duke 1999). Rhizophora seedlings specifically respond very poorly to canopy openings after becoming established in the shade (Duke 1999). The presence of gaps formed by a break in the canopy, those which exist on river banks and those on accreting mud flats all present a range of light conditions which affect the survival and growth of mangrove plants.

Mangroves have a range of physiological and morphological adaptations to high levels of incident solar radiation or insolation (Hutchings and Saenger 1987) Insolation is one of the few factors not correlated with levels of tidal inundation but by position relative to the canopy. Light levels above the canopy are not affected by height of the substrate. Light levels under the canopy are determined by the nature of the canopy. Only on riverbanks and prograding shores are high light levels associated with lower intertidal levels (Myers 1935; Smith 1987a). At low light levels, levels of photosynthesis in mangroves are positively correlated with light level (Attiwill and Clough 1980). Above saturation point for light, for any particular species, levels of photosynthesis plateau. Photosynthesis may be inhibited at higher light levels, as increased light levels are associated with increased leaf temperature (Andrews *et al* 1984). As temperature increases, the stomatal conductance decreases, this explains some but not all of the decrease in net photosynthesis (Andrews *et al* 1984).

Various authors have noted the light and shade requirements of different species based on observations in the field and from culture experiments. Some species appear to be shade tolerant, both as seedlings and as adults; others are shade intolerant. *Avicennia, Ceriops* and *Rhizophora* appear in both groups (Table 2-3). These inconsistencies require investigation.

Table 2-3 Shade tolerance of Australian mangroves (Hutchings and Saenger 1987)

Genus	Shade tolerant	Shade intolerant
Acanthus		Macnae 1966, 1968
Acrostichum		Macnae, 1966
Aegialitis		Macnae 1966,1968
Aegiceras	Clarke and Hannon 1971 Thom Wright and Coleman 1975	
Avicennia	Clarke and Hannon 1971 Attiwill and Clough 1980	Macnae 1963, 1966, 1968 Thom, Wright and Coleman 1975
Bruguiera	Macnae 1966, Macnae and Kalk 1962,	
Ceriops	Macnae and Kalk 1962, Thom, Wright and Coleman 1975	Macnae, 1966 1968
Excoecaria	Saenger 1982	
Lumnitzera		Macnae 1966,1968
Osbornia	Saenger 1982	
Rhizophora	Macnae 1966	Macnae 1968
Sonneratia		Macnae 1968
Scyphiphora		Macnae 1966
Xylocarpus	Saenger 1982	

2.2.5 Differential dispersal of propagules

Mangrove seeds and propagules are generally water dispersed. Carried downstream during ebb tides and periods of high river flow, and upstream during flood tides. Mangrove propagules moving back into the mangroves face a tangle of trunks, prop roots and pneumatophores.. Rabinowitz (1978a) hypothesised that it was tidal sorting of propagules of different sizes which contributed to zonation in mangrove forests in Panama. In these forests, species appear to be distributed from the low to high intertidal zones in a manner inversely related to their propagule size. The two species with smaller propagules, *Avicennia* and *Laguncularia* were restricted to high intertidal zones, a result of their propagules being carried inland by the tides. *Rhizophora*, with the largest propagules were restricted to the lower intertidal, the result of the larger propagules, tangled in the prop roots, being unable to reach the higher zones.

Rabinowitz, (1978a) also tried to use dispersal properties of mangrove propagules such as floating and rooting time to explain zonation. Not all propagules require the same length of time to develop roots, *Avicennia* and *Laguncularia* need 5-7 days, whereas *Rhizophora* and *Pelliciera* need 11-15 days (Rabinowitz 1978a). Based on these, the zonation should have shown the smaller propagules to be more successful on the lower intertidal, where inundation appears at shorter intervals, with all species favoured at the high intertidal, with longer periods between inundation to allow for successful establishment.

Jimenez and Sauter (1991) used the mechanism of tidal sorting, in conjunction with sea level rise, to explain the invasion of the high intertidal *A. bicolor* forest by *R. racemosa,* in a mangrove forest in Costa Rica. They attributed the movement of the larger propagules into the area to the increased number of high tides that covered the forest following sea level rise (Jimenez and Sauter 1991).

The mechanism of tidal sorting of propagules has not been supported in other regions. *Sonneratia* spp, which is common in the low intertidal, has relatively small seeds of 10-15 mm in length (Tomlinson 1994). In discussing *Sonneratia*, Rabinowitz (1978a) erroneously referred to the entire fruit, which falls from the tree while still green before releasing the small angular seeds (Tomlinson 1994). *Sonneratia* is commonly found at the seaward fringe of the mangrove. Similarly the seeds of *Aegiceras* spp and *Avicennia* spp, are small and the adults are typically found in the low intertidal zone (Watson 1928; Bunt *et al* 1982a; Wells 1982) as well as in the highest intertidal (Wells 1982; Johnstone 1983; Smith 1988a; Osborne and Smith 1990). Saenger (1982) found seedlings of all species in all plots in his work on the mangroves of Port Curtis in eastern Australia. The largest propagules, those of *Rhizophora stylosa*, were found across the entire population gradient. The amount of dispersal of mangrove propagules that occurs is highly variable. Yamashiro (Yamashiro 1961), working with *Kandelia* in southern Japan, painted propagules before they fell from the parent tree. He found that most were carried at least 50m from the mother tree within 30 days. Komiyama (1992) working with *Rhizophora* propagules reported that most did not move out of the forest. Seasonal flood rains and high spring tides, both of which occur during the period of propagule abscission in many tropical regions, have the potential to increase movement of propagules away from the parent tree.

2.2.6 Inter-specific competition

Competition experiments between species usually involve growing the species under investigation, both individually and together, and interpreting the resulting growth and survival data. This is then used to interpret observations made in the field. Studies of competitive interactions between mangrove seedlings are rare. Smith (1988b) grew *C. australis* and *C. tagal* in mono and poly cultures at salinities ranging from 0 to 60 $^{0}/_{00}$. Competition was gauged by comparison in growth of each alone with that of growth in the presence of the competitor. The results suggested that *C. tagal* would be the superior competitor at low salinities (0-15 $^{0}/_{00}$) whereas *C. australis* would be the superior competitor at 45 $^{0}/_{00}$. In the field however, both are shifted to regions with higher salinities than their growth optimum as measured in the laboratory. Smith (1988b) hypothesised that both might be out-competed at lower salinities by species such as *Heritiera littoralis*, *Xylocarpus granatum* or *B. gymnorhiza*.

2.2.7 Differential predation on propagules across the intertidal zone

Predation on seeds has been recognised as an important process in determining community structure in a number of forests, (Janzen 1971; Connell 1971; Holmes and Price 1986; Hubbell 1980; Asquith *et al* 1997). Propagules of mangroves are known to be consumed by a number of predators including long tail macaques (*Macaca fascicularis*) (Chan *et al* 1984), molluscs (*Melampus coeffeus* and *Cerithidea scalariformis*) (Smith *et al* 1989) and crabs (family Grapsidae) (Watson 1928; Smith *et al* 1989).

Smith and colleagues have shown that consumption of mangrove propagules by sesarmid crabs (family Grapsidae, subfamily Sesarmidae) greatly affects natural regeneration and influences the distribution across the intertidal zone (Smith 1987a; Smith 1987c; Smith *et al* 1989; Osborne and Smith 1990; Smith and Duke 1987). In a series of experiments in Australian mangroves they tethered propagules in the forest and observed the amount of consumption over time, finding that on average 76% of seeds were consumed by sesarmid crabs (Smith 1987b; 1988a). As the distribution of sesarmid crabs is not uniform across the intertidal zone (Smith 1988a), differential predation has the potential to affect survival of seedlings differently across the zone. The amount of predation differed significantly among propagules of mangrove species, decreasing in the order *A. marina* >*B. exaristata* =*C. tagal* >*B. gymnorrhiza* =*R. stylosa* (Smith 1987a). The nutritive quality of propagules varied among species and explained approximately 97% of the variance in the amount of predation among the five species. Smith (1987b) also examined seed predation in relation to tree dominance and distribution in mangrove forests. He found that there were significant differences in the predation rates on seed, in forests with differences in the dominance of conspecific adults. Predation rates were highest where conspecific trees were rare or absent. McKee (1994) working in Belize found that for *R. mangle* and *L. racemosa*, predation rates were highest where conspecifics dominated the canopy. Only the predation rate for *A. germinans* was consistent with intertidal dominance of trees. Thus while predation on *A. germinans* may explain the distribution of the trees, the predation levels of *R. mangle* and *L. racemosa* do not in the cases studied, indicate that predation may affect distribution.

In a comparison of seed predation in tropical tidal forests from three continents, (North America, south east Asia and Australia), Smith *et al* (1989) found that variation in the amount of predation on *Rhizophora* among regions is partly attributable to differences in the composition of the predator guilds between the forest studied. In Florida, crabs are minor consumers and three genera of snails are more important, whereas in south east Asia and Australia, the predator guilds are dominated by grapsid crabs (Smith *et al* 1989).

Crabs are not the only organisms feeding on propagules. In Florida mangroves, Onuf *et al* (1977) have shown that infestations of a scolytid beetle that occur in the propagules of the mangrove *R. mangle* while they are still on the tree, significantly reduce propagule viability when they fall. Reports of scolytid damage in Indo-Malaysia and Australasia regions all report scolytid damage on propagules on the substrate (San Valentin 1986). (Lapis and San-Valentin 1982; Rau and Murphy 1990; Browne 1961). Surveys by Robertson *et al* (1990) of the percentage of mangrove seeds/propagules that had been damaged by insects and other agents (sesarmid crab and physical abrasion) were carried out in 12 mangrove dominated estuaries or embayments along approximately 1200 km of the tropical Queensland coast. These surveys showed that 20-80% of eight of the common mangrove tree species in north Queensland are damaged by insects. A scolytid beetle *Coccotrypes fallax*, was the major cause of damage to propagules of *R. stylosa* (Robertson *et al* 1990). The beetle is common throughout south east Asia (San Valentin 1986; Rau and Murphy 1990). Robertson *et al* (1990) tested the effect of an unidentified scolytid found infesting *R. stylosa* in north Queensland forests and found that survival and growth of seedlings in a shadehouse were not affected. This contradicts observations by Smith (1987 that most of the mortality in *R. stylosa* propagules in field trials was caused by an unidentified scolytid.

These and other contradictory observations of the effect of insect attack on mangrove seeds or propagules (Saenger 1982; Wells 1982; Hutchings and Saenger 1987) suggest more work needs to be done on the effects of insect seed predation on mangrove community structure.

2.3 *The nature of scolytid infestation in mangroves*

2.3.1 Predation on mangroves.

Various organisms had been reported as infesting mangrove propagules in different countries of the world (Rabinowitz 1977; Murphy and Meepol 1990; Robertson *et al* 1990). In particular in the new world mangroves, *R. mangle* and *R. harrisoni* are reported to have propagules attacked by a scolytid identified as *Coccotrypes rhizophorae* (Rabinowitz 1977). In the Old World mangroves, *R. mucronata*, *R. apiculata* and *R. stylosa*, as well as *Bruguiera* spp and *Ceriops* spp are reported as having propagules attacked by *Coccotrypes fallax* (Browne 1961; Murphy and Meepol 1990). In order to study any possible effects of scolytid predation on community structure it is important to have an understanding of:

The natural history of scolytids. What are they, where do they live, what do we know of how they reproduce etc.

The host propagules in which the scolytids live and breed. Which mangrove species are involved, are the propagules available year round, to what extent do propagules move away from parent trees.

The effect of seed predation on community structure. Can predators or parasites affect the recruitment and survival of any host species to the extent that the structure of the community is affected?

Biogeographical considerations. What are the implications of all of the above when considered in relationship to the known distribution of different species of the propagules and scolytids being studied.

2.3.2 The Natural History of Scolytids

Scolytids are members of the family Curculionidae. They are small cylindrical beetles that spend almost their entire lives in the plant tissues in which they breed. Scolytid females lay eggs in chambers excavated from the tissues of the host. The adult female tends the young, removing a sawdust like mixture of borings and excrement (known as frass) from the burrow (Browne 1961). The larvae feed communally, resulting in a large irregular patch within the plant tissue (Kirkendall 1993). Scolytids are known to breed in bark, wood, pith, seeds and seed coats, leaf petioles, stems and roots of herbaceous plants and propagules of mangroves (Browne 1961; Kirkendall 1993).

Wood (1986) recognises 215 genera in the scolytids. Prior to his reclassification, *Coccotrypes* Eichhoff and *Poecelips* Schaufuss were considered as two difficult to separate genera, with similar biology and distribution (Browne 1961). *Poecelips fallax* (Egger) became *Coccotrypes fallax (*Egger*)* following Woods's revision of the family Scolytidae (Wood 1986). Similarly the scolytid which infested propagules in the western (Atlanto-American) group of mangroves is now *Coccotrypes rhizophorae.*

Coccotrypes is one of the numerically larger scolytid genera, with over 100 nominal species (Wood 1986). *Coccotrypes* are primarily borers in fruits and seeds (Brown 1961). When smaller seeds are attacked, the activity of the mother beetle and the larvae eventually hollow out most of the interior (Brown 1961). Most species are recorded from a variety of host families, showing little selectivity with regard to host species(Brown 1961). Brown (1961) provides several examples of seed-breeding species in which host selection is governed by size and texture of the host, indicating selectivity with respect to host condition. Many fruits are attacked only when they have fallen from the tree and successful breeding depends on a favourable moisture content (Kirkendall 1993)

Coccotrypes spp spend almost their entire lives in the tissues of their host, exiting only to find new host material or a place to overwinter (Brown 1961). Fertilisation of the female offspring is thought to take place within the brood chamber prior to dispersal (Kirkendall 1993). The evidence for inbreeding in *Coccotrypes* is based on the fact that they have a highly biased sex ratio. They are haplodiploid with any males produced dwarfed and flightless and thus unable to disperse (Kirkendall 1993).

C. fallax is known to infest propagules of *Rhizophora* spp lying on or speared into the mud (Rau and Murphy 1990). It does not appear to attack seedlings once they have become established (San Valentin 1986). The scolytid attack causes mortality to outplanted *R. mucronata* and *R. apiculata* (Lapis and San-Valentin 1982). In mangroves, which are viviparous, propagule consumption is the parallel of seed predation in terrestrial forest communities.

2.3.3 The propagules of Family Rhizophoraceae.

All members of the mangrove Rhizophoraceae reproduce viviparously, that is the embryo in the seed does not pass through a dormant phase, but continues development while on the tree. The resultant unit of reproductive dispersal being known as a propagule (Tomlinson 1994).

Propagules of the three genera of Family Rhizophoraceae differ from one another in several respects. *Rhizophora* propagules germinate while on the tree through extension of the hypocotyl. The cotyledons are without stipules and fuse to form a tubular collar that remains on the tree when the propagule falls. The hypocotyl of *R. stylosa* is 20 to 37 cm long (40 to 80 cm in *R. mucronata)* with a plumule protected by a stipule pair of first (aborted) leaves (Tomlinson 1994). A distinguishing characteristic are the characteristic H shaped trichosclerids which can be seen protruding from any broken surface of a propagule. *Bruguiera* propagules differ from other member of Rhizophoraceae in that the propagule consists of both fruit and seedling (hypocotyl). *B. gymnorhiza* propagule is up to 25 cm long, cigar shaped, blunt apically and slightly angular (Tomlinson 1994). *B. exaristata* propagules are similar in shape to *B. gymnorhiza*, but much smaller, up to 12 cm long. *B. parviflora* propagules are up to 15 cm long, truncate at the apex and usually less than 5 mm in diameter (Tomlinson 1994) . *Ceriops* propagules are described as up to 25 cm or more, warty throughout, fruit pointed apically. *C. tagal* differs from *C. australis* in that *C. tagal* has distinctly fluted hypocotyls (Tomlinson 1994).

In North Queensland mangrove propagules are found on the mud surface in the vicinity of parent trees following fruiting. Fruiting times for mangrove Rhizophoraceae are in the summer months with mature propagules falling January to March (*Rhizophora*), November to March (*Bruguiera*) and November to May (*Ceriops*) (Jones 1971; Saenger 1982; Duke et al 1984). The propagules of all mangroves are buoyant (Tomlinson 1994; Rabinowitz 1975; 1978a) and after falling, a proportion are dispersed by water. Rabinowitz (1978a) investigated the dispersal parameters including longevity and vigour of six Panamanian mangroves and found that the longevity of *Rhizophora* propagules was a year or more when floating in seawater.

The propagules initially float horizontally but rapidly assume a vertical position in sunlight (Banus and Kolehmainen 1975). Roots appear within 10 to 17 days and first leaves after approximately 40-50 days (Banus and Kolehmainen 1975). Roots and leaves appeared whether or not the propagule was floating or stranded, in light or in the shade, floating horizontally or vertically despite claims that contact with the substrate was required for root formation to occur (Teas and Montgomery 1968). Propagules are thus a latitude dependent seasonal resource in most Australian mangrove forests, with recruitment to the seedling stage usually occurring within two months of abscission, that is usually in the months January to April.

Propagules dispersed out of the forest through tidal movement or flood rains are lost to the seedling bank of the forest. This seedling bank is made up of the seedlings in the understorey whose growth is suppressed by heavy shade (Connell 1971). Rabinowitz (1978) working with four species of propagules which remained viable as seedlings for different lengths of time suggested that those species or genera represented in the seedling bank are likely to succeed in colonising the gap. Any process that reduces representation in the seedling bank, for example species specific predation, has the potential to affect colonisation of light gaps and hence the community structure in the area.

There are a range of factors which affect whether individual propagules remain in the forest area or are dispersed. Propagules of the mangrove Rhizophoraceae are pointed, and this is frequently expressed as an adaptation to promote self-planting (Tomlinson 1994). While it is not difficult to watch this happen it has been suggested the notion deserves little consideration (Tomlinson 1994). The forest floors of the zones dominated by *Rhizophora* and *Bruguiera* have large numbers of roots protruding from the surface or above the surface. These would tend to deflect falling propagules, reducing the number which speared in (Tomlinson 1994).

2.3.4 The effect of seed predation on community structure

Janzen (1970) and Connell (1971) both demonstrated the effect of seed predation on the potential for survival of seedlings, and related this to adult distribution of mangroves in forests. Crawley and Pacala (1991) demonstrated that the potential for herbivory to affect community structure is most likely to occur during the plant's recruitment.

Seed predation has the potential to affect the recruitment and survival of seedlings in mangroves (Smith 1987a; 1987c; Smith 1987c). Monophagous feeding, resulting in differential levels of predation, has the potential to influence the outcome of inter specific competition, thus determining the plant species that obtains dominance in a given community (Crawley and Pacala 1991). Reports on insect predation of propagules of mangroves in Australia refer to all species of propagules in the family Rhizophoraceae (Browne 1961; Robertson *et al* 1990). To date there has been no published detailed study on the scolytid *C. fallax*, the range of host propagules it infests or any measure of host specificity. If differential predation by *C. fallax* is a factor in observed zonation patterns in the mangroves, then knowledge of the host specificity of *C. fallax* is critically important.

2.3.5 Biogeographical considerations

Propagule production is an unusual method of reproduction, found only in mangroves and some seagrasses. It is most highly developed in the family Rhizophoraceae (Tomlinson 1994). Propagules of family Rhizophoraceae appear to be subject to predation pan-tropically by one genus of scolytid, that is *Coccotrypes* spp. *C. rhizophorae* have been reported in *Rhizophora mangle* in the new world mangroves (Woodruff 1970; Rabinowitz 1977; Onuf *et al* 1977), while *C. fallax* have been reported in *R. stylosa* , *R. mucronata*, *R. apiculata, B. gymnorhiza* and *C. tagal* in old world mangroves (Browne 1961; Murphy and Meepol 1990). An unidentified scolytid infesting propagules in Australia was reported by Smith (1987c). Co-evolution of Coccotrypes spp and members of the family Rhizophoraceae thus appears likely.

The biogeographical distribution of members of the family Rhizophoraceae implies a long term separation of the old world and new world species (Chapman 1984; Duke 1995). Allopatric co-speciation may have led to the existence of different species of *Coccotrypes* in the three genera of family Rhizophoraceae in the Old World. Alternatively, the host range for *C. fallax* may have been widened to include *Bruguiera* and *Ceriops*.

2.3.6 Importance of light gaps, disturbance and patch dynamics

The factors underlying species zonation patterns in mangroves are complex and despite several thousand publications concerning mangrove forests (Frith 1977; Rollet 1981), a clear understanding of the processes involved is just beginning to emerge. Research on terrestrial forests in the past few decades has introduced the concepts of gap-phase dynamics, natural disturbance and forest mosaics (White and Pickett 1985). It is important that the dynamics of mangrove forest systems fit within current theories and paradigms developed for other vegetation systems (Smith 1992).

Mangroves are opportunistic colonisers. The availability of light is one of the overriding factors in seedling growth and long term survival. In tests on the effect of light and intertidal position on seedling survival on *Rhizophora*, *Ceriops*, *Bruguiera* and *Avicennia*, all species within the high intertidal survived better in light gaps than under the canopy (Smith 1987a). Any gap, whether in the form of newly available substrate not surrounded by existing vegetation formed as a result of changing sea levels or accreting sediment, or in the form of a canopy gap as a result of storm, lightning strike, or tree fall will be opportunistically colonised. The colonising species will depend on the conditions on the site (water depth, wave action, salinity, period of inundation) and propagule availability at that time. Succession within light gaps may be altered by the size of the gap, the prevailing climatic conditions, the timing (level of survival of shade tolerant seedlings from the previous season) and the length of time before new propagules arrive on site (Clarke 1995).

Osborne and Smith (1990) have shown that the rate of predation on *Avicennia* propagules by grapsids is significantly different under the canopy and in light gaps, and that levels of predation in a light gap are affected by the size of the light gap. Ellison and Farnsworth (1993) demonstrated that seedlings in canopy removal areas had higher survivorship, grew twice as fast and had less than half the herbivory of seedlings growing beneath an intact canopy.

Avicennia, *Ceriops* and *Rhizophora* are all listed as both shade tolerant and intolerant (see Table 2-3). Smith (1987c) has shown that in the case of *Avicennia*, predation levels are decreased in areas associated with higher light levels. McMillan (1971) has shown that un-rooted *Avicennia* propagules are killed by high temperatures, associated with high light levels and shallow water. Extrapolating these two disparate reports, it seems logical to hypothesise that *Avicennia* recruit in a window of opportunity in which abiotic conditions reduce predation, and frequent inundation and deeper water levels keep temperatures below lethal limits during the period of recruitment, while not exceeding the depth criteria for recruitment. This description fits that of the known distribution of *Avicennia* as a pioneer species in the low intertidal. In the uppermost intertidal (above the range of its predator) *Avicennia* may have the potential to recruit during prolonged periods of rain and cloud cover.

Knowledge of factors affecting the survival and recruitment of propagules is fundamental in determining the composition of the adult community in future years since it is typically the seedling stage that experiences the highest mortality (Harper 1977). In order to understand what is happening in a mangrove forest it is necessary to adopt an approach that integrates a number of concepts regarding recruitment, survival and growth of seedlings. These include:

the environmental niche for each species, which includes adaptations to physio-chemical gradients on the site, defining the upper and lower limits in which the seedlings could recruit.

competition, including competition for light, space and nutrients.

predation and/or herbivory, both of which have the capacity to significantly change recruitment levels.

information on the heterogeneity of the landscape which provides refuges from predation for example presence/absence of rocks, fallen branches, cracks or crevices etc. This must be considered on a range of scales.

gap dynamics, including size, frequency and timing (with respect to season) of disturbance which initiated gap formation

history of the site- mangrove fauna and flora have the potential to change many of the abiotic parameters of the site.

2.4 Conclusion

Extensive work has been carried out in describing mangrove zonation, with more recent work emphasising the complexity of associations in some systems (Bunt 1996). Correlations between species and single factors in the environment have been demonstrated, but multi factor experiments have been limited. Predation on propagules of *Avicennia* has assisted in understanding the disjunct distribution of the genus. Predation on *Rhizophora* spp propagules could also be used in part to explain the disjunct distribution of adult *Rhizophora*. Many other anomalies in species distribution are not explained by any of the existing hypotheses. Smith 1992 summed up the status of the six most common hypotheses (Table 2-2-4), I have added a seventh.

Table 2-2-4 Status of several hypotheses proposed to explain mangrove zonation adapted from Smith (1992)

Hypothesis	Status
Zonation represents land building and plant succession	Not supported by the data
Geomorphological control	Geomorphological factors that regulate sediment supply, soil type, texture, accretion and erosion all play an important role in setting the framework within which mangrove forests develop. Climatic factors, particularly rainfall and fresh water run off are also important.
Physiological adaptation to gradients	Application of the results of single factor experiments to the field situation is tenuous at best. Extensive controlled, multi-factor, experiments are needed to fully test this hypothesis. Based on salinity tolerances two groups of mangroves can tentatively be identified: one with an extremely broad range and the other with a narrower range of tolerance.
Tidal sorting of propagules	Not supported by the data.
Differential predation on propagules	More important for some mangroves (eg Avicennia) and in certain regions (eg the Indo-Pacific) than for other groups or regions.
Interspecific competition	Very limited data indicate that competitive interactions occur which could influence zonation.
Importance of light gaps disturbance and patch dynamics.	***Only recently applied to mangrove forest zonation, increasingly seen as important in other forest dynamics.***

CHAPTER 3

STUDY SITES AND GENERAL METHODOLOGY

3 Study Sites and General methodology

3.1 *Mangroves in North Queensland*

This study was carried out during October 1993 to March 1997 in Cairns which is located on the north east coast of Australia at 16° 03' S , 145° 44'E (Figure 3-1). The coastline in this region is protected from wave action by a string of offshore reefs comprising the Great Barrier Reefs, approximately 25 to 35 km off shore.

Protection provided by the reef system is not sufficient to allow mangrove development on the more exposed areas (Dowling and McDonald 1982). Bays, sheltered by headlands, which are protected from the prevailing southmost trade winds, provide habitat within which mangroves can become established (Dowling and McDonald 1982). The largest portion of mangrove habitat in the Cairns region is associated with the sheltered areas adjacent to estuaries and rivers. In this way mangrove communities are isolated from one another, the mangrove lined estuaries forming 'islands' of trees, separated by unsuitable habitats, but linked by water (Beach Protection Authority, Queensland 1984).

Three locations approximately 5km apart were selected in the Cairns region in order to study levels of infestation by scolytids of mangrove propagules. The locations chosen are all adjacent to a river or a creek and located on the Barron River Delta within Trinity Bay. The mangrove forests of the three locations are separated from one another on land by disturbed areas, urban housing and roads but are linked by water in Trinity Bay (Figure 3-2).

Figure 3.1 Location of Study area within Queensland

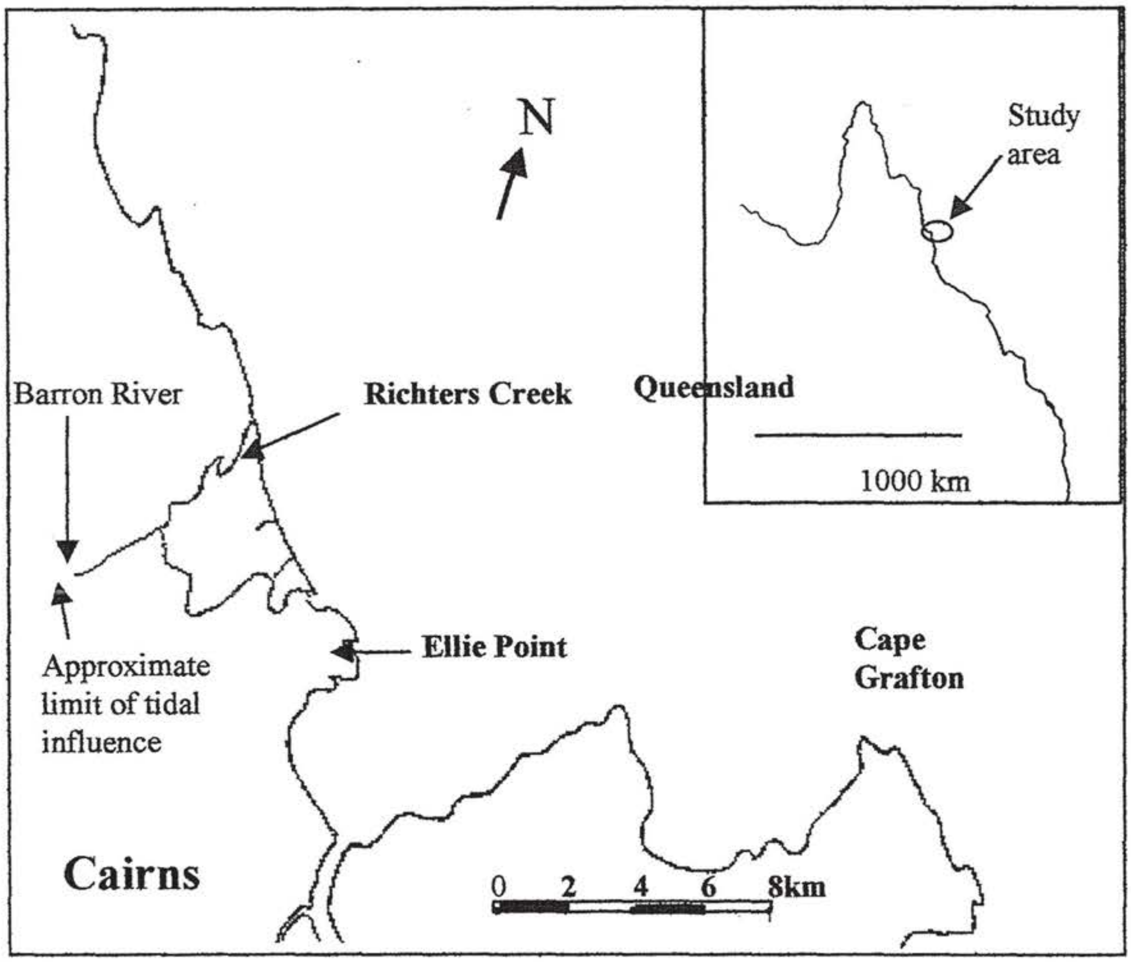
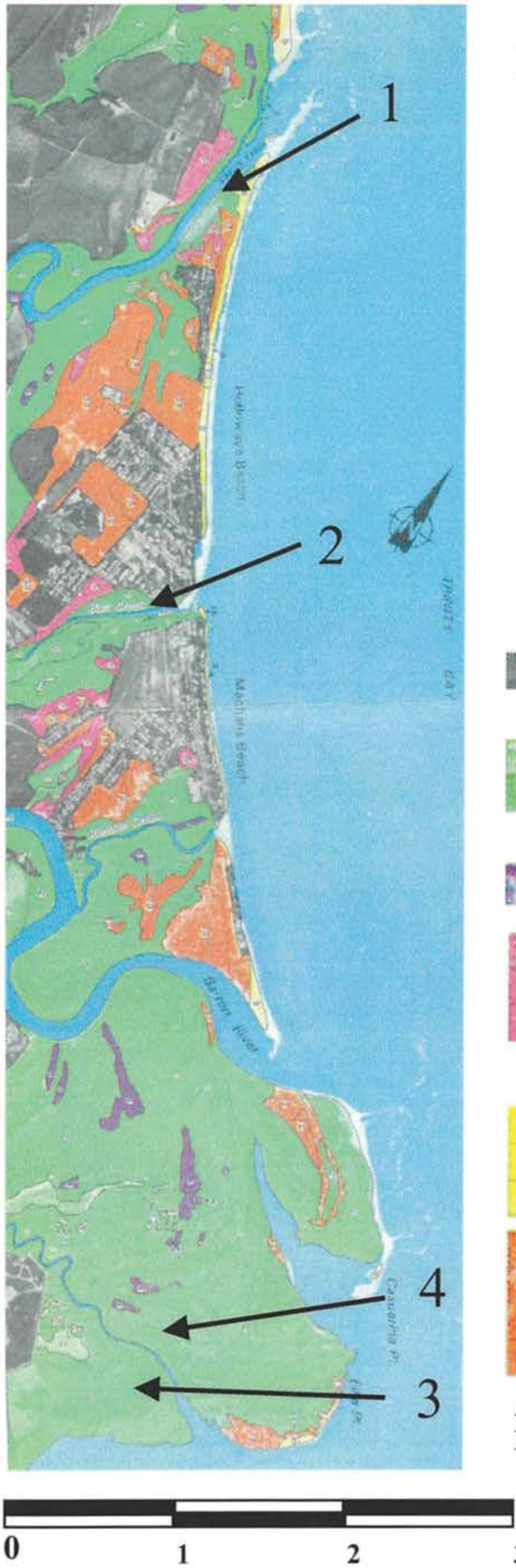


Figure 3.2: Site Location and vegetation



Legend

1 **Richters Creek mangroves**

2 **Barr Creek mangroves**

3 **Airport mangroves**

4 **Ellie Point grow out site**

Disturbed areas

Mangrove and saltmarsh

Stranded beach ridges

Freshwater swamp

Frontal beach ridge vegetation

Hind beach ridge vegetation

Adapted from Coastal Vegetation Map 6.2 Beach Protection Authority Report 1984

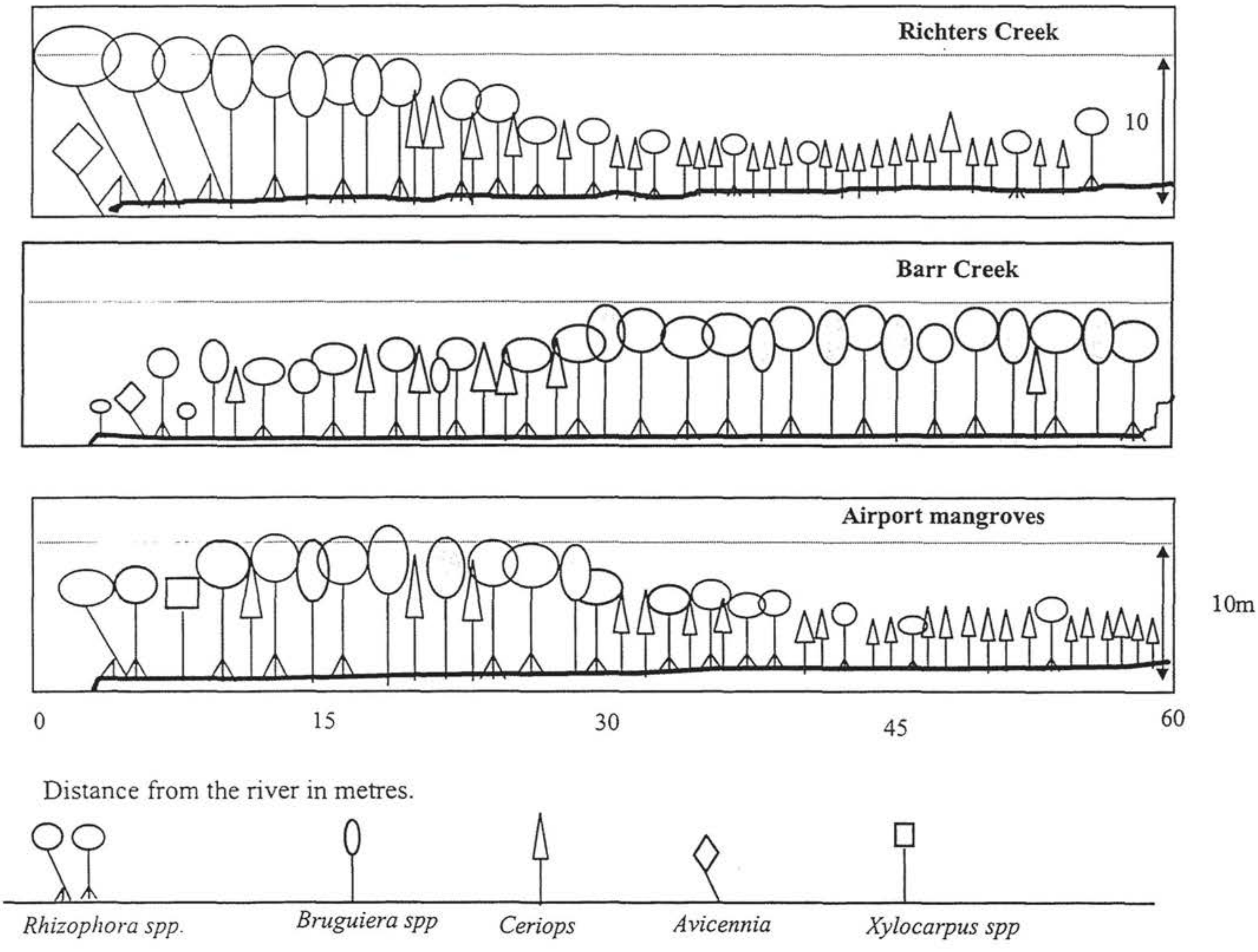
The long term trend of coastline development in Trinity Bay has been towards accretion (Beach Protection Authority, Queensland 1984), within this trend numerous medium and short term cycles of erosion and accretion have occurred. The Barron River Delta during this time has evolved mainly through meander development and river mouth switching. Barr Creek, Richters Creek and Little Barron River are part of this system, though at present only Richters Creek is permanently connected to the Barron River, with Barr Creek and Little Barron River connected only during flood periods. The substrate at each site is muddy sand and sandy mud in back barrier regions laid down through quaternary accretion systems (Beach Protection Authority, Queensland 1984).

All locations used in this study fall within the 'riverine forest ' type which is defined as 'Flood plains along river drainage's, which are inundated by most high tides and flooded during the wet season (Lugo and Snedaker 1974).
Tidal range in Cairns Bay is approximately 3.3m with mean sea level 1.678m (Queensland Department of Transport 1996). Mudflats occupy the tidal level from -0.15 to 1.35m Australian Height Datum (AHD) that is from lowest astronomical tide to mean mid tide level (Bird 1972). Above this level there is a zone of impersistent *Avicennia* spp seedlings merging into an *Avicennia* fringe, extending to the lower limit of *Rhizophora* spp at approximately 1.95m AHD. The mangrove zone extends to an AHD height of 3m. Above this level swamp forests or saline flats are found (Bird 1972). On river banks, the *Avicennia* zone is often reduced or absent. All sites were located in the 1.9m to 3m AHD level.

3.1.1 Location and Site selection

Locations were chosen on the basis that each contained representatives of all three mangrove genera of the Family Rhizophoraceae. Figure 3-3 shows the vegetation profiles of all three locations, indicating the presence of *Bruguiera*, *Ceriops* and *Rhizophora*. *Avicennia* spp were found close to the river at Richters Creek and Barr Creek. Several *Xylocarpus* spp were found close to the river at the Airport mangroves. (Figure 3-3) but overall *Bruguiera*, *Ceriops* and *Rhizophora* dominated the locations. The species composition of all three locations was established by counts of trees with dbh (diameter at breast height) of 10cm or more, with dominance in any area based on proportional canopy cover of each species. The value, 10 cm dbh, was chosen as preliminary counts had shown trunk diameters in the size range 7 to 13 cm were uncommon, trees with dbh> 10 cm had reached the canopy and tended to be much larger, seedlings and saplings in the understorey had dbh << in the three locations.

Figure 3.3 Stylised vegetation profile of the three locations



Sites within locations

Two sites within each location were established separated by a distance of approximately 30 metres. Each site extended along the bank of the river for approximately 50 metres and back at right angles as far as the 3m AHD line. The high intertidal limit of the mangroves made up the 4th side. This was easily identified by the vegetation change from mangrove to hind dune or salt flat vegetation which occurs at the 3m AHD level. Surveyors tape markers were tied to large trees at intervals along the boundaries. The immediate river bank and a distance of 1m in from the bank was not sampled as there was a danger from salt water crocodiles (*Crocodylus porosus*) which inhabit all river systems in the region. In each site a permanent transect, 50 m long and two metres wide was marked out. In all cases the transects were in areas dominated by adult *R. stylosa.*

Location 1 Richters Creek

Richters Creek (Figure 3-4), more accurately known as the Thomatis/ Richters system is a small creek which, during the floods of 1932 became linked with the Barron River system forming the northern mouth of the Barron River (Beach Protection Authority, Queensland 1984). The Barron River flows year round, though dry season flow is minimal. The river is tidal during the dry season and mangroves line the banks for a distance of at least 3km upstream from the river mouth.

Within each site the area closer to the river is dominated by *Rhizophora stylosa.* These occur in pure stands or in association with *Ceriops* spp or *Bruguiera* spp (Figure 3-5). The landward zone is dominated by *C. australis* and *C. tagal* with occasional *R. stylosa.*

Figure 3.4 Richters Creek sites

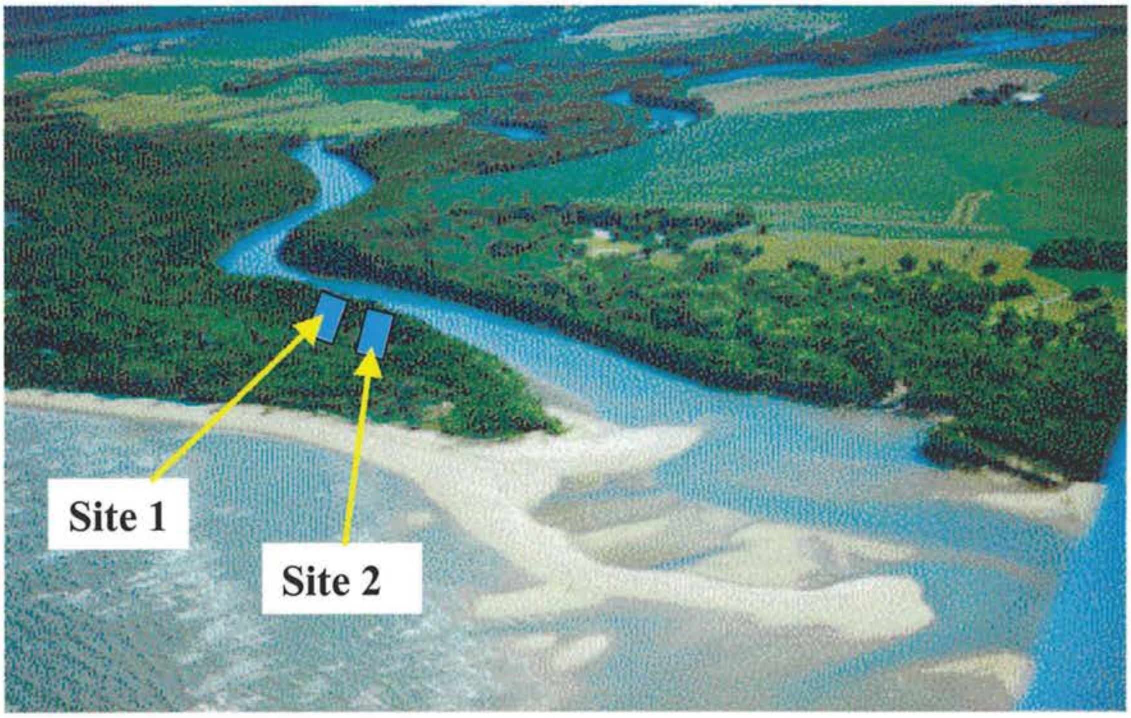


Figure 3.5 Richters Creek Site 2, typical vegetation on transect through site

Location 2 Barr Creek

Barr Creek is a small estuarine creek which forms part of a declared wetland Reserve and functions as an important flood overflow for the Barron River Delta (Beach Protection Authority, Queensland 1984). Most years the mouth remains open all year, but on occasions a sand barrier closes the mouth during the dry season Beach Protection Authority, Queensland 1984). When the mouth closes, the normal tidal influence is moderated, with water having to seep through the sand bar separating the creek from the open sea. This results in a tidal change of up to 3m in the adjacent sea being reduced to one metre or less in the creek. The rate at which drainage occurs is reduced. Rain in the area can result in the mangroves being flooded with fresh water, which drains away over a period of days to weeks, rather than with the normal daily tidal flushing.

Closing of the river mouth occurred in the middle of 1993 and it remained closed until March 1994 when heavy rains and flood conditions flushed the estuary and broke open the seaward sand barrier. The mouth remained open for the remainder of the survey period. This change in inundation pattern altered the abiotic conditions on the substratum during 1994 resulting in the mud surface drying out in dry weather even during spring tide periods.

At other times following rain and prior to the opening of the mouth, standing water to a depth of 4 to 10 cm was noted. A storm water drain that collects storm water run off from the adjacent suburb enters the location at the back of the mangrove between the two sites.

Several species associations are represented, *R. stylosa* with *B. gymnorhiza*, *R. stylosa* with *B. exaristata* and *R. stylosa* with *C. tagal* combinations being the most common (Figure 3-7). *B. parviflora* was not recorded at this location.

Figure 3.6 Barr Creek sites

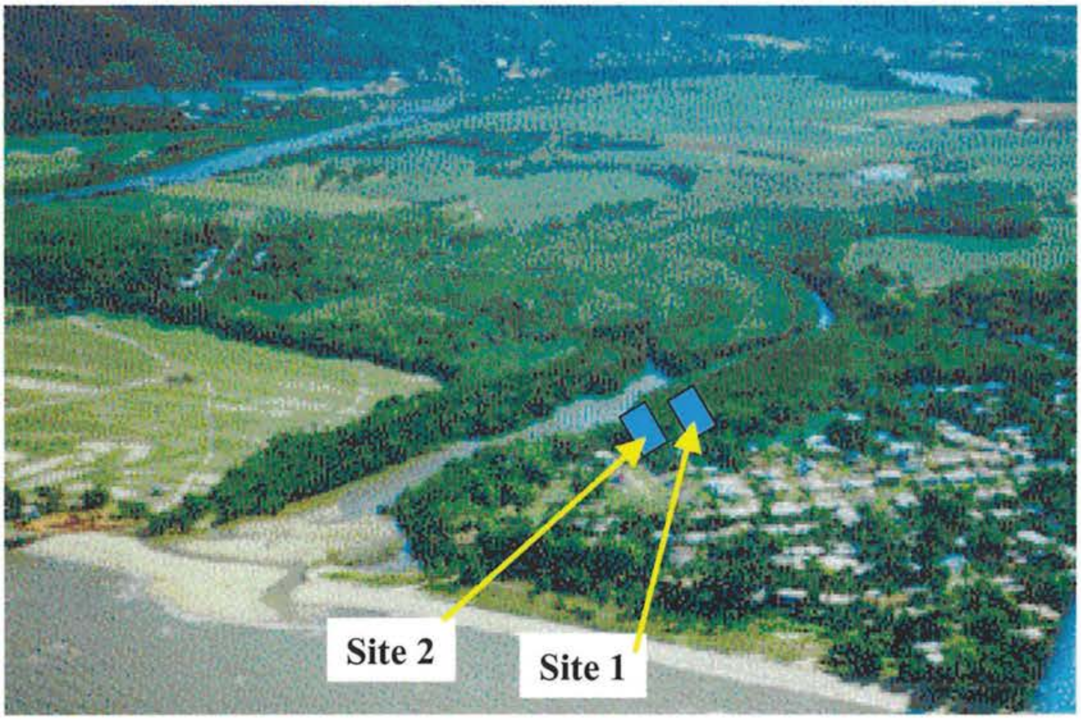


Figure 3.7 Barr Creek Site 1, typical vegetation on transect through site.

Location 3 Airport Board walk Mangroves

The sites are adjacent to the 'Little Barron River (Figure 3.8). The Little Barron is between 2 and 3 km in length and serves as a flood overflow during the wet season. Drainage from the adjacent airport storm water system is split between The Barron River, Salt Water Creek and the Little Barron entering upstream from the sites. The species composition of the location is patchy, with *R. stylosa* /*B. gymnorhiza*, *R. stylosa* /*B. parviflora* and *R. stylosa* / *C. tagal* combinations. (Figure 3-9)

Site 2 at the Airport differed slightly from all other sites through the presence of a nest of ants on the mud adjacent to the river bank. The nest was covered by water from mid tide onwards. It was presumed that the nest was *Polyrachis sokolova*, which in Australia is found only in the lower intertidal, in the *Ceriops* and *Rhizophora* zone (Hogarth 1999). The nest is up to 45 cm deep and has two entrance holes which are blocked by soil which collapses in on them when the advancing tide reaches the nest. Food remains found in the nest include small decapod and amphipod crustacea, lepidopteran larvae and other insects (Hogarth 1999). There is a possibility that *P. sokolova* are predators on *C. fallax*.

Figure 3.8 Airport Sites

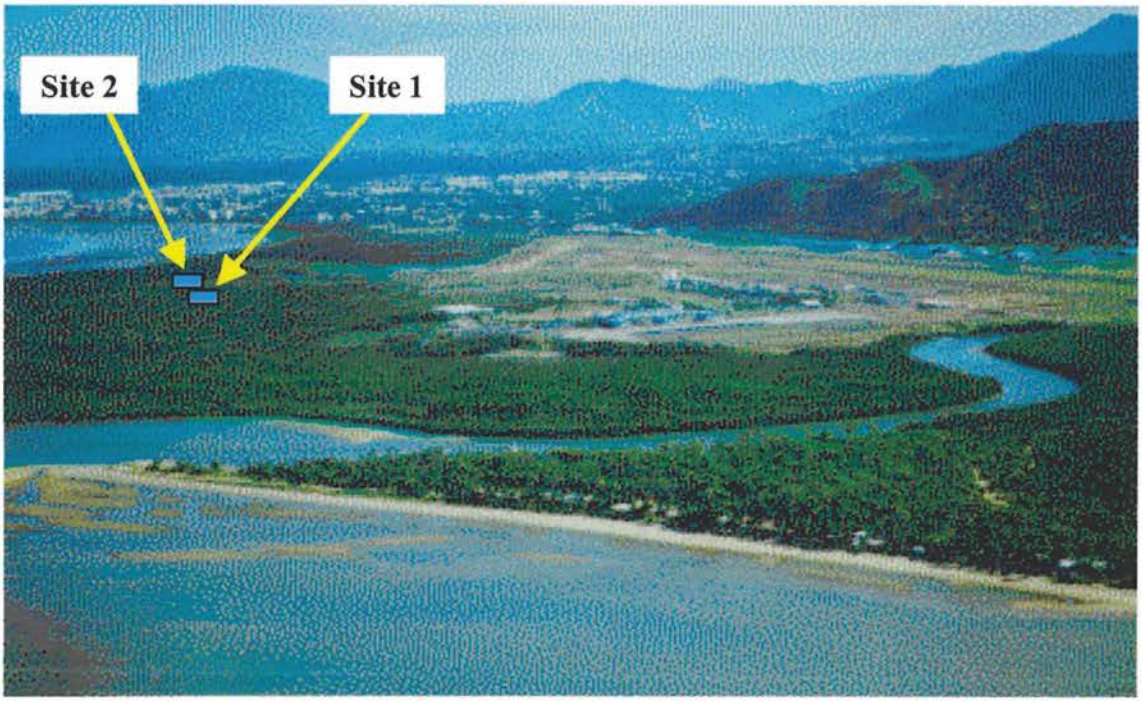


Figure 3.9 Airport mangroves Site 1, typical vegetation on transect through site.

Grow out site

In January 1995 an area for growing out propagules was established (Figure 3-10). All planting of propagules occurred in an area recently cleared of mangroves for a survey adjacent to the airport. This site met all the requirements for the grow out site which included

that it be in the tidal inundation zone in which *Rhizophora* normally grow

that the substrate was suitable for growth of *Rhizophora*

that there was sufficient light for growth (*Rhizophora* seedlings are shade intolerant)

That it was not exposed to direct sunlight for large periods of the day, ie. the overhead canopy reduced effect of direct sunlight to less than three hours a day,

Light gap site

The site to establish any difference in level of *C. fallax* infestation in shade and light gaps, required that the site be suitable for *Rhizophora* growth, be supplied naturally with propagules, yet not have any established trees. Without a disturbance of some sort, any site meeting this description would soon be covered in seedlings and saplings. Any site that did not recruit seedlings naturally would not qualify. Mudflats that meet these criteria occur on naturally accreting systems and in logged areas. In Cairns, for a variety of political, economic and aesthetic reasons, the city council has a policy of clearing all seedlings from the mudflat on the foreshore fronting the Esplanade (Galloway 1982). Every year a contract is given out to manually remove any seedlings that have survived the dry season, the majority of these seedlings are *Rhizophora* spp (Galloway 1982). Without active intervention (namely seedling removal) this area would behave in a manner similar to that of the southern portion of the inlet where the *Rhizophora* zone has advanced considerably over the last 50 years (Bird 1972; Galloway 1982)

Seedlings recruiting in this area receive no shade between the hours of 7 am and 5pm, unlike those in the adjoining forest, where light levels are much lower. At the northern end of the esplanade, there is a large area of mangrove immediately adjacent to the cleared area. This mangrove is dominated by *R. stylosa* and *R. apiculata* with an *A. marina* fringe on the seaward side.

Figure 3.10 Ellie Point grow out site showing tagged seedlings

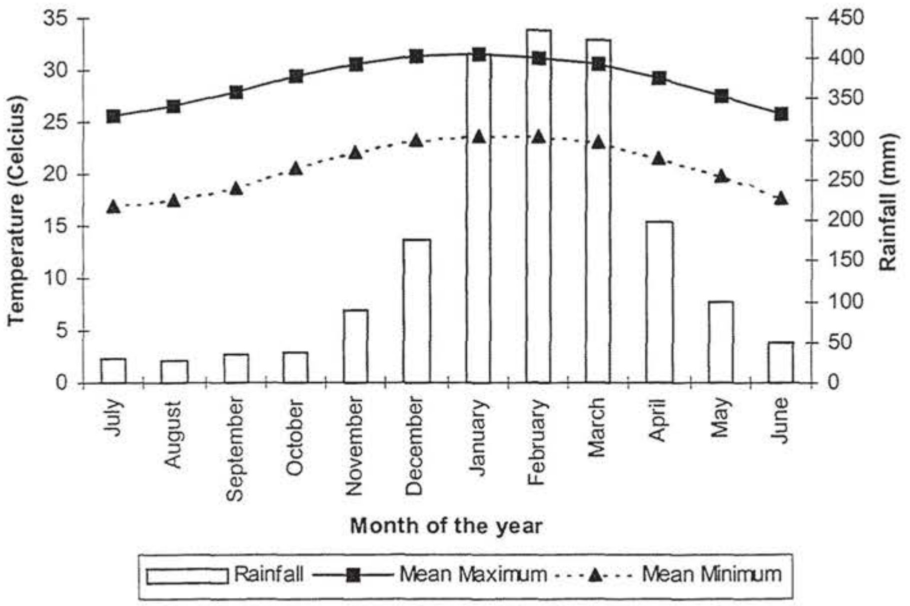
a: Growth of seedling measured from the top of the hypocotyls to the point where the last pair of leaves emerge.

3.1.2 Meteorological Data

The average yearly rainfall for Cairns is 2225 mm falling over 145 days per year (Bureau of Meteorology 1999). Heavy rains occur during the wet season, January to April (Figure 3-11). Flood rains are associated with low-pressure systems and cyclones in the Coral Sea and Gulf of Carpentaria. During periods of heavy rain up to 300mm may fall in a 24-hour period (Bureau of Meteorology 1999). This wet season coincides with the period of propagule abscission (Duke 1984), propagules falling during this time have the potential to be widely dispersed as flooding rivers carry them out to sea.

The hottest months are January and February, with average maximum temperatures of about 32^{0}C. July is the coolest month, with average maxima about 26^{0}C and average minima of about 17^{0}C (Figure 3-11). Seedling growth is reduced during the cooler months. Insect growth rates are temperature dependant (Mathews and Kitchling 1984), and reproduction may cease entirely during the cooler months.

Figure 3-11 Mean monthly rainfall, maximum and minimum temperatures for Cairns (Bureau of Meteorology).



Insolation levels (energy transferred through sunlight) can be measured as total energy incident on an object, including reflected and refracted radiation and is given in tens of kilojoules per square metre. The region receives approximately 12.5 hours of daylight in summer, with insolation levels rising from zero at dawn and peaking between the hours of 10.30 and 13.30. Average insolation levels for the months of propagule dispersion and recruitment (October to April) for Cairns are given in Figure 3-12.

Insolation levels vary with cloud cover. Mean levels tend to be higher in October, November and December as these have more hours of sunlight (ie fewer hours when cloud obscures the sun) than January, February and March, the 'wet' season months. Cloud cover decreases the incident radiation dramatically. Daily radiation levels plotted for a whole month give a graphic illustration of the daily variability, while still maintaining the normal distribution curve for insolation over the 12.5 hours of sunlight (Figure 3-13).

Figure 3-12 Mean Insolation levels as measured at the Cairns Bureau of Meteorology weather station for the months October 1997 to April 1998

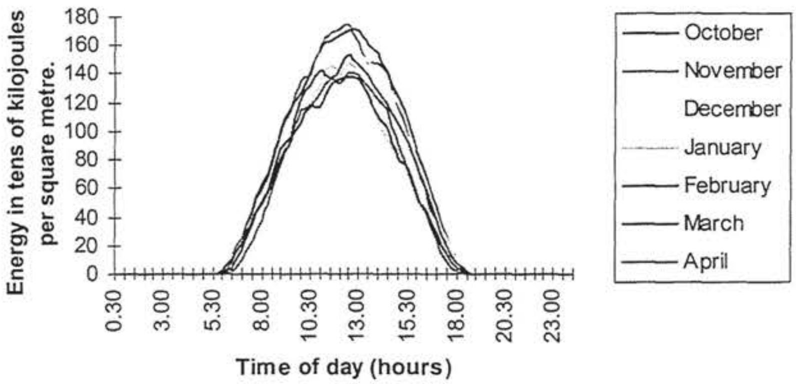


Figure 3-13 Daily radiation levels in Cairns, January 1998. Compiled from data provided by Bureau of Meteorology, Cairns. Each line represents the daily radiation levels for one day of the month of January 1998.

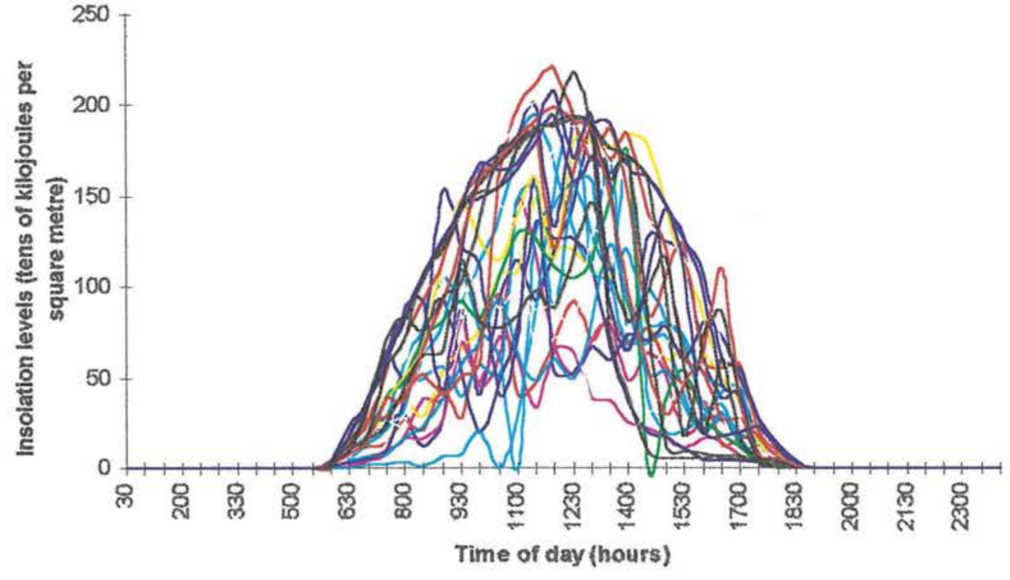
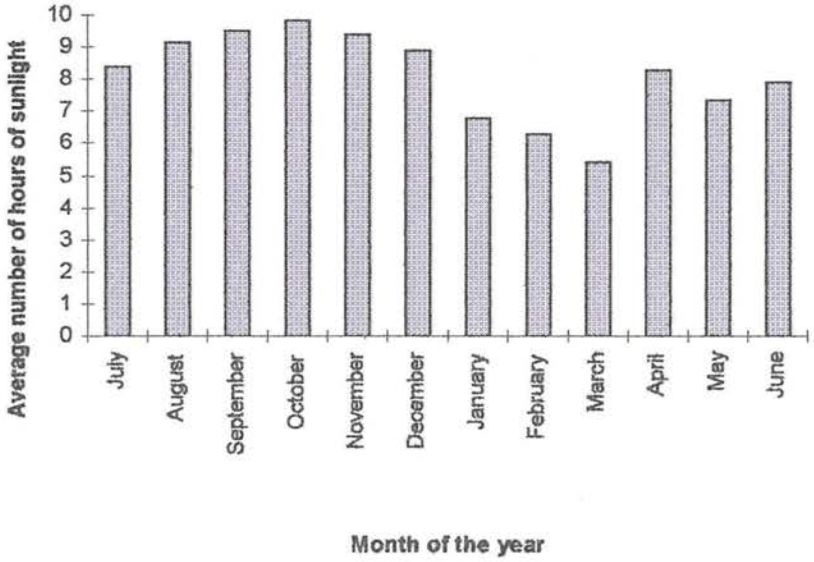


Figure 3-14 Average number of hours of sunlight in Cairns.



Compiled from information supplied by the Bureau of Meteorology, Cairns.

3.2 General Techniques and definition of terms

3.2.1 Potential host species

Previously published reports of *Coccotrypes* spp infestation (Onuf et al 1977; San Valentin 1986; Smith 1987a; Rau and Murphy 1990; Robertson et al 1990). indicated that infested propagules were all members of the tribe Rhizophoraceae. In order to determine host specificity within the tribe, locations were sampled to determine the range of species from three genera in Family Rhizophoraceae in the area and choose sites that maximised species representation within the tribe. The mangrove tribe of the *Rhizophoraceae* consists of four genera, *Kandelia*, *Bruguiera*, *Ceriops*, and *Rhizophora* of these three, *Bruguiera*, *Ceriops*, and *Rhizophora,* are found in the Cairns area. In the study sites the following species within each genus were identified.

In *Bruguiera* Lamark; *Bruguiera exaristata* Ding Hou, *B. gymnorhiza* Lamk., and *B. parviflora* Wight and Arnold ex Griffith were identified.
In *Ceriops* Arnold; *C. tagal* (Perr.) C.B. Robinson and *C. australis* (Perr) C. B. Rob. were identified.
In the genus *Rhizophora* L; four species were identified, of these only three *R. stylosa* Griff. and *R. apiculata* BL. and *R.*x *lamarckii* Montr. were identified growing in one or more of the sites. *R. mucronata* Lamk. propagules were occasionally found on the substrate.

All sites were chosen on the basis of having mature trees of most of the above species present. All species identified in the study sites are listed as occurring in the region (Table 3-1). Identifiable propagules of all species are not all present all year round.

Table 3-1 Mangrove Rhizophorae found in the Cairns region and those found in study sites.

Species	Duke 1994	Present in study sites
Bruguiera cylindrica	x	
Bruguiera exaristata	x	x
Bruguiera gymnorhiza	x	x
Bruguiera parviflora	x	x
Bruguiera sexangula	x	
Ceriops decandra	x	
Ceriops tagal var tagal	x	x
Ceriops tagal var australis	x	x
Rhizophora apiculata	x	x
Rhizophora stylosa	x	x
Rhizophora mucronata	x	
Rhizophora x lamarckii	x	x

3.2.2 Identifying characteristics of members of the mangrove tribe of Family Rhizophoraceae.

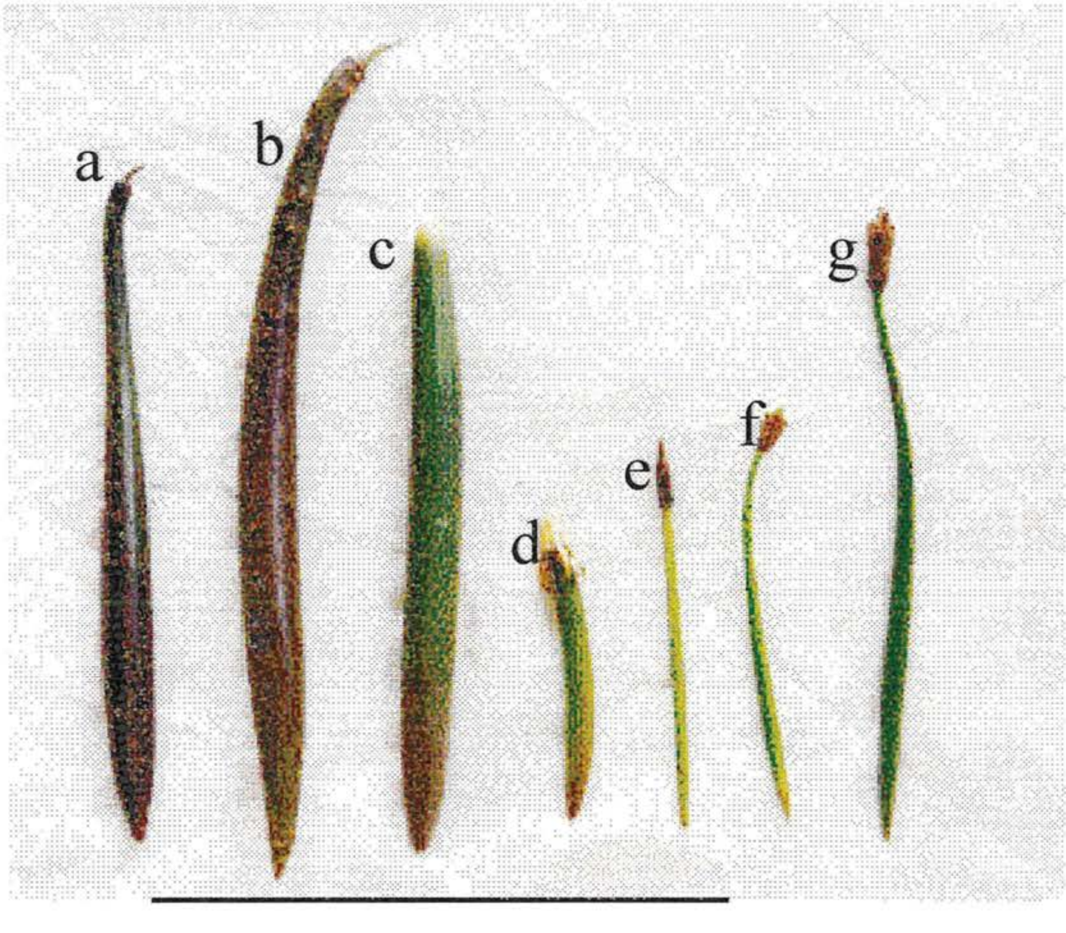
Gross morphological features including root structure, bark, leaf size and shape make differentiation between mature members of the three genera straightforward. Floral characteristics can be used to identify trees to species level with little difficulty. Descriptions and keys are provided in (Tomlinson 1994; Duke and Bunt 1979; Lovelock 1993; Lear and Turner 1977). All of these however rely on a combination of characteristics to identify to species level because of the range and overlap of individual characteristics (**Table 3-2**). This can, on occasion, present a problem with identifying propagules already detached from the parent tree.

Table 3-2 Mean measurements (cm) for propagules of *Rhizophora* species, with {range} and [number of components measured]. Taken from Table 4 (Duke and Bunt 1979)

Character	*R. apiculata*	*R. .lamarckii*	*R. stylosa*	*R. mucronata*
Hypocotyl L	28.2 {20-37} [104]	18.7 {14-28} [4]	42.0 {26-65} [116]	58.7 {40-80} [79]
Hypocotyl W	1.68 {1.2-2.0} [104]	1.2 {1.0-1.3} [4]	1.58 {1.2-2.1} [116]	1.69 {1.2-2.1} [79]
Collar W	0.8 {0.6-0.9} [104]	0.73 {0.6-0.9} [4]	1.07 {0.8-1.4} [116]	1.02 {0.8-1.3} [79]

Despite this overlap in individual characteristics, with experience it is generally easy to identify most propagules. This is in agreement with the finding by Duke and Bunt (1979) who found that although identification of species can easily be confused when direct distinctions are made through measurements of phenotopic detail, it was established that , with practice, *Rhizophora* species could be distinguished at a distance on tree foliage and habit. Similarly in this study is was possible to distinguish propagules of different *Rhizophora* species through less definitive attributes such as the difference in curvature of the propagules over the lower third, central and upper third of the hypocotyl (Figure 3-15)

Figure 3.15 Propagules of Family Rhizophoraceae found in the study sites.



Legend

a *R apiculata*

b *R. stylosa*

c *B. gymnorhiza*

d *B exaristata*

e *B. parviflora*

f *C. australis*

g *C. tagal*

Propagules which did not have the typical *R. apiculata* shape or the length which characterises *R. mucronata* were grouped in with *R. stylosa*, the most common of the *Rhizophora* spp in each location. *R. mucronata* tend to be found upstream from the locations used in this study (Tomlinson 1994) and no *R. mucronata* trees were identified on any of the sites. On occasion *R. mucronata* propagules were found washed into the location, these were examined for evidence of *C. fallax* infestation

Immature propagules, detached by high winds or dropped by stressed trees, may not yet have attained the identifying characteristic shape of *R. apiculata* or the distinctive length of *R. mucronata*. Similarly, where propagules are speared into the mud, the lower third of the propagule, used in distinguishing between *R. stylosa* and *R. apiculata* may be hidden. Where this occurred, the propagules were deemed to be *R. stylosa*, the most common tree species in all sites. The hybrid *R lamarckii*, tends to be infertile and not produce mature propagules (Duke and Bunt 1979). *R. lamarckii* made up less than 2% of their sample of 303 propagules. It was not considered to be a significant portion of the *Rhizophora* spp propagule population and no attempt was made to identify *R. lamarckii* propagules as distinct from immature *R. stylosa* propagules in this study.

Propagules of *B. gymnorrhiza*, *B. parviflora*, *B. exaristata*, *C. australis*, *C. tagal*, *R. stylosa* and *R. apiculata* (Figure 3-15) were identified using descriptions from Lovelock 1993, Tomlinson 1994, Duke and Bunt 1979 and confirmed by Dr U. Kaly, Department of Marine Biology, James Cook University.

Some reports indicate scolytid infestation took place while the propagules were still on the tree (Onuf *et al* 1977). Given the height of mature *Rhizophora* in Cairns and the difficulty involved in obtaining unbiased samples of propagules on trees, collections were limited to propagules on the mud.

3.2.3 Definitions and clarification of terminology.

The unit of propagation is a propagule (a seedling which germinated on the parent tree) and not a seed. The term 'germination' is not used in reference to propagules, as in viviparous mangroves this takes place on the tree, before formation of the propagule. As the propagule spends time in the water during the dispersal phase, it is convenient to use the terminology associated with larval dispersal of marine organisms.

Thus the period when the propagule attaches to the substrate by the formation of roots is recruitment. Loss of propagules prior to recruitment will be attributed to 'pre-recruitment mortality'. Prior to recruitment the hypocotyl will be known as the propagule, after recruitment it is a seedling. Death of a seedling is recorded as seedling mortality. Emergence of the first two leaves on the seedling is taken as evidence of recruitment. Leaf production is associated with root production and in the field any intact seedling with two leaves is firmly rooted.

Propagules lying loose on the mud are more likely to float away on the flood tide than those speared into (and held by) the mud. However the mud surface is irregular and propagules on the mud are found at all angles to the horizontal.

Propagules 'lying' on the mud are those that were at less than 30° to the horizontal. In classifying intermediate cases whether or not the tip of the propagule was buried in the mud substrate was taken into account.

Propagules 'speared' into the ground are those with the majority of their length clear of the ground, the lower end embedded in the mud, usually making an angle of greater than. 30° to the horizontal. As propagules are seldom seen to fall and 'spear in' the manner in which the propagules attain the position other than a direct fall from a tree may be any of the following or a combination thereof.

Self elevation is the phenomenon whereby propagules lying on the mud grow roots from the distal portion into the mud, followed by bending of the propagule to

elevate the upper two thirds of the hypocotyl. Seedlings with this 'J' shape are common although long term survival may be reduced (McKee 1995b).
Propagules floating with the root end of the propagule even slightly lower than the tip, will tend to be caught in irregularities of the substrate. Subsequent partial flotation of the tip will then lead to the distal portion becoming more securely embedded in the substrate.
Movement by predators. It is common to see propagules sticking out of crab holes. Damage to the propagule varies from a few claw marks to consumption of a large proportion of the propagule. For the purpose of data collection, propagules in crabholes are classified as 'speared' as experience indicated they would recruit in this position.

No attempt is made to distinguish the process by which propagules attained their position with respect to the mud surface (Appendix 1). The interchangeability of the positions is recognised and taken into account in the interpretation of the results.

CHAPTER 4

INFESTATION OF PROPAGULES BY *C. FALLAX*; HOST SPECIFICITY AND SEASONAL VARIATION IN LEVELS OF INFESTATION

4 Infestation of propagules by C. fallax; host specificity and seasonal variation in levels of infestation.

4.1 Introduction

The scolytid beetle, *Coccotrypes fallax* was described as infesting propagules in mangrove forests in Malaysia (San Valentin 1986), Philippines (Lapis and San-Valentin 1982), and Thailand (Rau and Murphy 1990). In Australia Robertson *et al* (1990) reported on an unidentified scolytid affecting the survival of *Rhizophora* spp seedlings. Zimmerman (1992) reported on the presence of *C. fallax* in the mangroves at Hinchinbrook, North Queensland. This was the only official record of *C. fallax* in Australia in the literature. Information on host propagules of *C. fallax* suggested that the scolytid reported by Robertson (1990) was in the genus *Coccotrypes* and could be *C. fallax*.

Reports on the host plants for *C. fallax* in the Indo-Pacific region include propagules of most of the members of the mangrove tribe of the Family Rhizophoraceae (Browne 1961; Lapis and San-Valentin 1982; Rau and Murphy 1990; San Valentin 1986; Wood 1960). There was no data given to identify which of the genera or species were the preferred host, or if the scolytid was host specific or feeding opportunistically on available propagules.

There were conflicting reports as to whether the scolytids infested the propagule prior to abscission, ie. while the propagules were still on the tree (Onuf *et al* 1977), or after abscission, while the propagules were on the ground (Rau and Murphy 1990; San Valentin 1986). Propagules are the reproductive unit in mangrove Rhizophoraceae, and are dispersed by water (Tomlinson 1994). Whether propagules are infested prior to dispersal (while on the tree) or after dispersal has begun (while on the ground) has the potential to affect the ability of the host species to colonise new locations. If infestation occurs while on the tree, the period of host availability begins before propagules begin dispersal. If, however, propagules are infested on the ground the level of infestation, rate of change of infestation level and rate of dispersal of propagules has the potential to influence the effect of infestation on the community.

Mangrove propagules are a seasonal resource, falling in the summer months (Duke 1984). There is usually a time lag between any increase in host population and subsequent increase in predator numbers (Krebs 1994). The extent of this time lag may affect the number of propagules that escape predation by dispersing away from the parent tree.

Propagules that fall from the tree may spear into the mud, or land up lying on the mud. Propagules are dispersed away from the parent tree rapidly (Yamashiro 1961). There were no reports which indicated whether the position of the propagule on the forest floor, that is whether it is speared into the mud or lying on the surface affected the likelihood of the propagule becoming infested before moving away from the parent tree. The level of infestation of dispersing propagules has implications for both dispersal of the infesting scolytid and the colonising ability of the propagules.

4.2

Identification of infested propagules

The life cycle of *C. fallax* means that the adult scolytid emerges only to fly or move onto another host propagule prior to boring in (Browne 1961). This means that the only visible sign of infestation is often a small entrance tunnel (Browne 1961), infesting scolytids are very rarely seen on the outside of a propagule. A reliable means of identifying infested propagules would be useful in studying the effect of infestation on recruitment, where dissection of the hypocotyl to establish infestation would not be required.

This lack of information on *C. fallax* infestation in Australia left many questions unanswered, specifically

What specie(s) of scolytid infests propagules in North Queensland?

Is infestation confined to a few isolated forests or is the beetle found in forests across the majority of the host propagule range?

Which species of propagules are infested by the scolytid, and is one or more species the preferred host?
Is host selection correlated with species, mass of propagule or weight of propagule?
When does infestation occur, on the tree or while on the ground?
What proportion of propagules become infested and do these levels change over the season?
Do levels of infestation vary at different locations and during different years?
Does the position a propagule, after landing on the mud, affect the likelihood it will be dispersed away from the parent tree?
Is there a method of identifying infested propagules by external signs only without disturbing their position on the forest floor?

4.3 Methods

To obtain information on host species infested by *C. fallax* in North Queensland a number of propagules, representing different species within the Family Rhizophoraceae, were collected from three locations in Cairns over a two year period. These propagules were dissected and examined for evidence of infestation. In addition possible external indicators of infestation were noted and checked against the results of the dissection in order to assess the reliability of these indicators in predicting;

whether or not a propagule had ever been subject to scolytid attack

whether or not the propagule was still infested by a viable colony of *C. fallax*.

the level of infestation ie. number of viable scolytids present.

4.3.1 Sampling within the Cairns region

Propagules were collected from three locations, Richters Creek, Barr Creek and the Airport (see Chapter 3), two sites at each location. During the dry months (May to November) sites were visited monthly to check for the presence of propagules on the ground. Presence of newly fallen propagules would have indicated possible food source and habitat for *C. fallax* during winter other than propagules from previous season. Sites were sampled at two weekly intervals from December to April. Propagules of the three genera, *Bruguiera*, *Ceriops* and *Rhizophora* all fall to the mud within this period (Duke 1984, Tomlinson 1994).

The three locations were sampled on consecutive low tides during daylight hours. As all sites are in the intertidal zone, sampling hours were restricted to those when the tide was low enough to allow access to the whole site. In the summer of 1993/1994, twenty propagules of each species were collected from within each site whenever possible. Not all species were present at each site, especially early in the season therefore it was not possible to find 20 propagules of each species each time. Each propagule, with a tag recording date, site and location, was placed in an individual plastic bag to minimise the possibility of cross infestation occurring prior to examination of the propagules.

The following season (1994/1995), having established a method of external identification of infestation, propagules were assessed on site.

4.3.2 Methods of identifying infested propagules.

Propagules collected in the sampling program used to find the host range of *C. fallax* were used to measure the reliability of assessing infestation from external signs only. In the laboratory, each propagule was wiped clean of mud and sand after presence or absence of frass was noted. Propagules were then measured (length and wet weight), and other external evidence of infestation noted (boreholes, discolouration etc) prior to dissection to establish the presence of *C. fallax*. The presence or absence of frass at the mouth of the borehole was recorded. Dissection was done on a wooden cutting board using a sharpened stainless steel knife to split the propagule lengthways. This exposed tunnels, which were then further exposed either with cuts or by breaking the propagule along the line of weakness.

Where propagules were infested, the number of adults, eggs, larvae and pupae were counted. Where an adult was cut in half, an estimate of the number of whole adults represented by the body parts was made.

Adults differ in colour according to time since pupation, newly emerged adults are pale, darkening over time (Browne 1961). In this way it was sometimes possible to distinguish between the parent and offspring even after pupation. Adults were identified using the description in Wood (1960). This describes females only. Specimens of both male and female scolytids found in the propagules were sent to C.S.I.R.O. Canberra for confirmation of identification. Notes were made of infestation or damage by other organisms.

A method of identifying infested *C. fallax* through the production of frass was established (See Appendix 1) and this allowed for field estimates of infestation levels without disturbing the propagules in any way.

4.3.3 Data collection in transects

Fixed transects 25 m long, 2 m wide were established in both sites at each of the three locations for the start of the second season of data collection (October 1994 to June 1995). Within this transect, numbers and health, (clear or infested) of propagules were recorded. Examination of the results at the end of the season, indicated that important information (eg. how many propagules had fallen recently and how many had moved off the transect) was hidden within the seasonal change in propagule numbers.

During the third season changes in numbers and infestation levels of cohorts of propagules was recorded. A cohort in this context refers to a group of propagules that all fell within a specified time period within the season along the transect. This involved tagging of all propagules on the transect. Tagging of fallen propagules was carried out by inserting a tagged bamboo skewer into the mud adjacent to the propagule (Figure 4-1). A second tagged stake, recording infestation, was inserted next to any infested propagules. Tags on each skewer were made with different colours of pressure sensitive plastic 'Dymo' tape. The skewers indicated the position of the propagules. Observations during pilot studies had shown that the skewers did not interfere with the movement of propagules at high tide.

When propagules were dispersed away from the transect during high tides in the interval between assessment dates by water movement, the tags were removed from the substrate during the next data collection day. Newly fallen propagules are relatively easy to distinguish from those of a previous cohort by the colour changes that occur when propagules are repeatedly immersed in muddy water. In this way it was possible to identify when a propagule had been moved a short distance within the transect, versus propagules which were newly fallen. Data for each cohort was recorded each survey date on the number of propagules lying on the mud, the number speared into the mud and the number recruited as seedlings (possessing at least 2 leaves) for both infested and clear propagules.

Figure 4.1 Tagged propagules on the forest floor at Richters Creek. Bamboo skewers with 'Dymo' tape markers were used to indicate the period in which the propagules had fallen.

Tagged propagules could be identified as part of a cohort, ie. identified with respect to the period in which they had fallen. This data was then used to compare the mean length of time the propagules in a cohort had been on the ground with the level of infestation within that cohort. The number of propagules of each cohort and the position of the propagules on the mud (lying or speared) which were lost from the transect, by water dispersal or consumption by predators could also be estimated. The data on cohort and propagule position was only available for the final year of data collection.

4.3.4 Manipulation and analysis of data

Host specificity

To determine whether propagules of *Rhizophora*, *Bruguiera* and *Ceriops* were infested equally, (ie H_o ; No difference in frequency of propagules infested) chi – square values were calculated and checked for statistical significance. Similarly, tests were done to see whether propagules of the different species of *Rhizophora* were infested at equal rates.

Variation in infestation levels:- location, season and year effects.

Data on proportion of propagules infested were collected for three locations, over 5 months for three years. This was analysed with a three factor ANOVA (randomised block analysis, Model III) to determine significance of location, year and seasonal effects and any interactions. Infestation levels were recorded as proportion of propagules infested. The infestation data was transformed before analysis, using the transformation $p' = \text{arcsine} \sqrt{p}$ (Zar 1984) to normalise the distribution.

Regression analysis

Tagging of propagules as described in the methodology section permitted cohorts of propagules to be monitored through the season. The intervals between sampling dates was calculated to give the number of days on the ground. As propagules could have been on the ground for as long as 14 days prior to tagging, the mean length of time on the ground for the cohort was calculated as time since tagging plus 7 days (estimated average time propagules were on the ground before being tagged) The proportion of propagules showing signs of infestation was then plotted against the time spent on the ground. Regression analysis was carried out for each cohort at each location (two sites at each location) using SPSS.

The slopes and the intercepts of the regression lines between cohorts and locations were analysed using a two factor ANOVA to determine whether pooling of results was justified. Only cohorts with >10 propagules at each site were used, these being the cohorts which fell during the months of January, February and March, the major months for fruiting of *Rhizophora* and this included 4 of the 7 cohorts.

4.3.5 Sampling in selected *Rhizophora* spp forests on the Northern and Central Eastern Australian Coastline.

Coccotrypes fallax is not recorded in the literature on Australian mangroves other than one report by Zimmerman (1992). The range of *C. fallax* would be a factor in the potential for *C. fallax* infestation to affect recruitment of *Rhizophora* spp and hence zonation within mangroves. To assess the range of *C. fallax* infestation within North Eastern Australia, it was necessary to sample sites over the range of the host genus *Rhizophora* in this region.

Rhizophora spp propagules in *Rhizophora* forests were examined for the presence of *C. fallax* in locations between Port Douglas (16^0 28' S, 145^0 27 E) and Southport (27^0 59 S, 153^0 24 E). The date, location and presence or absence of *C. fallax* was recorded for each location. Presence or absence or *C. fallax* was determined by dissection as described in this chapter. Propagules collected in other locations by volunteers were also examined (Table 4-1). Volunteers from the University and associated organisations were asked to collect twenty *Rhizophora* spp propagules while on field trips. These propagules were airmailed to the laboratory and assessed for presence of *C. fallax* before being destroyed.

Table 4-1 Locations from which *Rhizophora* spp propagules were collected to check for presence of *Coccotrypes fallax*. Latitude and longitude details compiled from information provided by Environment Australia (1997)

	Location	Latitude	Longitude	Collection Details
1	Normanton	17^{0} 40 ' S	141^{0} 04 ' E	volunteer 1995
2	Weipa	12^{0} 38 ' S	141^{0} 53 ' E	volunteer1995
3	Cooktown	15^{0} 29 ' S	145^{0} 15 ' E	volunteer1996
4	Port Douglas	16^{0} 28 ' S	145^{0} 27 ' E	1995
5	Cairns	16^{0} 55 ' S	145^{0} 46 ' E	1993
6	Fitzroy Island	17^{0} 56 ' S	145^{0} 56 ' E	1993
7	Innisfail Harbour	17^{0} 42 ' S	146^{0} 09 ' E	1993
8	Cardwell	18^{0} 16 ' S	146^{0} 01 ' E	1994
9	Lucinda	18^{0} 31 ' S	146^{0} 20 ' E	1993
10	Orpheus Island	18^{0} 37 ' S	146^{0} 30 ' E	1993
11	Townsville	19^{0} 16 ' S	146^{0} 48 ' E	1993
12	Magnetic Island	19^{0} 09 ' S	146^{0} 50 ' E	volunteer 1995
13	Home Hill	19^{0} 39 ' S	147^{0} 24 ' E	1994
14	Bowen	20^{0} 01 ' S	148^{0} 15 ' E	1995
15	Airlie Beach	20^{0} 16 ' S	148^{0} 43 ' E	1995
16	Mackay	21^{0} 09 ' S	149^{0} 11 ' E	1995
17	Yeppoon	23^{0} 07 ' S	150^{0} 44 ' E	1995
18	Gladstone	23^{0} 50 ' S	151^{0} 15 ' E	1995
19	Bundaberg	24^{0} 52 ' S	152^{0} 20 ' E	1995
20	Maryborough	25^{0} 31 S	152^{0} 41' E	1995
21	Caloundra	26^{0} 48 ' S	153^{0} 08 ' E	1995
22	Brisbane	27^{0} 28 ' S	153^{0} 01 ' E	1998
23	North Stradbroke Island	27^{0} 36 ' S	153^{0} 27 ' E	1998
24	Southport	27^{0} 59 ' S	153^{0} 24 ' E	1999

4.4 Results

4.4.1 Propagules of Family Rhizophoraceae infested by scolytids.

The scolytids collected from infested propagules were identified as *C. fallax* by Elwood Zimmerman, Division of Entomology, CSIRO Canberra (pers. comm.). Infestation by *C. fallax* occurred more frequently in propagules of the genus *Rhizophora* (18.% infested) than either *Bruguiera* (0.96%) or *Ceriops* (0.60%).(χ^2 =175, df =2, $p<0.01$)(Table 4.2).

Selection at species level within the genus *Rhizophora*.

There was no significant difference in levels of infestation between propagules of *R. stylosa* and propagules of *R. apiculata*. (χ^2 =1.01, df=1, $p>0.05$ Yates correction applied). *R. mucronata* was eliminated from the analysis as expected frequencies were less than 5 (Zar 1984). Trees of *R. mucronata* were not found growing in the area. The few propagules found were washed into the site late in the season when infestation levels were high (see Section 4.4.8).

Table 4-2 ***C. fallax*** **infestation of mangrove propagules in the Family Rhizophoraceae over two seasons in Cairns mangroves.**

Species of propagule	Number examined	Number infested	% Infested
R. stylosa	1387	*254*	18.31%
R. apiculata	261	41	15.70%
R. mucronata	10	5	50%
Total *Rhizophora* spp	**1658**	**300**	**18.09%**
C. australis	290	0	0%
C. tagal	209	3	1.43%
B. gymnorrhiza	457	9	1.97%
B. exaristata	478	2	0.42%
B. parviflora	628	4	0.64%
Total non-*Rhizophoran* spp	**2062**	**18**	**0.87%**

Infestation levels within individual propagules.

Six hundred and ninety *Rhizophora* spp propagules were dissected and the number of *C. fallax* in each stage of the life cycle recorded. One hundred and nineteen of the propagules were infested, that is, had a minimum of one *C. fallax* individual present. This was always an adult female. Infestation levels within propagules varied widely, ranging from a single adult, with no eggs, larvae or pupae, to propagules with as many as 60 eggs or 45 larvae (Table 4-3).

In some propagules reinfestation appeared to have occurred, with up to 40 adults in one propagule. Reinfestation in this context would be either infestation by a second female prior while larvae from the first brood were still present, or, one or more of the emerging females ovipositing in the propagule in which she pupated. No infested propagules were found without an adult female present. Where many females were present it was not possible to distinguish between parent and offspring as the new generation had already darkened. Some heavily infested propagules had numerous adults and no juvenile forms indicating that dispersal did not immediately follow pupation.

Table 4-3 Mean numbers of the different stages of *Coccotrypes fallax* life cycle recorded in infested propagules of *R. stylosa*.

	N	Minimum	Maximum	Mean	Std. Deviation
No. of adults	119	1	40	4.75	6.50
No. of eggs	119	0	60	2.96	8.75
No. of larvae	119	0	45	5.27	9.99
No. of pupae	119	0	28	.93	3.79
Total all life stages	119	1	*67	13.91	15.28

* maximum number of all life stages in any one propagule.

The average brood size could not be calculated from the above data, which was confounded by propagules with large numbers of adults. Brood sizes (mean = 9.36, std dev = 5.36 n=22) were calculated from data of propagules with single infestations, that is those containing only one adult with at least one egg, larvae or pupae to show that reproduction had occurred.

4.4.2 Correlation of level of infestation by *C. fallax* with mass and length of propagules of Family Rhizophoraceae.

Observed levels of infestation of *C. fallax* within propagules correlated with both mass of propagules (Pearson correlation 0.757, n=7, $p < 0.05$) (Figure 4-2) and length (Pearson correlation 0.907, n=7, $p < 0.01$) (Figure 4-3). The smaller species with respect to mass of the propagules had very low levels of infestation and *Rhizophora* spp which are larger had much higher levels of infestation (Figure 4-2). The exception was *B. gymnorrhiza* which had mean mass of propagules greater than *R. apiculata* and less than *R. stylosa*, but had very low levels of infestation (Figure 4-2).

Similarly the smaller species with respect to length (*B. exaristata* and both *Ceriops* species) had very low levels of infestation (Figure 4-3). *R. stylosa* and *R. apiculata* , the two longest propagules had very high levels of infestation (Figure 4-3). *B. parviflora* and *B. gymnorrhiza* were both infested at low levels despite having length ranges that overlapped with *R. stylosa* and *R. apiculata*.

Figure 4-2 Mean mass (and range) of propagules in Family Rhizophoraceae arranged in order of their level of infestation by *C. fallax*.

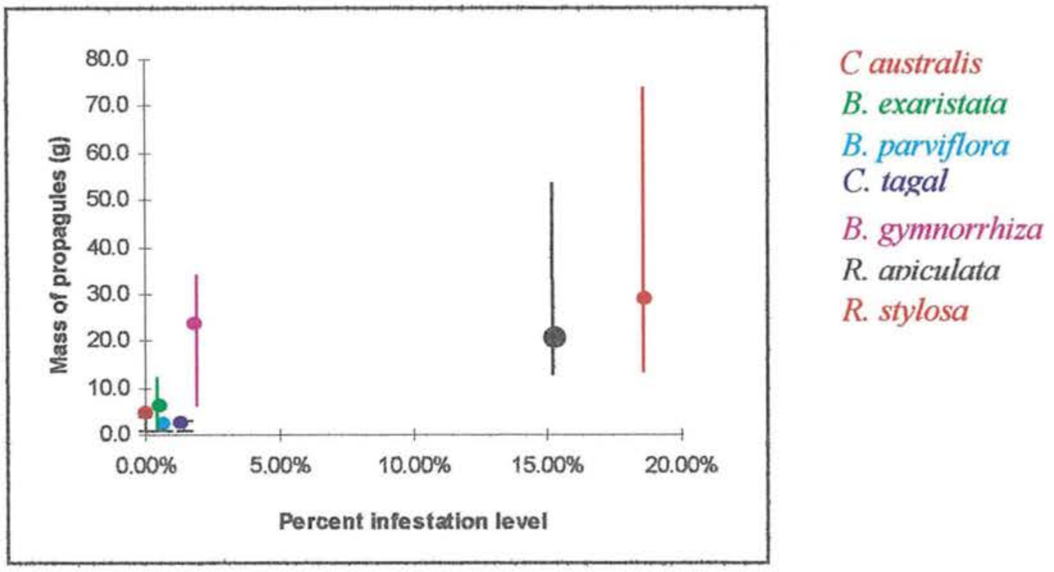
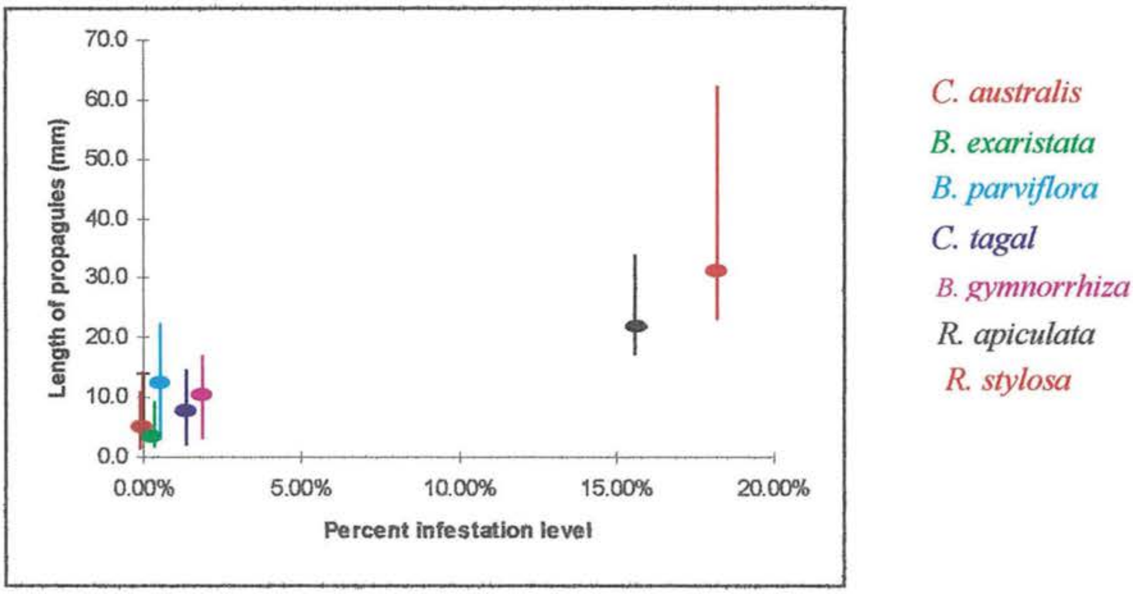


Figure 4-3 Mean length (and range) of propagules of Family Rhizophoraceae arranged in order of their level of infestation by *C. fallax* .



4.4.3 Assessing infestation using external signs only

95.5% of 771 propagules examined which were clear of scolytids had no external boreholes. Of the 119 propagules that were infested with *C. fallax*, all had at least one borehole. The number of scolytids inside infested propagules was positively correlated with the number of boreholes visible ($r = 0.663$, $p<0.01$, $n = 119$). As can be seen in Figure 4-5, a propagule with only one borehole may contain anything between zero and 23 *C. fallax* individuals (adults, eggs, larvae and pupae). A propagule with two boreholes may have anything between zero and 67 individuals. Similarly, the number of external bores was positively correlated with number of adult scolytids ($r = 0.548$, $p < 0.01$, $n = 119$, Figure 4-4). In each scatter graph a statistically significant linear relationship can be fitted, eg total scolytid number = 0.435*number of boreholes or total adult number = .548*number of boreholes.

Presence of boreholes in a propagule cannot be taken as evidence of active infestation. In many cases on dissection (35 out of 154 where boreholes were noted), it was observed that the tunnel was empty, no live scolytids were present. Active infestation was always associated with the presence of a sawdust like mixture of faeces and debris (frass) at the borehole ($\chi^2 = 210$ df = 1, $p < 0.001$, Yates correction applied).

These results were combined to produce a key to identify infested propagules by external observation only (See Appendix 1). All field assessments of infestation levels in propagules err on the side of under-assessment of rate of infestation. As infestations tended to reach 100%, under estimation was the more conservative choice.

Figure 4-4: Correlation of adult scolytid numbers with external boreholes.

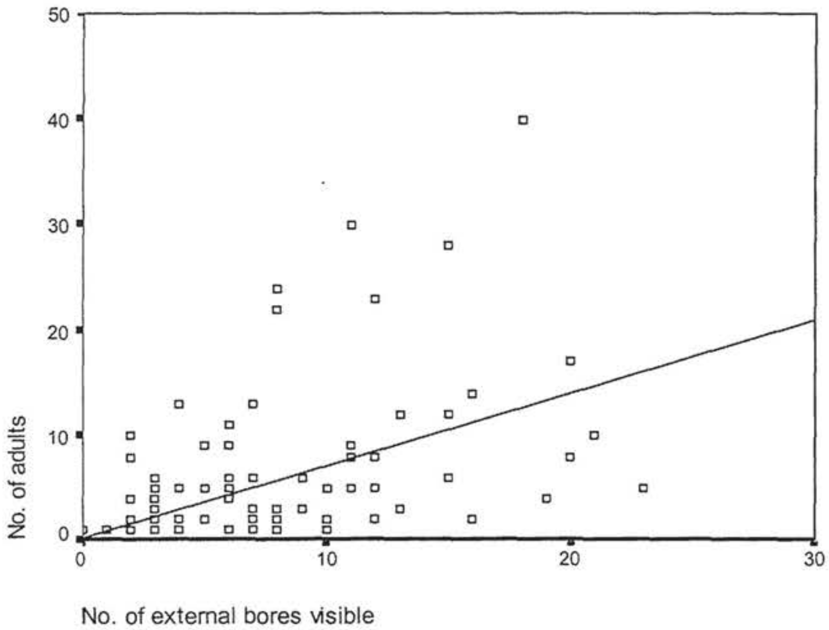


Figure 4-5 Correlation of total scolytid numbers with the number of external boreholes.

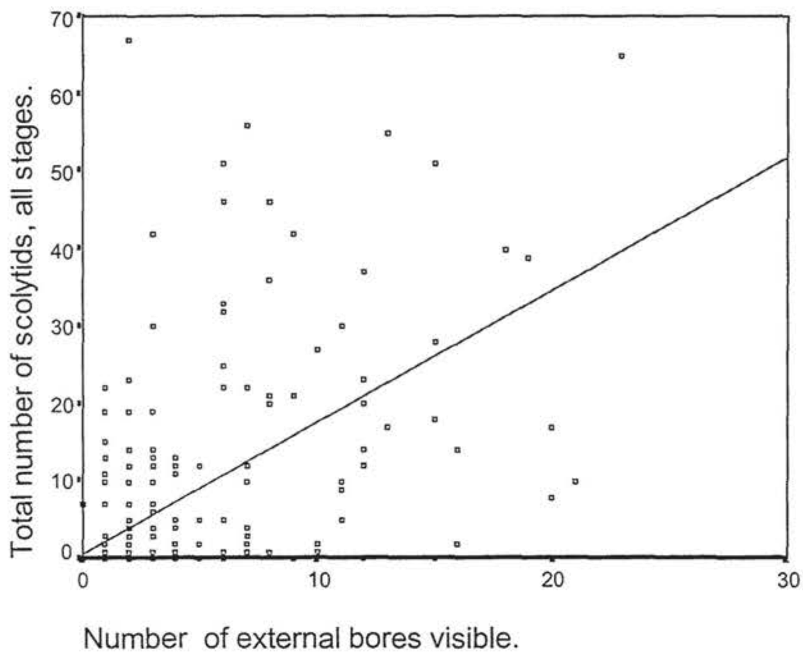
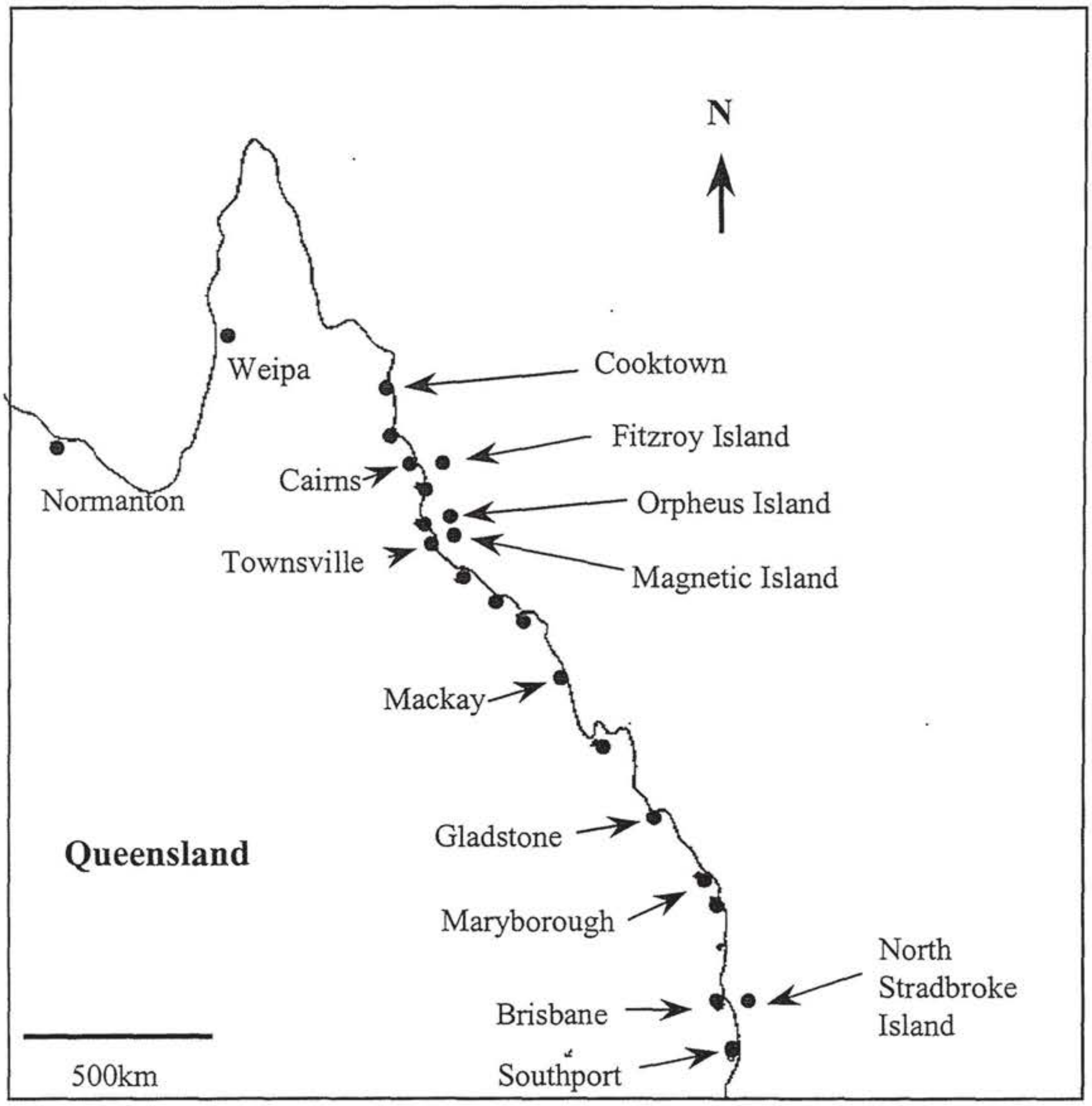


Figure 4.6 Locations of Rhizophora forests in Queensland which were checked for scolytid infestation and in which propagules infested with *Coccotrypes fallax* were found.



Legend

- Locations sampled at which *C. fallax* was found

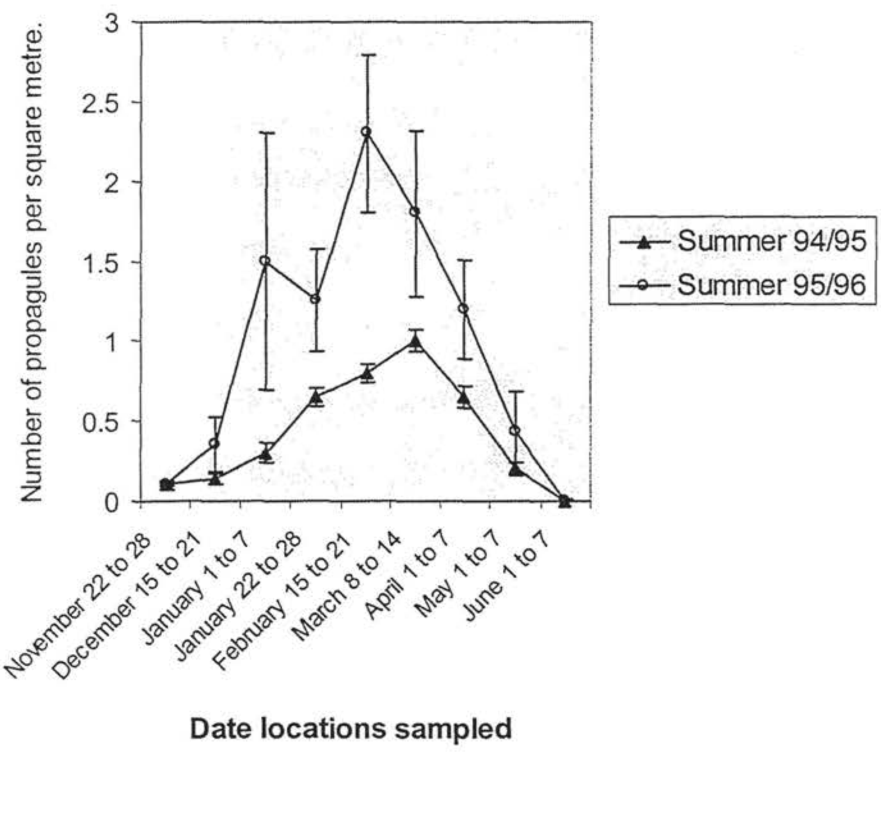
4.4.4 Range of *C. fallax* in Queensland

C.fallax were found in propagules of *R. stylosa* in all 23 Rhizophora zone locations checked, as well as at the six sites in Cairns. Four of the sites were islands located 2 to 5 km off shore (Figure 4.6).

4.4.5 Variability in numbers of *R. stylosa* propagules on the ground.

The number of propagules on the ground was significantly different at different dates during the year (F= 7.610, df = 5,9, p= 0.001) and in different years (F = 22.834, df = 5,1, p = 0.001), with no significant date/year interaction. In both years propagules started falling in November in small numbers, the majority falling in January and February (Figure 4-7). There was a large difference in the density of propagules at all locations during the two years, with densities peaking at 2.3/m^2 in 1995/6, significantly higher than the peak of 1.0/m^2 reached in 1994/5 (Figure 4-7). The November of 1994 was the fourth driest November on record (Cairns Meteorological Office). There was no location effect between the three locations, Richters Creek, Barr Creek and the Airport mangroves, (F=1.469, df =2,9 p = 0.239).

Figure 4-7 Change in the mean number (±SE) of *R. stylosa* propagules on the ground over two seasons, locations pooled.



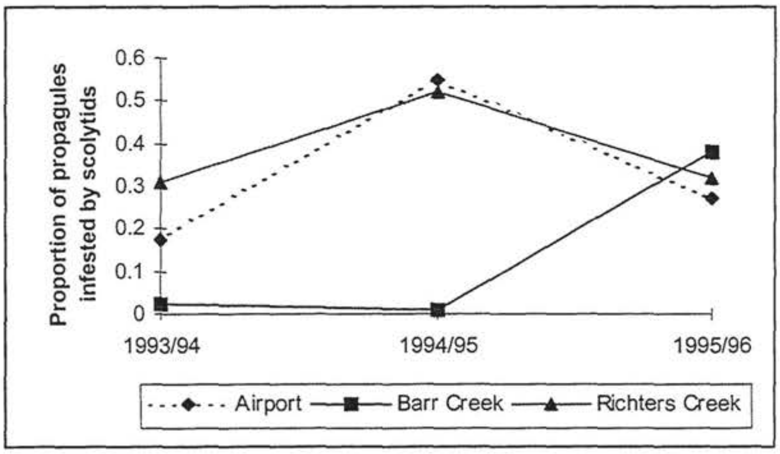
Loss of propagules from transects.

Propagules which speared into the substrate were less likely to be lost from the transect than propagules which ended up lying on the mud ($F=21.013$, $df = 1, 34$ $P<0.01$). Only 18.2% of 'speared in' propagules were lost between the first and second survey date, whereas 71.4% of propagules lying on the substrate were lost. Analysis beyond the initial two week period was confounded by the changes within the propagules which remained on the transect. Propagules lying on the substrate, that did not float, away self-erected, adventitious roots holding the base of the propagule in position while the hypocotyl curved so the upper portion became erect. These would then be recorded as being 'speared' rather than lying. Propagules speared into the mud recruited as seedlings and hence were no longer counted as propagules. No propagules recruited (developed leaves) while in the horizontal position.

4.4.6 Effect of location, season and year on levels of infestation of scolytids in *R. stylosa* propagules.

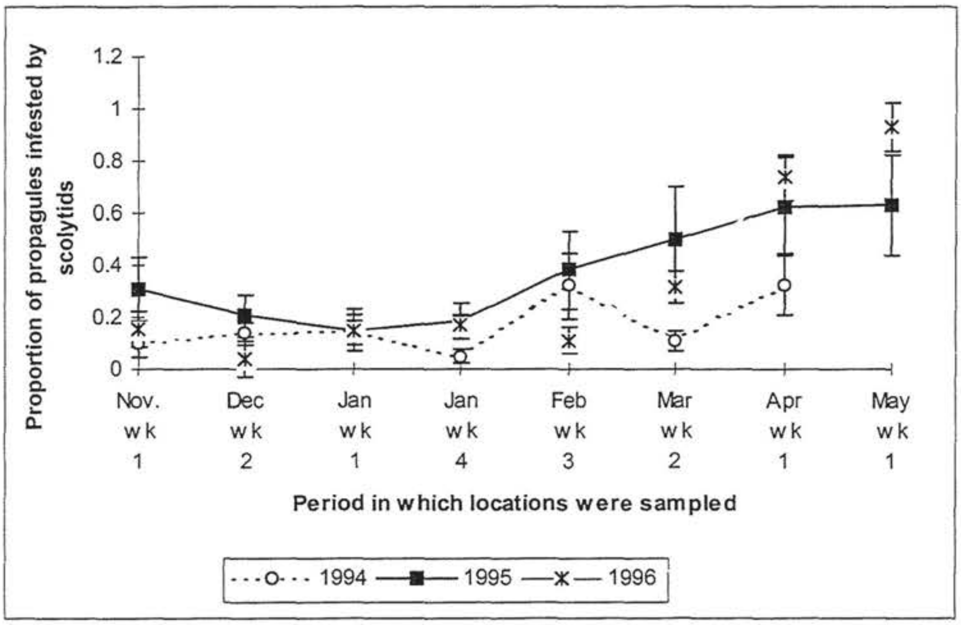
There was a significant year by location interaction in the proportion of infested to clear propagules checked over the three years ($F = 22.160$, $df = 4$, $p = 0.000$). Richters Creek and Airport Mangroves had similar levels of infestation, that is, low in 1993/4, rising in 1994/5 and dropping again in 1995/6. Barr Creek was the exception, with very low levels of infestation for both 1993/4 and 1994/5, increasing in 1995/6 to be comparable with the other two locations (Figure 4-8).

Figure 4-8 Changes in yearly level of infestation of *R. stylosa* propagules by *C. fallax*, at three locations.



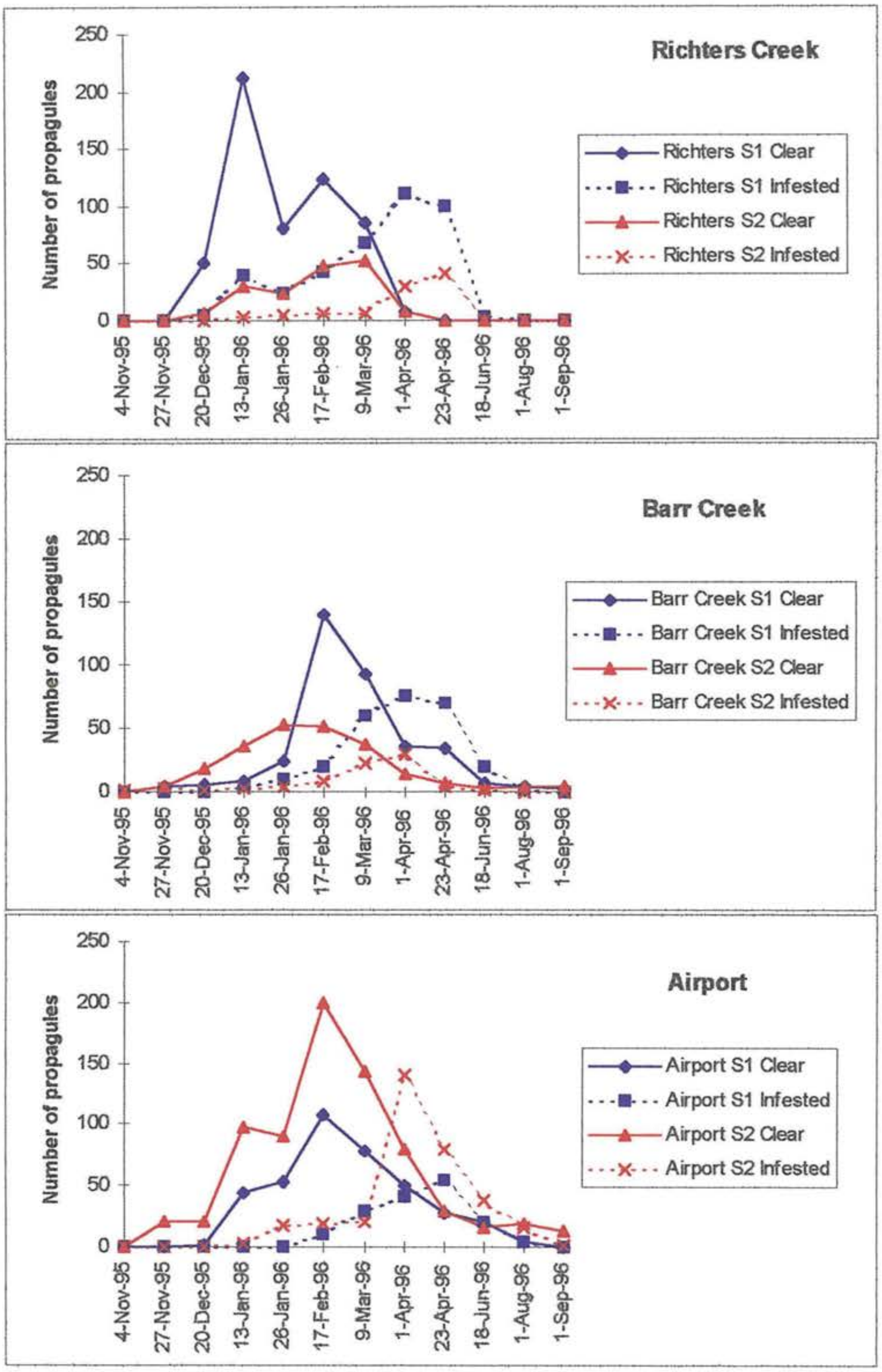
There was also a significant date by year interaction (F = 2.566, df = 13, p = 0.006, Figure 4-9). The proportion infested stayed relatively low and fluctuated in January and February during the period of greatest propagule fall. The proportion infested then started increasing in March and continued to increase in April and May. The summer of 1994 was different in that the proportion of infested propagules dropped in March, decreasing to 11% infested following a period of exceptionally hot weather. This decrease in 1994, and subsequent lower levels of infestation for the remainder of 1994 (Figure 4-9) even though infestation levels initially had been similar to other years produced the year by date significant interaction identified in the analysis.

Figure 4-9 Changes in proportion of propagules infested by scolytids over the fruiting seasons of 1994, 1995 and 1996. (Points indicate means ±SE).



While the proportion of propagules infested generally increased as the season progressed, the number of infested propagules peaked in April/ May and decreased after that as the number of propagules decreased. Propagule numbers decreased as they (propagules) were consumed by predators, removed from the forest floor by flood rains and high tides or recruited (became seedlings). The pattern of infestation following propagule fall is shown in Figure 4-10. Clear (uninfested) propagules are represented by solid lines, infested propagules by dotted lines.

Figure 4-10 Changes in numbers of infested and clear propagules at 6 sites in 1996.



Note that the pattern of an initial peak of clear propagules followed by a peak in infested propagules two to three months later occurs over a range of propagule densities.

4.4.7 Patterns in infestation change over a season.

The density of propagules on the ground varied from over 200/ 50m^2 transect to less than 60/ 50m^2 transect (from 4/m^2 to 1.1/m^2). Despite this, the pattern of change is consistent at all 6 sites. At each site, the number of clear propagules increases rapidly from November when the first few propagules fall. The number of infested propagules is initially low but increases over time, equalling and then exceeding the number of clear propagules in March or April, depending on the site. In each case the maximum number of infested propagules recorded is close to 50% of the maximum number of clear propagules recorded for that site. This pattern occurred over a range of densities (50 per 50m^2 and 200 per 50m^2) of propagules. In each case, the number of propagules on the ground by June was close to zero. The propagules remaining on the ground at this time were unlikely to recruit as they were speared in upside down, or were infested with the upper portion of the propagule desiccated, decayed or broken off.

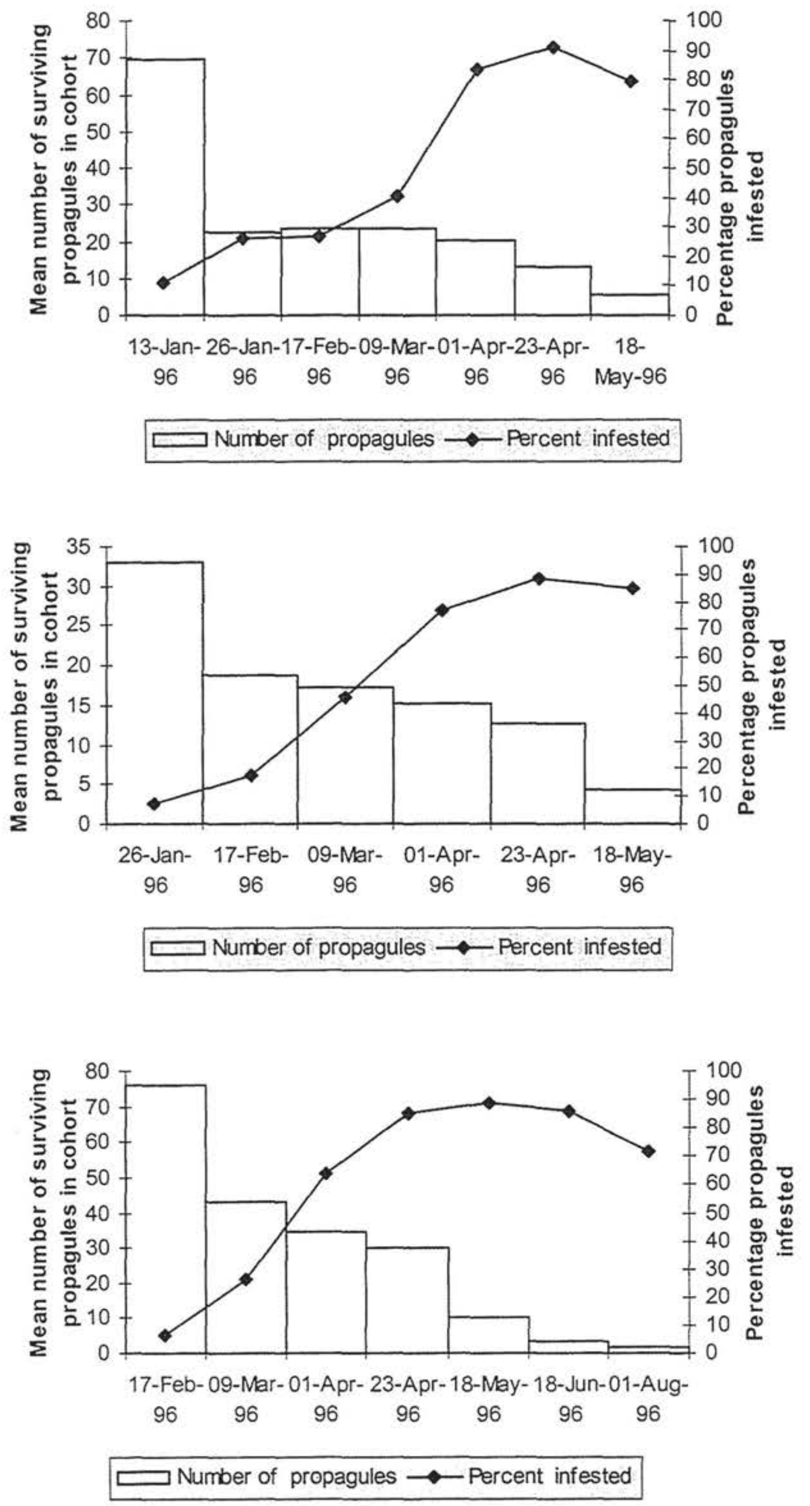
4.4.8 Timing of propagule infestation.

In 1996, propagules were tagged the first time they were observed on the transect. All propagules tagged on that date were then followed to observe the changes in the numbers of clear vs. infested propagules. In each cohort the same pattern emerged, ie. the proportion of propagules infested by *C. fallax*, increased over time, while the total number of propagules decreased. Figure 4-11 shows averaged figures for all locations for the cohorts of propagules first recorded on site for 13 January, 26 January and 17 February 1996 respectively.

Infestation levels of propagules dispersed away from the forest location

The largest drop in propagules (propagules being moved off site) occurred in the first fortnight when the proportion of infested propagules was low (Figure 4-11). The proportion of infested propagules recorded on the initial assessment day of each cohort stayed low even as the season progressed. This contrasted with the propagules which remained on the site and showed a steady increased in the proportion infested as the season progressed.

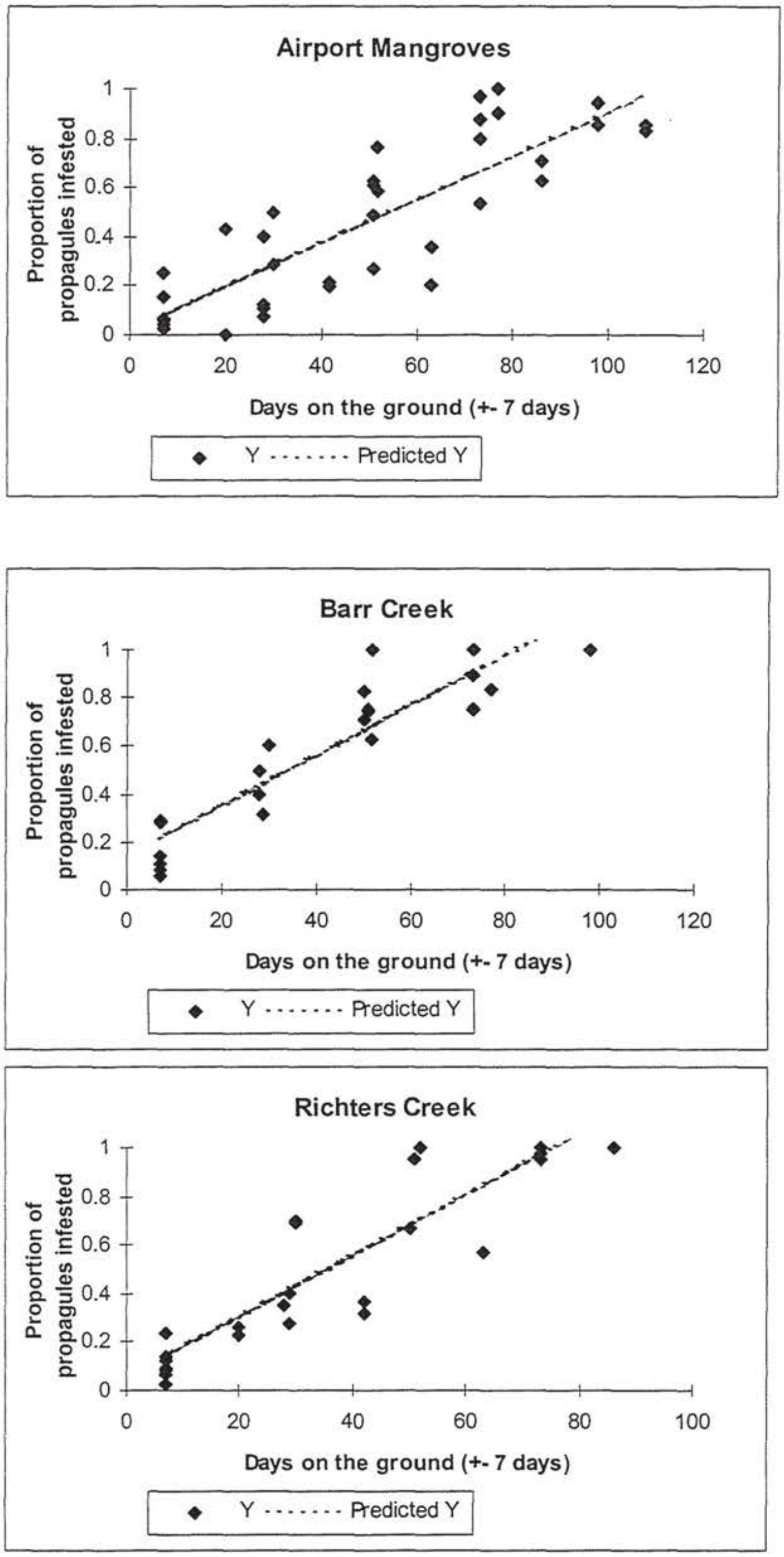
Figure 4-11 Average number of propagules on transects at three locations with the percentage infested by *C. fallax*, for three cohorts of propagules for four months following arrival of the propagules on the transect.



Regression analysis of proportion of propagules infested against time spent on the ground.

The proportion of infested propagules on the transect was regressed against the number of days the cohort of propagules had been on the ground at each location. The dates on which locations were visited were just over two weeks apart. Propagules tagged for the first time could therefore have been on the ground for up to two weeks. To adjust for this, 7 days was added to the number of days on the ground when plotting regression lines. The 'coefficients of x' (the rate of increase of infestation) for each regression line plotted (4 cohorts at each of 3 locations) were subjected to two way analysis of variance. (See Appendix 2 for graphs and tables). This indicated that there was no difference between cohorts ($F=2.81$; $df = 3,6$; $P = 0.13$) but that the rate of increase at the locations was different ($F = 7.28$; $df = 2,6$; $P = 0.025$). Analysis of variance of the line intercepts (level of infestation on first examination showed no significant difference between cohorts or locations. The resulting regression lines for each location (cohorts pooled) show that at all three locations in 1996, any propagules remaining on the transect for over three months were likely to become infested (Figure 4-12). The time to 100% infestation varied between locations, occurring most rapidly at Richters Creek (60 to 70 days) and taking longest at the Airport mangroves (100 days) (Figure 4-12).

Figure 4-12 Regression plots for proportion of propagules infested against number of days the propagules had been on the transect for three locations.



4.5 Discussion

4.5.1 Range of *C. fallax*

Prior to this study, *C. fallax* had been reported in Australia only once (Zimmerman 1992). In this survey it has been demonstrated that *C. fallax* infestation is widespread, extending over the range of *Rhizophora* on the eastern coast of Australia and the Gulf of Carpentaria. While not finding the scolytid at any particular site would not have proved anything, *C. fallax* was found at every site surveyed which fulfilled the minimum requirement of having *Rhizophora* spp growing in the forest. Further searches of mangroves at the limits of distribution of *Rhizophora* are likely to find areas where *C. fallax* is not present at any given time.

The method of dispersal of *C. fallax*, within the host propagule, suggests that statistical methods could be used to predict the probability of infestation of *Rhizophora* forests based on the supply of propagules to the area from distant sites and the level of infestation at the sites of origin. Islands and accreting mudflats could be free of *C. fallax* infestation during initial colonisation, only to have infested propagules arrive on site and introduce the scolytid at some later date. It is interesting to note that Hawaii, where *Rhizophora* was introduced, has no record of scolytids infesting propagules. Hawaii is considered beyond the limit of colonisation by propagules by natural means, the Pacific forming a barrier to propagule dispersion (Duke 1995). This limit to colonisation by scolytids carried in dispersing propagules would not apply on the coast of Australia, where coastal currents distribute propagules and *C. fallax* was found on the four islands checked. In Australia the scolytid was found from the Gulf of Carpentaria in the north to close to the limit of *Rhizophora* distribution in the south. *C. fallax* infestation thus has the potential to affect *Rhizophora* communities over this range.

4.5.2 Propagules infested by *C. fallax*

Infestation was shown to be correlated with length and mass of propagules within the mangrove Rhizophoraceae. It was also shown to be significantly higher in propagules of the genus *Rhizophora* than in either *Bruguiera* or *Ceriops* spp. In terms of mass, *Bruguiera gymnorrhiza* propagules are in the same range as *R. stylosa* and *R. apiculata* ie. relatively large propagules. *B. gymnorrhiza* propagules, however, were not infested by *C. fallax* at the same level as *Rhizophora* propagules. It is possible therefore to hypothesise that *C. fallax* are able to identify suitable host propagules and discriminate against *B. gymnorrhiza* propagules for some reason unknown to us.
The ability of herbivores to identify their host plants is well-documented (Bernays and Chapman 1994). Food selection by insects may be based on mechanical or physical selection (presence of hairs, texture of cuticle), visual selection (colour) or chemical selection (odour and taste) (Jolivet 1998). It is possible that *C. fallax* can identify propagules of the different genera the mangrove Rhizophoraceae by any one of a number of selection criteria.

C. gedeanus use feelers to measure the diameter of the potential host (Browne 1961), which gives some indication of the size of the propagule. *Coccotrypes* spp larvae consume the tissue of the host propagule and a certain minimum volume of host tissue would be required in order for all larvae to gain the required nutrients and energy to complete the life cycle. Further studies would be required to demonstrate the hypothesis that all *Ceriops* (mass 1 to 4 g) species and the smaller *Bruguiera* species do not meet this minimum and hence are not preferentially selected by *C. fallax*. The normal brood size of *C. fallax* is 11 to 16 (Browne 1961) and it is possible smaller propagules (ie. *B. exaristata*, *B. parviflora*, *C. australis* and *C. tagal*) have insufficient quantities of nutrient tissue to allow for successful completion of all larval stages. Experiments to quantify the mass of tissue consumed by the adult and developing larvae through to the time the new adults disperse, would allow prediction of the minimum mass of host tissue required for reproduction.

Other factors or a combination of other factors such as physical and chemical cues, may also be involved in host propagule selection by *C. fallax*. This hypothesis is supported by the fact that *B. gymnorhiza* has relatively large propagules but shows minimal infestation by *C. fallax*.

The isolated incidents of *C. fallax* infestation in *Bruguiera* and *Ceriops* propagules occurred early in the season when there were reduced numbers of Rhizophora spp propagules on the ground and may be associated with lack of availability of the preferred host. Time spent searching for a suitable host may be a factor in the decision to infest *Bruguiera* or *Ceriops* spp. Both *Bruguiera* and *Ceriops* spp begin to fall during November and December, whereas *Rhizophora* spp begin in January (Jones 1971, Saenger 1982, Duke *et al* 1984). Any adult leaving the host in which it had over-wintered in November or December would encounter *Bruguiera* and *Ceriops* propagules on the ground, whereas *Rhizophora* propagules would still be on the tree. This may explain the presence of the scolytid in propagules in which they were not found later in the season when *Rhizophora* (preferred hosts) were available.

How or why the scolytids discriminate between propagules is not the major focus of this thesis. The results clearly show that they do and factors which may be involved (mass and diameter) have been identified. The important fact is that distribution of *C. fallax* between propagules of the different genera of the family *Rhizophoraceae* was found to be heavily biased towards *Rhizophora* species. Any effect of infestation by *C. fallax* on propagules therefore would have the potential to affect *Rhizophora* spp propagules to a much greater extent than any of the other members of the mangrove Rhizophoraceae.

Differential predation by monophagous predators has been shown to affect community structure (Crawley and Pacala 1991). For example predation on *Avicennia* propagules by sesarmid crabs has been shown to affect forest structure in mangroves (Smith 1988a). If it can be shown that *C. fallax* infestation affects recruitment of propagules or survival of seedlings the evidence that *C. fallax* infestation has the potential to affect forest structure will be strong.

4.5.3 External assessment for use in field trials

Presence of a borehole alone is not evidence of active infestation by *Coccotrypes* spp. and despite the correlation between borehole numbers and adults, should not be used to imply presence of an active infestation. *C. fallax* are not the only organisms to attack mangrove propagules. Presence of frass from a borehole is positive evidence of active infestation. The development of a reliable method of external assessment of *C. fallax* infestation (see Appendix 1) without the need to touch the propagule made it possible to monitor changes in infestation levels without disturbing the propagules or affecting their recruitment. In the analysis, significant correlations were found between the number of external boreholes and both the number of adults and the total number of all life stages in the propagule. Despite this statistical significance, the biological and practical significance of these relationships is very limited. Intuitively, it makes sense that the more boreholes a propagule has, the greater the number of scolytids are likely to be found inside. In practice, the huge variability (for example 2 boreholes with between 1 to 10 adults or 1 to 68 total scolytids of all stages, Figure 4-4 and Figure 4-5), means the relationship is not useful for predictive purposes. It is not likely to give meaningful information as to the effect of infestation on the survival of the propagule.

4.5.4 Levels of infestation.

The effect of insects on plants and seeds cannot simply be extrapolated to plant populations. In natural communities plants produce a large number of propagules (seeds) per unit area. Only a small fraction of the seeds will develop into productive plants (Schoonhoven *et al* 1998). In most plant communities, recruitment in the subsequent plant generation is micro-site limited. Therefore, the reduction in seed must reach a certain degree before it affects the number of adult plants in the next generation (Schoonhoven *et al* 1998).

The level of predation on propagules that can be tolerated is dependent on the plant species' life history traits. Plants with a long life cycle which produce large propagules and in which the period in the seed bank is short have a higher probability of being affected by seed predation than those with many small seeds which remain viable for long periods (Louda 1995). Mangrove Rhizophoraceae fit the description of those with a higher probability of being affected by seed predation. It was necessary however to demonstrate that the level of predation by *C. fallax* was high, and attempt to find what factors affected the proportion of propagules affected

Differences between locations and years

Propagule numbers were seasonal and varied from location to location with propagule density at some sites being 5 times greater than at others (Figure 4-10). Propagule numbers also varied between years, with on average over twice the number of propagules falling in 1995/96 than in the previous year, which had been one of the driest on record. The ability of the parent tree to regulate the effort put into reproduction and abort propagules was documented by Farnsworth and Ellison (1997). The number of propagules reaching maturity is only a small proportion of the original number, environmental stress and predation being two factors implicated in early abscission of the propagule. The numbers of propagules available for dispersal to colonise new sites and for regeneration in existing forests is thus seasonal, dependent on location and subject to yearly variation.

The position in which a propagule lands on the substrate has the potential to affect whether it will remain in the vicinity of the parent tree, or be dispersed. There is much discussion in the literature on the shape of *Rhizophora* propagules and the potential to spear into the mud (Tomlinson 1994). Within the mangrove Rhizophoraceae, *Bruguiera* is described as part of the late successional vegetation (Johnstone 1983), whereas *Rhizophora* has many of the features of a coloniser. Propagules which are dispersed have the potential to contribute to the establishment of new *Rhizophora* communities (Banus and Kolehmainen 1975). Those propagules that spear in have the potential to increase the size of a new colony where a single tree has become established on an accreting mud flat. In newly colonised substrate it is anticipated that a greater proportion of propagules are likely to spear in as there are fewer roots from adjoining trees covering the surface. Seedling survival is greater from speared in propagules than from those stranded on the surface (McKee 1995b). The ability of propagules to spear into the mud might thus have a role in establishing new colonies which is not apparent in established forests.

Propagules which do not spear in end up lying on the mud surface. Propagules lying on the substrate have a high probability of floating away from the parent tree before they become infested. Seventy three percent of tagged propagules lying on the mud were moved off the transect before the next survey. That is they dispersed when the level of infestation of all propagules was still relatively low (less than 10%). Infestation by *C. fallax* is thus not likely to have the same effect on the ability to colonise new substrate as it does on the propagules attempting to recruit within the *Rhizophora* forest.

Other factors affecting levels of infestation of *C. fallax* in propagules were those associated with the locations and the year in which the mangrove was surveyed. With one exception there was a strong seasonal increase, at each location each year, following the seasonal availability of the host propagules. The exception was at Barr Creek in 1994, which had significantly lower levels of infestation. This followed a period of elevated temperatures, a heat wave that lasted for several days. This indicated that climatic variables, specifically maximum temperatures may be important in determining infestation levels in mangrove forests.

Barr Creek mangroves in 1994 were not subject to daily tidal inundation as a sand bar blocked the creek mouth. Propagules and substrate in the intertidal range at Richters creek and Airport mangroves would have been cooled by water during high tide. This did not occur at Barr Creek and C. *fallax* numbers in this location were extremely low for the whole of 1994. The mouth of the creek was open in 1995 and *C. fallax* were found in patches in small numbers. Infestation levels increased to those of the other two locations in 1996. All mangrove locations had decreases in *C. fallax* numbers following the periods of high temperature in 1994, but these were temporary (Figure 4-9). Local conditions and yearly climatic variations appear to affect levels of infestation at different locations. Locations in which the temperature regularly rises above 39 ^{0}C may have endemic low levels of *C. fallax* infestation, which only increase during unusually mild seasons.

Timing of infestation

While attack by *C. rhizophorae* is reported for propagules still attached to the trees in Florida (Onuf *et al* 1977), this study demonstrates that the majority of infestation occurs while propagules are on the ground. Some propagules may be infested while on the tree, but the ratio of infested to clear propagules in each cohort when first recorded, is low. There is a direct correlation between the time a propagule within a cohort remains on the forest floor and the level of infestation within that cohort. Sites were sampled at two to three week intervals. Therefore it is possible that propagules tagged as first recorded on the transect, for example on 13 January, may have fallen at any time since the last survey date, ie. 20 December. This was taken into account when plotting the graphs. These (ratios of infested to clear propagules) show that very few propagules are infested while still attached to the tree.

This finding of the scolytid attacking fallen propagules is consistent with the descriptions for the genus in Browne (1961) in which members of the genus *Coccotrypes* are described as attacking fallen fruit. It is also supported by fact that in other host-scolytid relationships, the host tree fights back through the production of a copious flow of sap which has the potential to drown the beetle or make their tunnels uninhabitable (Browne 1961; Crowson 1981). If the propagule on the tree were a suitable habitat, a food supply would be available year round as the time from flower primordium to mature propagule is 3 years in *R. apiculata* (Christensen 1977) and 1 to 1.5 years in *R. stylosa* (Duke *et al* 1984). The potential for the reproductive effort of the tree to be severely affected would suggest that some factor, which prevents infestation while still on the tree, exists. The population of *C. fallax* is limited by the relatively short period during which propagules are available for infestation. During this time they have been shown to infest up to 100% of the propagules which remain within the mangrove forest. Propagules infested by *C. fallax* have much of their tissue consumed by the larvae. Many seedlings are destroyed by water born flotsam (Blanchard and Prado 1995; Qureshi 1990). Floating debris is likely to have a similar effect on infested propagules, reducing the number of surviving scolytids available for infesting propagules the following season. This is consistent with the low numbers found infesting propagules early in the season.

4.5.5 Summary

The most important points demonstrated in this chapter are

Results of this study show that *C. fallax* attacks *Rhizophora* spp propagules at much higher levels than *Bruguiera* and *Ceriops* spp.
Infestation of *Rhizophora* propagules by *C. fallax* in Eastern Australia is widespread.
The levels of infestation vary between locations but approach 100 % in the intertidal zone where *Rhizophora*, *Bruguiera* and *Ceriops* dominated the locations surveyed.
The majority of infestation by *C. fallax* occurs while *Rhizophora* propagules are on the ground.
Most propagules washed away from the forest are not infested.

These results demonstrate that if *C. fallax* infestation does affect survival of seedlings in *Rhizophora* forests, then the interaction has the potential to be applicable over a large proportion of Australian mangroves. The effect of *C. fallax* infestation on *Rhizophora* propagules is discussed in Chapter 5.

CHAPTER 5

THE EFFECT OF INFESTATION BY *C. FALLAX* ON PROPAGULES AND SEEDLINGS OF *R. STYLOSA*.

5.1 Introduction

Insect predation on plants occurs on every part of the plant by one or more species of predator. The foliage, buds and flowers, fruits and seeds, twigs and branches, bark surface, under the bark, roots and even dead foliage and wood may all be exploited by insects (New 1986). Moderate levels of herbivory on adult plants by insects do not usually result in the death of the plant, although in cases where the plant is stressed by other factors, herbivory may be associated with plant mortality.

Predation on seeds and seedlings by insects can result in loss of viability of the seed or death of the young seedling (Crowson 1981; Gullan 1994). Insects may damage seeds in a variety ways. They chew into seeds and damage the embryo, they consume the whole seed, they damage the seed coat and thus allow penetration of other pathogens etc (Crowson 1981).

Predation on propagules where the propagules, or parts thereof, are consumed has been shown to have the potential to affect community structure (Smith 1988a). Predation by scolytids, however, differs from predation by crabs or vertebrates. When crabs consume a propagule, it is accepted that it will not survive. Infestation by *C. fallax* is internal; the female bores into the propagule, constructing a tunnel and a single communal chamber in which she lays her eggs (Browne 1961). The female stays to tend the larvae, which live, feed and pupate communally. The consumption of hypocotyl tissue by the feeding larvae is incremental, increasing over time. Infestation is thus less obvious and the damage being done by the feeding larvae is not visible. The first section of this chapter looks at the effect of *C. fallax* infestation on individual propagules.

C. fallax takes 39 to 53 days to complete the life cycle from egg to young adult (San Valentin 1986). *Rhizophora* propagules establish roots and develop leaves (recruit as seedlings) in 40 to 50 days (Banus and Kolehmainen 1975). This similarity in time period means that there is the possibility that infested *Rhizophora* propagules may recruit as seedlings during the early part of the life cycle of the scolytid. Therefore the ability of infested *Rhizophora* propagules to recruit may not reflect the ability of the infested seedlings to survive. Similarly, seedlings infested soon after recruitment may be affected to a greater or lesser extent than seedlings established in the previous season. No details on the effect of *C. fallax* infestation on the different stages ie. propagule, young seedling (first few weeks) and older seedling (well established) is available in the literature.

Biological systems are inherently variable and the level of infestation (measured as the proportion of propagules on the substrate infested by *C. fallax*) varies between locations and between years (Chapter 4). While the first part of this chapter looks at the effect of the infesting scolytid on the individual propagule, the second portion looks at the effect of *C. fallax* on recruitment of *Rhizophora* propagules as part of the community, the survival of these propagules over the following months as well as correlation between levels of infestation and survival of seedlings in the field.

Timing of infestation may be important if seedlings have a method of defending themselves against attack by *C. fallax*. San Valentin (1986) reports that *C. fallax* does not infest propagules while still attached to the tree or after the propagules have become established as seedlings, but gives no data to support the statement. Seedlings differ from propagules in that the seedling, through the root system has access to water, which is not available to the propagule. Browne (1961) reports on the production of a copious flow of sap in plants attacked by scolytids. This either drowns the beetle or renders their tunnels uninhabitable. Crowson (1981) attributes the fact that the majority of wood borers develop in dead rather than living wood to the danger of being drowned by sap flow in living trunks or branches.

It is possible that propagules, with no access to water, may be suitable for *C. fallax* infestation whereas seedlings may be able to flood scolytid tunnels if attacked. To assess the level of infestation on established seedling it was decided to study seedlings that recruited in the previous year and were free of infestation at the start of the season. The differences in levels of infestation by *C. fallax* in these established seedlings and the current season's propagules were then compared. If seedlings are subject to the same level of attack, there should be no difference in infestation levels.

This chapter looks at

the result of *C. fallax* infestation on individual propagules and seedlings.

the difference in recruitment and survival of infested propagules compared to non-infested controls in plantings in the mangroves.

the correlation between levels of infestation of propagules and the subsequent survival of seedlings at three locations over three years.

the difference in the rate of infestation between propagules and established seedlings.

whether newly recruited seedlings are as resistant to infestation as established seedlings.

The results are then integrated to provide a hypothesis of how *C. fallax* infestation affects *Rhizophora* propagules and seedlings and what factors may affect the success or otherwise of *C. fallax* attack on *Rhizophora* propagules.

5.2 Methodology

5.2.1 Qualitative observations on the internal changes in *Rhizophora* propagules following infestation by *C. fallax*.

Individual propagules infested with *C. fallax* were dissected and the damage inflicted by the feeding *C. fallax* larvae noted. Photographs of propagules infested with varying levels of infestation at different times of the year were taken. Seedlings which were visibly affected, that is in which the upper portion of the hypocotyl was desiccated or in which the shoot (stem and leaves) above the hypocotyl no longer had sufficient cell turgor to keep the stem supporting the leaves, were examined. This was done to ascertain what qualitative internal changes had occurred in the propagule that had caused the external signs. No attempt was made to quantify the extent of the damage at this stage, as the variables (eg. position of the tunnel within the propagule, length, breadth, shape, volume, presence/absence of fungi etc) which might impact on the survival of the propagule were unknown.

Seedlings that recruited early in the season and were infested by *C. fallax* relatively late in the season were also examined to see if the presence of roots and leaves affected the survival of *C. fallax* in the hypocotyl.

5.2.2 Methods of following changes in levels of infestation, recruitment, and loss of viability in the field.

Seedlings that had recruited in the period February to June 1995 were tagged by inserting skewers with tags into the mud adjacent to the seedling. Their status (clear/ infested, surviving/dead) was recorded at each survey date. Propagules and newly recruited seedlings were tagged and followed in cohorts during the period of propagule abscission and up to four months after recruitment (determined by production of the first two leaves) or loss of viability of the final propagules.

Information gathered in previous studies was used to set parameters on which to make decisions on the viability of propagules/seedlings in the field. Those that had lost the upper third of the hypocotyl or where this section had become desiccated were deemed not viable. Similarly, where roots had formed and the propagule or seedling was then broken, separating the rooted section from the rest of the propagule, it was deemed that the upper portion, being detached from the substrate, was not likely to regrow roots.

Survival of a seedling was based on the continued existence of a non-desiccated hypocotyl and the potential for re-budding. Defoliation by leaf eating herbivores was not taken as indicating non viability, as the propagules have the potential to produce adventitious buds on the hypocotyl (Tomlinson 1994). All sites were monitored at two to three week intervals and recovery (change in status from infested to clear) recorded.

5.2.3 Recruitment and survival in experimental plantings.

An experiment was run to determine the effect of infestation on the survival of propagules and subsequent growth of seedlings. Propagules were sorted in the laboratory into two groups (infested and clear) using the method described in Chapter 4. Weight and length data for each propagule were recorded to allow post hoc comparisons with these as potential factors, should analysis indicate these were significant covariates. All propagules were marked with a unique identifier using Artline 400XF paint markers. Pilot tests had indicated that these marks remained on propagules speared into the substrate for at least a year. This marking of propagules meant that propagules could be identified in the field when planted. Skewers with tags duplicating the information on the propagule were inserted into the mud next to each propagule. In this way if predators or water borne debris removed a propagule or seedling, the missing individual could be accounted for.

Sixty clear and sixty infested propagules were planted in six plots of 20 propagules, with equal numbers of clear and infested propagules mixed before planting. The six plots were all in a light gap in the mid intertidal zone with *Rhizophora* adults on each side of the gap. The light gap, the result of a survey line, cut through the mangroves, running North-South. It was approximately 5 metres wide at ground level. Planting was standardised by inserting propagules, to a depth equal to 20 to

25% of the length of the propagule into the substrate (Qureshi 1990). Planting was randomised by ballot with propagules from each group in each plot.

Plots were rectangular with gaps of approximately 50 cm between plots. This enabled close inspection of propagules and seedlings without disturbance of the substratum near their roots. Plantings took place in February 1996. Recruitment was defined as the production of two leaves, and these needed to be visible before a propagule was rated as having successfully recruited. Survival of seedlings was monitored until infested seedlings were either dead or no longer showing any signs of infestation, a period of 9 months.

5.2.4 Infestation levels in seedlings recruited prior to infestation by *C. fallax*.

To determine whether established seedlings are infested by *C. fallax* in the same way as propagules, seedlings that had recruited in the previous year were tagged, and their status noted. In the shade, seedling growth is slow. The majority of seedlings from the previous year still have only two leaves, that is they are very similar in appearance to newly recruited seedlings. On each subsequent survey the status of each seedling was checked to see if it was still alive and whether or not it had become infested. If seedlings were equally attractive as propagules with respect to *C. fallax* infestation, it was anticipated that levels of infestation of seedlings and propagules would show similar changes over the season as the *C. fallax* population increased.

5.2.5 Comparison of levels of infestation and seedling survival.

Two sites at each of three locations were surveyed over a three-year period. The number of propagules on the ground peaked during March (Chapter 4). The percentage infestation (number of propagules infested/total number of propagules on the ground*100 for each site) in March was plotted against the number of seedlings which successfully recruited at that site and survived to October. Any negative effect of *C. fallax* infestation on seedling survival in the field should be reflected as a negative correlation of infestation and seedling numbers.

5.2.6 Analysis

Cohort data was recorded in an Access database and queries written to extract relevant information. This was then exported to Excel and graphed to identify patterns of infestation. Analysis of variance was carried out using Excel. Where data was in the form of a proportion (p), for example, the number of propagules infested compared to the total number of propagules on transect, the data was normalised by arcsine$\sqrt{p}$ conversion (Zar 1984).

Results of the trial planting was recorded in SPSS and analysed using the GLM Univariate model III. The variable in the model was the state of the propagules ie infested or uninfested.

5.3 *Results*

5.3.1 Effect of *C. fallax* infestation on individual propagules.

The effect of *C. fallax* on the internal tissue of a propagule depends on the level of infestation (how many females have bored into the propagule to lay eggs) and the length of time since first infestation. The feeding larvae and female adult, consume the tissue of the hypocotyl. The tunnels are irregular in shape and the surrounding tissue appears to remain healthy. Seedling death seems to occur once the tunnel transverse cross section approaches that of the propagule at that point. The leaf and stalk tissue of heavily infested seedlings are limp, the cells lacking cell turgor required to hold the leaves erect. The effect of *C. fallax* infestation can be seen in the following photographs in Figure 5-1. The two photographs show a seedling with the signs of stress which were observed to precede death and the same seedling split vertically to show the internal damage caused by the feeding larvae of the infesting scolytid. Figure 5-2 shows the entry tunnel and feeding chamber of a newly infested propagule. Figure 5-3 shows the development of the tunnel as the larvae feed on the spermatophagous tissue of the hypocotyl.

Figure 5-1 External and internal views of a seedling infested by *C. fallax*

Note that the leaves of the newly established seedling are drooping while small quantities of frass extruding from entrance holes are the only other external indication of infestation. Internally it can be seen that portions of the tissue of the hypocotyl have been consumed and the resulting cavities within the hypocotyl are filled with frass. The cavity or feeding tunnel marked 'A' extends across the entire cross section of the hypocotyl and is probably responsible for preventing movement of water up the conducting tissue from roots to leaves.

Figure 5.2 Photograph of a dissected newly infested propagule.

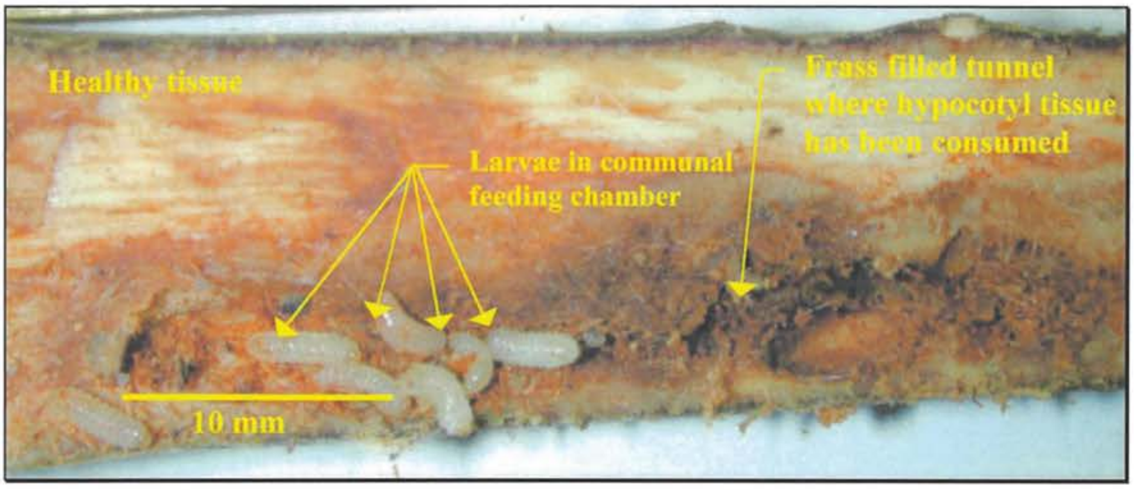
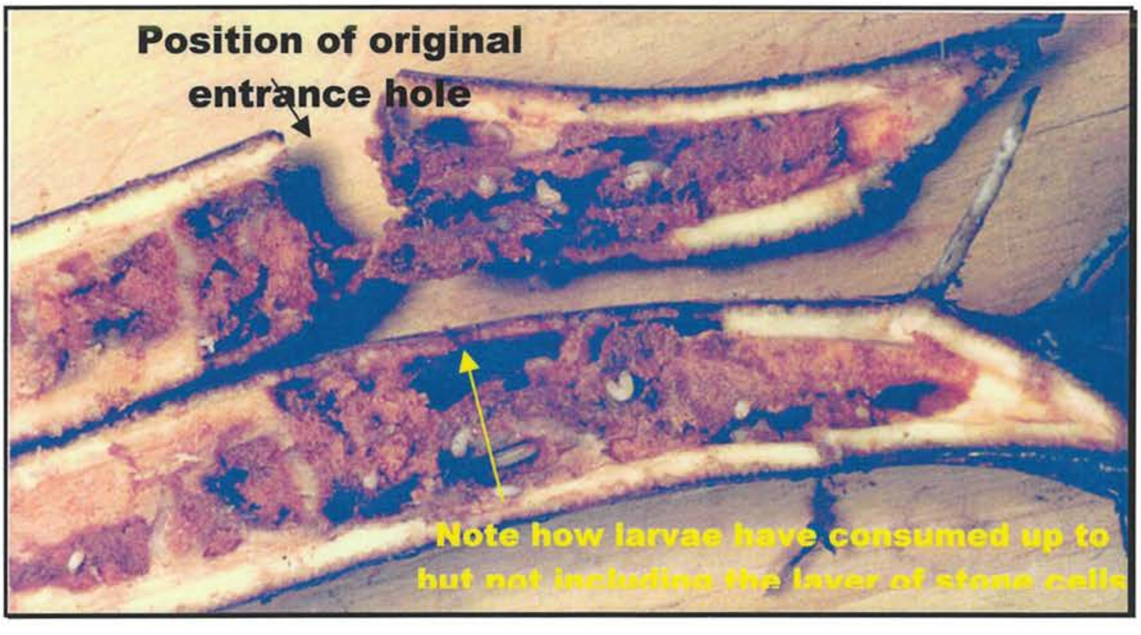


Figure 5-3 Photograph showing damage caused by larvae feeding on a propagule.



The sequence of events which occurs when a propagule is attacked by an adult scolytid was reconstructed from the appearance of tunnels in the dissected propagule and the associated second generation life stages that is, presence of eggs, larvae, pupae and new adults.

Initially a female *C. fallax* arrives on the surface of the propagule, after choosing a site for the tunnel she chews her way in, excavating a tunnel circular in cross section. The diameter of the tunnel is only fractionally larger than the cross section of the female, just over a millimetre in diameter. The length of the tunnel is normally at least the length of the female, ie. 2 to 3 mm long. At the end of the tunnel the female begins excavating a communal egg chamber. This is small, usually an oval chamber with dimensions in the order 4 mm by 4 mm by 5 mm. In this she lays 8 to 12 eggs in a cluster.

Larval feeding is communal, and the feeding tunnel increases in size as the larvae grow. The shape of the tunnel is irregular, sometimes forming one large chamber the width of the propagule, leaving only the epidermis untouched. At other times the larvae may eat out a long narrow tunnel, less than a quarter of the diameter of the hypocotyl, but up to 5 cm long. The tunnel may be straight or twist and turn, it may widen out or reverse in direction as it reaches the epidermis. Although the shape of the tunnel is irregular, there are two points of consistency. The epidermis is never consumed, leaving a layer of cells between the tunnel and the outside (see Figure 5-3), and the single entrance is used to discard frass.

5.3.2 Observation on *C. fallax* infestation on newly recruited seedlings.

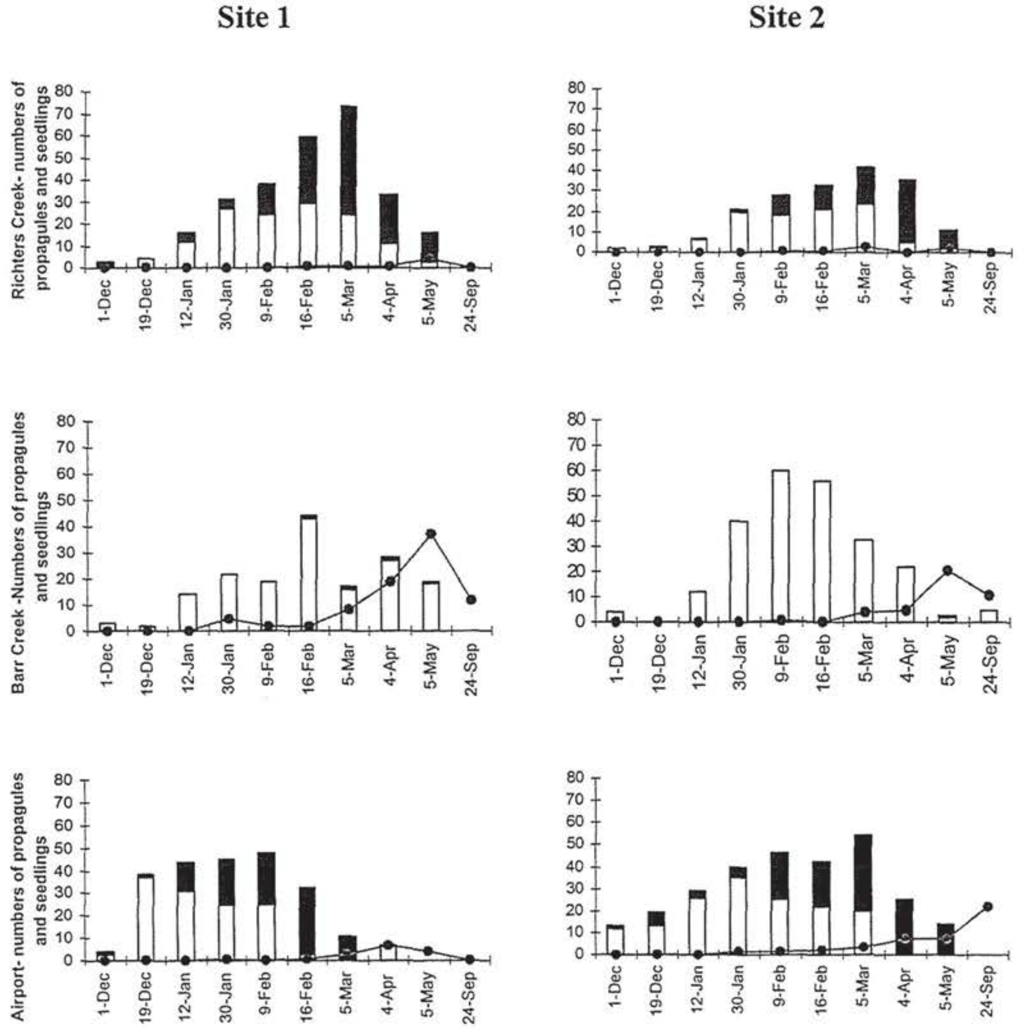
Late in the season seedlings, which had already established roots and leaves before *C. fallax* infestation occurred, were collected. Dissection of these infested seedlings revealed tunnels in which the scolytids were either dead or missing. There was frequently moist or wet frass clogging these tunnels. No remains of eggs, larvae or pupae were detected in the decaying mass of frass but portions of the exoskeleton of the adult were noted on occasion.

5.3.3 Effect of *C. fallax* infestation on recruitment of seedlings in monitored transects.

Six cohorts of seedlings were followed at each location from the time they were first tagged on the mud in January, February or March 1996 through to October 1996. The same pattern of change occurred at each site at each location for each cohort. All cohorts started off with low levels of infestation (less than 10% infested), the number of infested propagules in each cohort rose to 100% at 5 of the 6 sites. During the first 6 weeks of monitoring many of the propagules recruited as seedlings. At five of six sites all seedlings in the cohort were dead within two months of the final members of the cohort becoming infested. The Airport Site 2 was the only site with less than 100% infestation and was the only site where seedlings survived until October.

In 1995, infestation levels were low in three sites, Airport Site 2, and both sites at Barr creek. Figure 5-4 shows the higher levels of recruitment (more than 10 seedlings/50m ^{2} transect) at these sites associated with the presence of propagules which had recruited without being infested by *C. fallax*. Sites 1 and 2 at Richters Creek and Site 1 at the Airport had no seedlings which were not infested by *C. fallax* and had no seedlings which survived to September.

Figure 5-4 Effect of propagule numbers and infestation level on seedling recruitment.



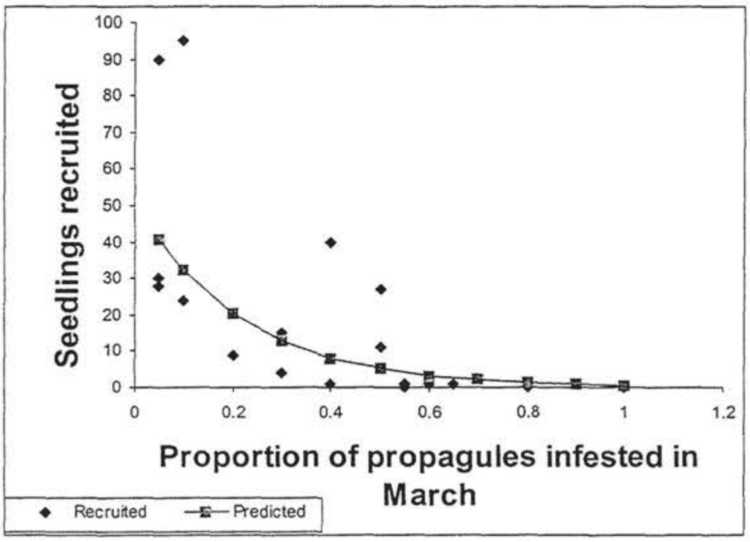
Legend: Infested propagules ▬ Clear propagules ▭

The line indicates the number of seedlings on the transect at each survey date.

Cohort data was only available for one year, but proportion of propagules infested and the number of seedlings recruited in each transect is available for three years. This includes the period in 1994 when the Barr Creek locations had returned to normal patterns of inundation, but had very low levels of infestation. Based on the patterns observed in the cohorts in 1996, the levels of infestation recorded at the end of the summer (March) were compared with the number of seedlings that remained alive in October. This was done for all six sites over the three-year period. Proportional levels of infestation ranged from 0.01 to 1 and recruitment from 0 to 90 seedlings/ $50m^2$ (Figure 5-5). The result shows that recruitment levels show a significant negative correlation with levels of infestation ($F=29.48$; $df=1,16$; $p = 0.00005$; $r^2=0.64$).

Recruitment is not plotted as number of seedlings per number of propagules, as the number of propagules changes constantly as a result of new propagules falling and existing propagules being removed through predation or water movement. Recruitment is not correlated with high numbers of propagules. For example Richters Creek sites consistently had the highest number of propagules and the lowest number of seedlings recruited (zero in three years of monitoring). It also had consistently high levels of infestation.

Figure 5-5 Regression line showing relation between levels of infestation and recruitment of seedlings.



The fitted curve indicates the possibility of a relationship of the form $y = a e^{-b x}$ where y is the predicted level of recruitment in October per $50m^2$, x is the proportion of propagules infested in March of that year and a and b are constants.

5.3.4 Effect of *C. fallax* infestation on established seedlings in monitored transects.

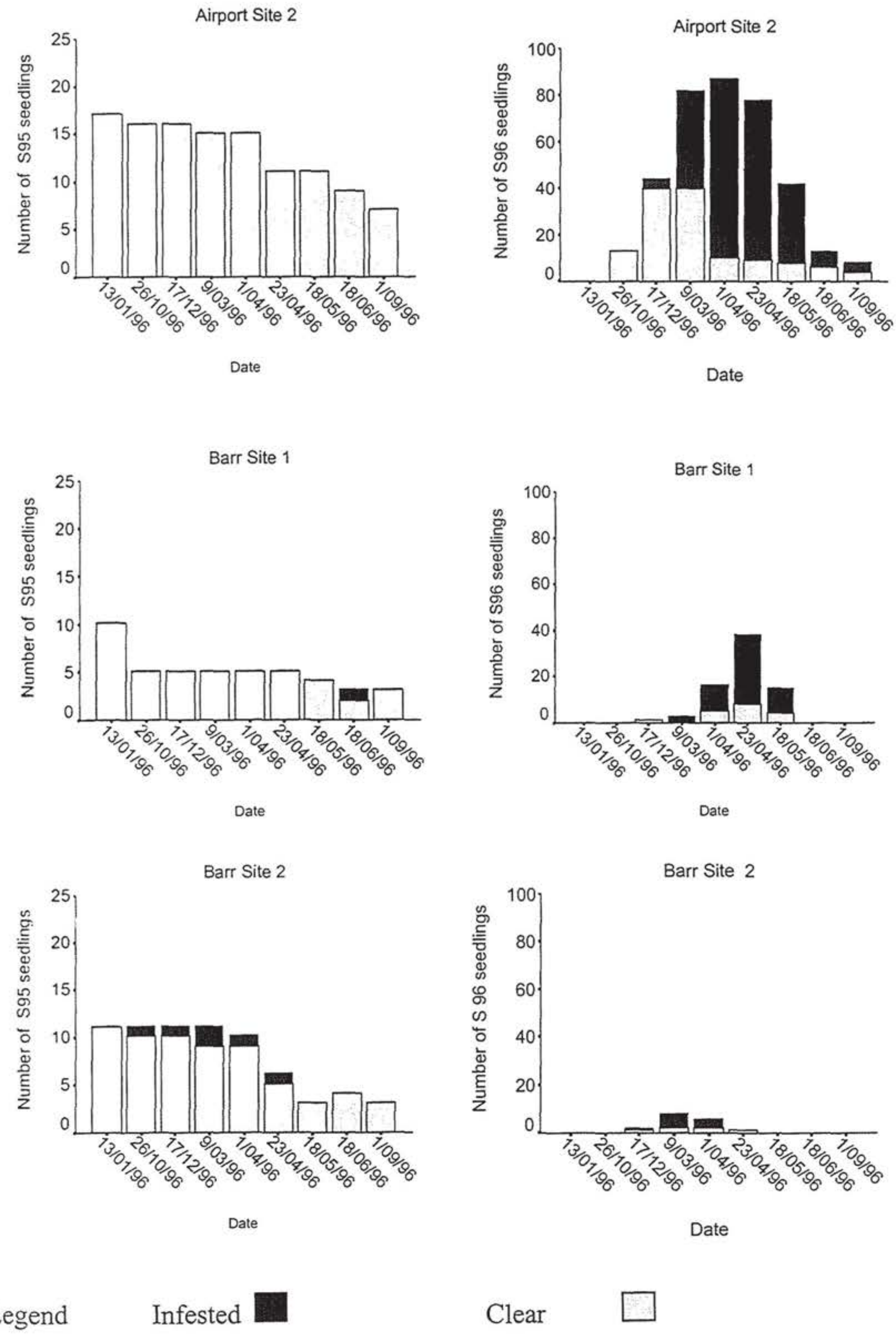
Seedlings which had recruited the previous season and survived the winter were designated S95 seedlings, indicating they had recruited in the period February to June 95. S95 seedlings in 1996 did not show the same rate of infestation as newly recruited S96 seedlings in 1996 (Figure 5-6). Very few S95 seedlings were infested whereas the majority of S96 seedlings were infested and failed to survive. Comparison is at three sites only as these were the only ones with S95 seedlings. S95 seedlings are less susceptible to *C. fallax* attack than newly recruited S96 seedlings ($F=31.07$; df 1,8; $p< 0.01$) and the death of S95 seedlings in the population is not correlated with the level of infestation in the surrounding propagule population.

The S95 and S96 seedlings were similar in size, having on average 2 to 4 leaves only. All S95 seedlings were located on the transects ie. under the canopy in fairly heavy shade. Occasionally seedlings were tagged as infested late in the season, but were subsequently found to be clear of scolytids The initial borehole was still visible, but lacked frass production even when the temperature rose and frass production from adjacent infested propagules had resumed.

5.3.5 Recruitment and survival in experimental plantings

There was no difference in recruitment between infested and clear propagules in the experimental plantings ($F= 1.98$; df 1, 18; $p= 0.18$). Survival of infested propagules as seedlings was, however, significantly lower than that of seedlings recruited from non-infested propagules ($F= 9.39$; df 1,18; $p<0.01$) with none of the infested group alive after 9 months while 47 % of clear control group were still alive at this stage.

Figure 5-6 Comparison of *C. fallax* infestation in S95 and S96 *Rhizophora* seedlings in 1996.



5.4 Discussion

5.4.1 Effect of infestation on individual propagules

The physical damage caused by infestation of *C. fallax* in *R. stylosa* propagules is readily visible when a propagule or seedling is cut open. Tissue destruction in the hypocotyl is variable and has two significant effects. One is the weakening of the hypocotyl, usually at the site of the borehole. The other is the interference with water transport to tissues above the tunnel.

The location of the site of infestation may have important long-term effects for the scolytids. A propagule which is speared into the substrate is subject to mechanical stress associated with water movements and floating debris during tidal inundation, this causes loss of propagules and seedlings (Qureshi 1990). Where a propagule or seedling is infested near the base, the moment of force exerted on the tunnel by water pressure acting on the length of the propagule, will be greater than if the tunnel is closer to the upper tip of the propagule. This increases the possibility that flotsam will snap the propagule at this point, thus destroying both the propagule and the *C. fallax* infesting the propagule.

Transpiration of water through the hypocotyl to the leaves is essential if photosynthesis is to take place. When *C. fallax* larvae feeding on the hypocotyl destroy the transport tissues, the continued survival of the propagule and/or seedling is at risk. The fact that *C. fallax* infestation does affect survival of seedlings was demonstrated in the grow-out trials. Recruitment of seedlings was not affected, supporting the hypothesis that it is only when the tunnel formed by the feeding larvae effectively prevents transport of water up the conductive tissue in the hypocotyl that survival of the seedling is threatened. The appearance of the heavily infested seedling (Figure 5-1) is what would be expected of a plant lacking sufficient water to maintain cell turgor in the cells of the leaf stalk.

The difference in results, (ie. that recruitment was not affected whereas survival of seedlings was affected) has implications for surveys in the field. To assess the effect of *C. fallax* on recruitment, levels of infestation of propagules needs to be compared to survival of seedlings several months later. The interval between infestation by *C. fallax* and death of the *Rhizophora* host is between two and three months. Any survey that looked at recruitment of seedlings, early in the season, as a measure of the effect of C. fallax infestation would give misleading results. A better measure is the survival of the seedlings over an extended period.

'One off' surveys will also fail to identify the level of movement of propagules on and off the site and the correlation between time spent on the ground and level of infestation within a cohort. The large numbers of uninfested propagules falling to the ground in February and March effectively 'dilute' the infestation levels when total numbers on the ground are surveyed. Only by studying cohort data was it possible to establish the close correlation between time on the ground and level of infestation within a cohort. Regressing the data showed clearly that the majority of propagules had become infested on the ground. This does not rule out the possibility of infestation occurring on the tree, it merely indicates that if it occurs it is not common in *C. fallax* infestation of North Queensland *Rhizophora* propagules.

The effect of large proportions of *Rhizophora* propagules being infested by *C. fallax* was demonstrated by looking at infestation levels of propagules and survival of seedlings. There was a significant negative correlation of infestation levels at the end of the fruiting season and the number of seedlings alive on the transect at the beginning of the following season. Relatively low levels of infestation have the potential to lower the level of recruitment significantly (Figure 5-5). Where infestation levels were less than 10% in March, seedling survival in October of that year was as high as 90 propagules per 50 m^2. When infestation levels reached 60%, no more than 3 seedlings survived per 50 m^2 (Figure 5-5). When this data is combined with the levels of infestation recorded in Chapter 4, it demonstrates the potential of *C. fallax* to affect the numbers of *Rhizophora* seedlings in the *Rhizophora* forest. This fits in with the data recorded for seedling survival of various cohorts.

All three measures of the effect of *C. fallax* on *Rhizophora* propagules, ie physical damage, grow out trials and correlation of infestation levels with survival of seedlings, support the hypothesis that infestation of *R. stylosa* propagules by *C. fallax* affects the survival of seedlings in the *Rhizophora* zone.

5.4.2 Infestation of established seedlings vs. newly recruited seedlings.

Infestation of established seedlings by *C. fallax* does not have the same effect as infestation of propagules. Both the rate of infestation and the effect of infestation on established healthy seedlings are much lower than on propagules in the same location. Established seedlings do not usually become infested (Figure 5-6). This may be related to the fact that seedlings have access to water via their root system and that when leaves are present, the flow of water associated with transpiration through the leaves is sufficient to flood the tunnels. Scolytids which infest twigs ring bark the twig before boring in, possibly to minimise flooding of the tunnels (Browne 1961; Crowson 1981). This increase in moisture in the tunnels appeared to have occurred in seedlings infested only after they had produced roots and leaves. Wet frass, clogging the tunnels, was associated with seedlings not showing signs of active infestation. These tunnels did not contain live scolytids, whether this was because the tunnel had been abandoned or because the infesting scolytid had died through predation, drowning or other causes could not be established. The presence of wet frass suggested drowning and this fits in with the known relationship between scolytids and host plants. The window of opportunity during which *C. fallax* can successfully reproduce in the tissues of the propagule appears to be limited to that period when the propagule is restricted in access to water, ie. after abscission and before it becomes well established as a seedling.

There appears to be a period early in the life of the seedling when it is susceptible to *C. fallax* infestation. Some tagged propagules recruited as seedlings prior to infestation yet the scolytids survived and eventually caused the death of the seedling (confirmed by examining the dead seedling). The factors that affect survival of *C. fallax* in newly recruited seedlings requires further study. Factors that would affect water uptake and transport through the propagule eg. pore water salinity, root mass when infested and leaf area when infested etc could possibly be important.

5.4.3 Evaluation of previously published data on *Coccotrypes* infestation in *Rhizophora* propagules.

Using knowledge of the physical effect of *C. fallax* infestation in *R. stylosa* propagules and the increase in loss of hypocotyl tissue over time, it is possible to interpret the conflicting results found in the literature. Any effect infestation has on a propagule will be associated with the effects of loss of tissue mass and function. Rabinowitz (1977) found infestation of *R. mangle* by *C. rhizophorae* had no effect on root production, since roots in infested propagules were produced above the scolytid feeding tunnel. This work was carried out with propagules kept floating in water. Root structures were isolated from the bulk of the propagule tissue by the scolytid tunnel therefore additional roots formed above the tunnel, with the combined root mass not significantly different from that produced by uninfested seedlings. This is consistent with the observation that the scolytid tunnels interfere with transport systems in the hypocotyl.

Robertson et al (1990) found no significant effect of scolytid infestation on growth of *R. stylosa* seedlings in greenhouse trials. Greenhouse growth experiments were abandoned in the present study after it was found that ants had attacked and removed the scolytids from the infested propagules. Robertson (pers. comm.) advised that the greenhouse used in the experiment reported in Robertson et al (1990), was not constructed to ensure exclusion of ants from the grow out trays. Therefore it was possible that ants had removed the scolytids from the propagules. As the damage caused by *C. fallax* consumption of hypocotyl tissue is cumulative and increases exponentially with time, removal of the larvae means the loss of tissue will stop. *Rhizophora* have the ability to seal off wounds to the hypocotyl and grow additional conductive tissue in the vicinity of the wound (Wier *et al* 1996). This has the potential to allow previously infested propagules to survive once the infestation is removed (see chapter 6). This raises the possibility that the perceived discrepancy in results between field and greenhouse trials is the result of an experimental artefact, namely marauding ants, and emphasises the need for experiments to be carried out in the field where ever possible.

Airport site 2 is the only site to have a nest of mangrove ants, *Polyrachis sokolova* that lives in burrows in the mud in the intertidal zone. *P. sokolova* is found only in the lower intertidal zone, nesting in the mud and foraging for food at low tide (Hogarth 1999). Examination of food remains in the nest shows a broad range of items, small crustacea, larvae and other insects (Hogarth 1999). This nest is only 4 m from the end of the transect where several seedlings survived despite all propagules in the area being infested (Figure 5-4). The possibility that these ants are predators on *C. fallax* in the field requires further investigation.

Smith (1987a) reported 100 % of *Rhizophora* seedlings in one area of the intertidal zone were killed as a result of scolytid infestation. The results of the present study support and extend his findings. The significant correlation between levels of infestation and recruitment of propagules can not imply cause and effect. However, when this is linked to the results of the planting experiment, in which care was taken to eliminate all variables except infestation, the evidence became more compelling. Infested propagules did recruit into seedlings, but none of these survived either during grow out trials or on monitored transects. The internal destruction of hypocotyl tissues provides evidence as to the mechanism causing seedling death. The appearance of infested propagules with reduced turgor in the tissues above the tunnel is consistent with damage to the conductive tissue in the hypocotyl.

In summary, *C. fallax* infestation does not affect recruitment of *Rhizophora* propagules, but damage done to becomes evident when survival of the seedlings is monitored. Established seedlings are not attacked by *C. fallax*. Levels of infestation of propagules as reported in Chapter 4 are correlated with very low levels of survival of *Rhizophora* seedlings.

CHAPTER 6

THE EFFECT OF SUNLIGHT AND HEAT ON SURVIVAL OF INFESTING SCOLYTIDS AND RECRUITMENT AND GROWTH OF HOST PROPAGULES

6.1 Introduction

Predation is often regarded as being of prime importance in determining species composition or in preventing competitive exclusion except where the effect of predation is reduced for some reason (Connell 1975). One situation where predation is reduced is where the prey species has the ability to live in refuges that the predator cannot invade because the conditions exceed their tolerance limits (Connell 1975). These limits may be one or a combination of the factors that combine to make up the environment of the host and which impact on the predator.

The mangrove environment is harsh due to the combination of periodic fluctuations and extremes in several of its physiochemical parameters (Saenger 1982). Blasco (1984), in discussing the climatic factors and biology of mangrove plants states that 'The basic climatic factor governing the geographical distribution of species is probably air temperature'. Krebs (1994) states 'Temperature and moisture are the major factors that limit the distributions of animals and plants'.

Most unshaded surfaces in the tropics heat up during the day. The surface temperature on the mud in a light gap can reach temperatures of 46^0C and water in shallow depressions in the mud has been measured at 36^0C (Edney 1961). Temperature control in leaves in the upper canopy, which are exposed to high levels of solar radiation (insolation) and where evaporative cooling is limited by access to fresh water, require special strategies. Ball (1988c) investigated optimisation of carbon gain in relation to water loss in a tropical mangrove forest and found that maintenance of favourable leaf temperature with minimal evaporative cooling was at the expense of light interception. Either evaporative cooling or a strategy to avoid high leaf irradiation (by assuming a more vertical position) was required to maintain the leaf temperature within the range favourable for photosynthesis. (Ball *et al* 1988c) Leaves constrained in the horizontal position rose from 4 to 11^0C above ambient air temperature which was approximately 30 ^{0}C.

The temperature to which propagules are heated may depend on the position of the propagule. Propagules speared vertically into the mud expose less surface area to direct sunlight at midday than propagules lying stranded on the mud. Position ie. horizontal (lying flat) or vertical (speared in) would depend on the method of delivery to the surface on which they were exposed to solar radiation. In propagules dispersed by water onto exposed substrates it might be expected that propagules were stranded in the horizontal position. Prior to root development, propagules do not have access to water for use in evaporative cooling. Control of internal temperature would be minimal and temperatures in the tissue would have the potential to rise. In infested *R. stylosa* propagules, the scolytid lives inside the propagule therefore any increase in temperature of the propagule would be experienced by the scolytid.

In general insects have an upper lethal temperature of between 40^0 and 50 ^{0}C (Mathews and Kitchling 1984) and heat is used to control the level of infestation of commercially important insect pests. Hot water immersion is used to kill infesting insects in a number of commercial operations where quarantine regulations prohibit the transport of insect pests in fruit and flowers for export (Hallman and Sharp 1990; Hara *et al* 1993). High temperature treatment (54 °C) is recommended to kill termites in timber (Woodrow and Grace 1998). These methods of control, which all use heat to kill infesting insects may have equivalents in the natural environment. That is, there could be habitats in the mangroves in which propagules are heated to the level at which scolytids infesting propagules are killed.

Daytime temperatures in the tropics can reach temperatures in excess of 40^0 C in the shade although this is unusual as the mean monthly maximum for Cairns does not exceed 35^0 C (Bureau of Meteorology 1999). It is possible that elevated temperatures in the shade may affect the scolytid under extreme heat wave conditions but not during average years. The temperature of soil exposed to full sunlight is usually several degrees warmer than those in the shade (Smith 1987), similarly leaves constrained in the horizontal position and exposed to solar radiation reach temperatures of up to 10C above ambient air temperature (Ball *et al* 1988c). Exposure to full sunlight would appear to have the potential to raise the temperature of the propagule.

All the sites used to study host specificity and levels of infestation in this study were under the canopy in the *Rhizophora* zone such that propagules on the substrate were in the shade. Levels of infestation in propagules exposed to full sunlight and information on the associated higher temperatures experienced by the propagules had not been studied. McMillan (1971) in an investigation of environmental factors affecting seedling establishment of *Avicennia germinans* (the black mangrove) found that exposure of *A. germinans* propagules to sea water temperatures of 39-40 ^{0}C was lethal. Smith (1987) reported on the die off of Ceriops seedlings following a heat wave in which daytime temperatures exceeded 45 °C for three successive days. Elster *et al* (1999) examined the impact of ecological factors on regeneration of mangroves and found that temperatures exceeding 45^{0}C affected both *A. germinans* and *L. racemosa*, but that *R. mangle* was more resistant to high temperatures. This suggested the possibility that the scolytids infesting *Rhizophora* propagules may be adversely affected by the temperatures experienced by propagules exposed to sunlight, whereas the propagules could survive.

This chapter explores the levels of mortality experienced by *C. fallax* in propagules at different temperatures. This is then linked to the effect of sunlight (insolation) on the internal temperature of the propagule. To establish the level of exposure to sunlight as a **cause** of lower *C. fallax* levels of infestation in propagules in exposed areas, it was necessary to demonstrate two things. Firstly that *C. fallax* inside *R. stylosa* propagules are sensitive to increased temperatures and secondly that these temperatures may be experienced by propagules in the field exposed to sunlight. Survival of *C. fallax* in propagules under different heat conditions was recorded and clear propagules exposed to the same range of conditions were planted out to see what affect the raised temperatures had on the recruitment and growth of seedlings.

6.2 Methodology

6.2.1 Overview

The links between temperature, time and survival of both host and scolytid were investigated under controlled conditions in the laboratory. Infested propagules were immersed in hot water at different temperatures for varying times. Survival of the scolytid was assessed by examining for frass production. The effect of the elevated temperature on the propagule was determined by planting the propagules in a small light gap in the *Rhizophora* zone and observing recruitment and growth of the seedlings. The temperatures and times chosen for this experiment were based on the figures given as upper lethal temperatures for insects ie. between 40^0 and 50^0 C after 30 minutes exposure (Mathews and Kitchling 1984).

The temperatures experienced by propagules in the natural environment were investigated by exposure of propagules to sunlight on both moist and dry substrates and while floating in water. Propagules dispersed by water and left stranded tend to lie flat on the surface before self-elevating (Egler 1948). Propagules floating vertically may have the tips embedded by abrasion (Davis 1940) or they may fall from the tree and implant themselves like little spears (LaRue and Muzik T.J. 1951). The surface area exposed to direct sunlight depends on the attitude of the propagule, vertical (speared in) or horizontal (lying flat) as does the area in contact with the substrate therefore the temperatures of propagules both speared in and lying flat were investigated. In addition the time taken for the internal tissues of the propagule to heat up were investigated for both immersion in hot water and exposure to sunlight.

The survival of infesting scolytids during short term exposure to sunlight was investigated by placing infested propagules in the mangrove in a large light gap, with controls in the adjoining shade. These were then checked to see how many of the propagules still contained active scolytid populations ie. in how many of the propagules the scolytids had been killed and how many still contained live scolytids. .This was recorded as proportion still infested. Assessment was done using the protocol developed from the results in Chapter 4. In addition, the actual level of active infestation in propagules stranded on a mudflat (in full sunlight) was then compared to the level of active infestation in the shade of the canopy in the adjoining forest. Light levels in the open range from 500 to 1900 kjoules/m^2 between the hours of 0800 and 1700 hrs, with levels under the canopy reduced by 80 to 95%, ie. to between 30 to 380 kjoules/m^2 (Chapter 3, section 3.1.2).

Experimental design and analysis

A series of treatments was designed to test the hypothesis that the mortality of *C. fallax* infesting *R. stylosa* propagules was affected by the temperature experienced by the propagule and to measure what effect these elevated temperatures had on subsequent recruitment and growth of the propagules.

A balanced experimental design was prepared with three levels of treatment. These were; health of the propagule (infested or clear), temperature of the water (40, 45 and 50 °C) and duration (time) of immersion (0, 5, 10, 15, 20 min.). Pilot studies indicated that this time period was appropriate a *C. fallax* died within 20 minutes at test temperatures. The results of the experiment were analysed at three stages. Initially the proportion of propagules still actively infested after the treatment was examined to determine the effectiveness of the treatment in reducing active infestation by *C. fallax*. Clear propagules (propagules which were never infested) were treated along with the infested propagules and both sets were planted out to gauge the effect of the treatments on recruitment. Controls in the form of clear and infested propagules, which were not immersed in hot water, were planted out at the same time. The effect of different treatment levels on growth was measured using increase in shoot length over time (Smith 1987a) using a modification of the method by Evans (1972).

To assess the differences in temperatures experienced by propagules in the field a second balanced design was drawn up with the following factors:

Light - two levels, under the canopy (shade) and in a light gap (sun)

Substrate moisture - two levels, inundated and allowed to drain (wet) and no added water for 4 days prior to treatment (dry).

Position- two levels, speared in vertically or lying flat.

Internal temperature of one propagule in each treatment level was recorded every hour between the hours of 9.00 and 17.00 hrs (repeated measure). This was analysed using the SPSS one way repeated measures ANOVA with 9 levels of temperature measurement (the within subject factor).

Table 6.1 Experimental design to investigate affect of light levels, substrate and position of propagules as factors affecting the internal temperature, survival of scolytids in propagules and subsequent recruitment of propagules.

Substrate	Light level	Position	No. of Propagules +1 for temp. measurement	No. of repeats	Repeated levels of temperature	Survival of scolytids assessed	Recruitment of clear propagules assessed
Wet	Full sun	Speared	5i +5c +1	3	9	n/5	m/5
Wet	Full sun	Lying	5i +5c +1	3	9	n/5	m/5
Wet	Shade	Speared	5i +5c +1	3	9	n/5	m/5
Wet	Shade	Lying	5i +5c +1	3	9	n/5	m/5
Dry	Full sun	Speared	5i +1	3	9	n/5	*
Dry	Full sun	Lying	5i +1	3	9	n/5	*
Dry	Shade	Speared	5i +1	3	9	n/5	*
Dry	Shade	Lying	5i +1	3	9	n/5	*

Exposure not done in field as the intertidal zone did not dry out following an early start to the wet season. Laboratory work only. i = infested propagules, c= clear propagules

To assess the survival of the *C. fallax* within propagules, infested propagules were placed in the mangroves and assessment of survival of infesting scolytids was carried out after one full day in the sun. Clear propagules, subjected to the same treatment combinations (wet substrate only), were planted out to assess the effect of treatment on recruitment of propagules. The design for effect on recruitment of *Rhizophora* propagules was not fully balanced as no dry substrate was available in the *Rhizophora* zone during the period (Table 6.1).

Transformation of results.

Results were recorded as the number of propagules still infested after treatment divided by the number in the treatment, ie. proportion of propagules still infested. This data was normalised using the conversion $p'=\arcsin\sqrt{p}$. Where one propagule or seedling was measured repeatedly as in growth data or change of temperature during exposure to heat, the results were analysed in SPSS version 8.0 using the General Linear Model- Repeated Measures Analysis software. Mauchli's test for sphericity was checked and where the data set deviated significantly, Greenhouse Geisser tests with associated lower degrees of freedom were used. (Note these gave the same results with respect to significance of results as the Huynh-feldt and Lower-bound tests). These tests permit use of the General Linear Model despite violations of the assumptions of sphericity required for repeated measures analysis

.

In the Post Hoc analysis of variance of survival of scolytids in propagules immersed in hot water, equal variance assumption was not met. In this case SPSS defaults to Tamehane and Dunnett T3 tests, and these were examined in analysing the results of this experiment.

Pooling of propagules following hot water treatment.

It was hypothesised that immersion in hot water would heat the propagule to levels at which the infesting scolytids would die. The propagules which were infested prior to treatment would then fall into one of two groups, those still infested (hot water treatment not lethal to scolytids) and those no longer infested (hot water treatment had killed the scolytids). The survival of these two groups as seedlings could then be compared. Any treatment that killed scolytids but also lowered the survival rate of the host propagule as a seedling would have less impact than one that did not affect seedling survival. It was important to compare the effect of the treatments on uninfested seedlings to see what effect they had on survival of the seedlings. Following assessment the propagules were regrouped as per Table 6.2.

Table 6.2 Pooling of treatments following assessment of new status of propagule.

Original status	Treatment	New group
Infested	Treatments that killed infesting scolytids	X
Infested	Treatments that did not kill scolytids	Y
Clear	Treatments that killed scolytids in infested propagules	$X^{\aleph}$
Clear	Treatments that did not kill scolytids in infested propagules	$Y^{\aleph}$

This grouping enables direct comparisons to be made between the survival of seedlings recruited from propagules that are still infested and those in which the infesting scolytid has been killed (comparison of X and Y for survival and growth). Any treatment effects on the propagule can be assessed by comparing the survival rates of the clear propagules (comparison of $X^{\aleph}$ and $Y^{\aleph}$).

6.2.2 Treatment methods

Propagules were collected from the forest floor of mangroves in the Cairns area. Care was taken to ensure propagules were not exposed to high temperatures or potential scolytid predators (ants) during transport, temporary storage or assessment periods. The method described in Appendix 1 was used to identify clear and infested propagules that were then placed into groups of five. Allocation of group to treatment was through random ballot. Ten propagules (5 clear, 5 infested) were immersed (simultaneously) for one of the temperature*time combinations (Table 6.3). The experiment was then repeated five times for each combination.

Table 6.3 Temperature and time combinations used in the heat treatment of propagules.

i =infested propagules, c = clear propagules

Treatment	Number of propagules per replication	Temperature of water	Time of immersion	Number of replications
A	5i + 5c	40	5	5
B	5i + 5c	40	10	5
C	5i + 5c	40	15	5
D	5i + 5c	40	20	5
E	5i + 5c	45	5	5
F	5i + 5c	45	10	5
G	5i + 5c	45	15	5
H	5i + 5c	45	20	5
I	5i + 5c	50	5	5
J	5i + 5c	50	10	5
K	5i + 5c	50	15	5
L	5i + 5c	50	20	5
Control	5i + 5c	-	0	5

Propagules were treated by immersing them in hot water in a 26 litre rectangular container made from white polystyrene. The close fitting lid was of the same material. No measurable temperature drop was recorded during the period of immersion of the propagules for periods of up to thirty minutes and temperature differentials between temperature of hot water and room temperature of up to 25^{0}C. Ambient room temperature was between 23 and 25 ^{0}C and maximum water temperature was 50 ^{0}C. All propagules were immersed in water at ambient temperature (23^{0}C) for 2 to 3 minutes forty eight hours prior to treatment to wash off mud and sand.

The water in the polystyrene container was adjusted to the required temperature by addition of hot or cold water as required, accompanied by vigorous stirring to ensure thorough mixing throughout the container. Five clear and five infested propagules were then placed in the water and the lid put on. Propagules in a treatment group were loosely attached to one another using rubber bands attached to a string. This allowed the five infested propagules (or 5 clear propagules) to stay as a group during treatment without being held against one another which may have restricted heat transfer to individual propagules. A tag on the string identified the clear group. The temperature in the water was monitored using a thermometer inserted through a hole in the lid. After the appropriate treatment time the propagules were removed from the water and spread out on a bench top to dry and cool down.

After treatment each propagule was marked with a code which identified the temperature*time treatment and a unique identifying number using a paint pen. The length and weight of the propagule and it's status (prior to immersion) were recorded. The treated propagules were then left on clean dry sheeting for 24 hours before being inspected for frass production. The white surface facilitated identification of even small quantities of frass exuded from a propagule. The propagules were rechecked after a further 24 hours after which they were planted out. The experiment was repeated 5 times and four of the five groups of propagules were then planted out. The propagules of the fifth group were dissected to verify that the method of identifying presence of viable scolytids in propagules ie. using frass production, gave a true indication of survival of *C. fallax* in the propagules under the treatment conditions.

All experiments were carried out in a single treatment container to eliminate variation caused by differences in containers. The sequence of treatments was allocated by random ballot to determine the order of treatments. Treatments were not carried out in sequence of increasing temperature or increasing time intervals. The water was changed after each treatment.

Following assessment of infestation status, propagules were planted out in a random block design to observe the effect of the heat treatment on recruitment of seedlings and the subsequent survival and growth of seedlings. 130 propagules were planted in a rectangular block approximately 50 cm wide by 130 cm long in a 5 by 26 array.

The propagules were speared into the ground approximately 10 cm apart to a depth of 20 to 25 % of their length. Position of propagules within the rows and allocation to rows was by random ballot . The 4 blocks were separated by gaps of approximately 60 cm so that walking between blocks to take measurements did not disturb the substrate close to the recruiting propagules.

Propagules were deemed to have recruited on the production of two leaves (Onuf *et al* 1977). The numbers of propagules which recruited (for each temperature*time combination) for both infested and clear propagules were recorded for each repetition of the experiment. Growth was measured using the method described in Smith (1987a). In this method, the length of the shoot from the top of the propagule to the base of the last pair of leaves is measured. This negates any effects of propagule size or depth of insertion into the substrate. This method was shown to produce consistent measures of growth as measured by biomass increase (Smith 1987a). The shoot lengths were measured at monthly intervals for the first 8 months of growth. The effect of the treatments on growth was determined using repeated measures analysis in SPSS General Linear Model with temperature, time and status as factors.

6.2.3 Effect of hot water immersion on the internal temperature of a propagule.

Individual scolytids were not submersed in hot water; the temperature experienced by the scolytid in the hypocotyl tissue would depend on the temperature of the surrounding tissue. Propagules vary in diameter and no reference to the heat conductivity of propagule tissue was found. In order to assess the temperature experienced by the scolytids inside the propagule, the temperature inside the propagule was recorded for the period it took to reach equilibrium with the hot water in which it was immersed.

A temperature probe was inserted inside the propagule at the widest point. The possibility of heat transfer along the probe was minimised by inserting the probe through polystyrene up to the point it entered the propagule, the gap being sealed with a small portion of a mouldable non setting plastic compound sold under the trade name 'Blue Tac'. This also minimised the chance of water flowing in along the probe and conducting heat.

The temperature was recorded at 30-second intervals following immersion. The experiment was repeated at 40, 45 and 50 °C with 10 propagules each time. The diameter of each propagule at the point where the probe was inserted was recorded. The results were analysed to find the effect of diameter of the propagule on the rate of increase in the internal temperature.

6.2.4 Effect of immersing propagules in hot water for extended periods and at higher temperatures on survival and growth of the propagule.

Prior investigations had indicated the most appropriate range of temperature time combinations to give a range of results for scolytid survival was between 40 and 50 °C for between 5 and 20 minutes. These investigations had indicated that the above combinations may not affect the levels of *R. stylosa* recruitment and survival. In order to gain an indication of what temperature*time combinations of hot water immersion would affect *R. stylosa* recruitment, clear propagules were exposed to treatment levels higher than those found to affect survival of *C. fallax* in the hypocotyl. These included extended exposure to water at 40, 45 and 50 °C, for periods of up to an hour and exposure to water at 55 and 60 °C. Temperatures of 53 °C have been shown to kill seeds and seedlings of *Avicennia* spp in Florida mangroves (Arora and Yanuraju 1998), but *Rhizophora* was reported to have greater tolerance to elevated temperatures (Elster 1999). Following treatment in hot water, the propagules were planted out as described previously. The propagules were monitored in the field for 8 months with respect to recruitment and growth as seedlings. The results were analysed to see if temperature and time of immersion did affect recruitment and growth of the propagules.

Selection of propagules and allocation to treatments and treatment protocols were as described above. The only difference involved the ability of the polystyrene container to maintain the temperature at the higher levels and for longer periods. This was compensated for by the addition of near boiling water to the container if the temperature fell more than one degree below the treatment level. The water was added in one corner (away from the propagules) and accompanied by rapid stirring to raise the overall temperature to the desired level.

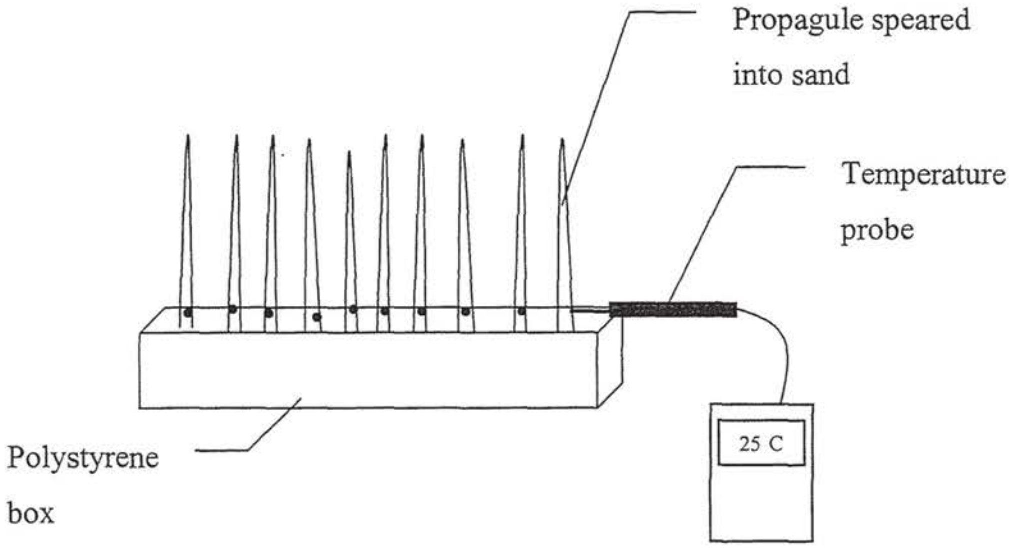
6.2.5 Factors affecting the internal temperature of propagules exposed to full sunlight.

It was hypothesised that the change in temperature of propagules exposed to sunlight would depend on the surface area of the propagule exposed to sunlight (ie. speared in or horizontal propagules) and the surface area in contact with damp or dry substrate. The level of insolation varies significantly during the day (Chapter 3, section 3.1.2), therefore, propagule temperatures at different times of the day were investigated.

Laboratory experiments.

Forty clear propagules were randomly assigned to 8 groups. The groups were then randomly assigned substratum and position treatments as for the field experiments (Table 6.1). Five propagules in the vertical group of position treatments were pushed into the substratum for approximately 20% of their length. The internal temperature was taken with a digital probe inserted approximately 1.5 cm above the substrate in the thickest part of the propagule (Figure 6-1). These experiments using propagules in pots supplemented the experiments done in the *Rhizophora* zone for which a dry substrate was not available. Propagules from trees in the upper intertidal zone may fall in areas which dry out between spring high tides. The effect of sunlight on these and on propagules which may become stranded on beaches temporarily while being dispersed could not be investigated in the mid intertidal zone used for the recruitment experiment.

Figure 6-1 Equipment used to determine temperature changes in propagules.



Those in the horizontal group of position treatments were placed with the probe entry point in view flat on the surface. Minor variations in the surface of the substratum were not smoothed out, nor were the propagules pressed on to the surface. Care was taken when inserting the probe not to increase the degree of contact with the substratum. Readings were taken at hourly intervals. Results were analysed using a repeated measures ANOVA to detect interaction effects of time of the day with the fixed factors of substrate water content and attitude of the propagule.

Rate of change of internal temperature to changes in light level.

To establish the rate at which propagules heated up when exposed to sunlight after a period in the shade, the temperatures in two sets of propagules were compared. One group was placed in sunlight at 09.00 hrs and left there all day- this was the control. The other group was moved between sun and shade positions at hourly intervals. This was done for propagules in both the speared in and lying positions, using damp sand in large garden pots as the support medium (Figure 6-1). Temperature readings were recorded at one-minute intervals using a Hastings data logger attached to a temperature probe. The data was graphed and the time taken for the propagule that had been in the shade to reach the same temperature as the control was compared for the two positions. Large light gaps imply large areas of sunlight reaching the substrate and hence potentially longer periods of exposure of propagules on the substrate to heating effects. The rate at which a propagule heats up may mean it does not reach temperatures lethal to *C. fallax* before being shaded, or that the time the scolytid is exposed to elevated temperatures is too short to affect the scolytid.

Variations in propagule size, colour, age, etc. may affect the rate at which incident light is absorbed as heat and the rate at which heat is lost to the surroundings. To estimate the variation in internal temperatures in a group of propagules in the same environment, the temperature from 10 propagules was taken in rapid succession. The mean ' between propagules variance' was calculated from these readings. This was repeated at various times of the day and for different positions and substrates. All temperatures were taken in clear propagules, which were not used in grow out experiments. All experiments were repeated three times on cloud free days using different propagules each time. This information was then used to estimate error terms where it was not possible to have replicate data for field temperature measurements.

Effect of sunlight on the temperature of *Rhizophora* propagules floating in water

The effect of exposure to sunlight on the ability of *C. fallax* to disperse in propagules transported by water was investigated by measuring the temperature of propagules floating in a large body of water (a salt water swimming pool) exposed to full sunlight. The propagules used in these experiments were discarded after testing, the presence of any chemicals in the pool were thus not relevant, as they were unlikely to influence the temperature of the propagule, the only measurement taken.

The internal temperature of the propagules was taken with a digital probe inserted into each propagule at the thickest part. Measurements in the pool were taken using Hastings data loggers set to record the temperatures of the propagules at 5 minute intervals. Air temperatures recorded at Cairns Meteorological Office were used as reference points for ambient air temperatures. The temperature of two propagules were recorded for a one week period at 5 minute intervals. The mean temperature of the propagule in the water and the temperature of the water taken at 1cm depth (average depth of the water surrounding the propagule) was then plotted for daylight hours. The results were analysed to test if there was any significant difference in the temperature measured inside the propagule and that of the water in which it floated.

6.2.6 The effect of light level and position on survival of *C. fallax* in *R. stylosa* propagules.

Propagules in the field could be exposed to sunlight where they had become stranded on the substrate or speared into the mud in a light gap. The effect on *C. fallax* in propagules exposed to sunlight in a gap needed to be investigated to confirm that the increase in temperature experienced by a propagule under these conditions did affect the survival of scolytids. Infested propagules were identified as described in previous chapters. Factors tested were position (speared in or lying) and light (sunlight or under the canopy) in a balanced design with 5 propagules in each group. The experiment was repeated three times using different propagules each time. Duration of exposure was one day between the hours of 0900 and 1630 hrs. Trials were carried out in the *Rhizophora* zone at Ellie Point in late February and March (see site description, Chapter 3), therefore the substrate was always wet.

Assessment of survival of *C. fallax* in the propagules was based on production of frass from the propagule over a 24-hour period back in the laboratory. Where no frass was produced it was recorded that the infesting scolytids had been killed. Where frass was produced it was taken as survival of the scolytids (Appendix 1).

6.2.7 The effect of exposure to direct sunlight on germination of *R. stylosa* propagules.

Clear propagules were exposed to the same combinations of light (light gap and canopy) and position (speared in and lying) as the infested propagules discussed in the previous section. After treatment they were planted out in a small light gap in the mid intertidal to assess effect of the treatment on recruitment. The results reflect the effect of the single days treatment, not recruitment of propagules left in that position to determine whether propagules for a day in an exposed position were affected by the exposure during that day. This effect (if any) could then be compared to the effect on the mortality of the infesting scolytid during an equivalent period.

6.2.8 Variations in levels of active *C. fallax* infestation in *R. stylosa* propagules in exposed and shade plots.

Experimental manipulation is useful in controlling variables, but it does not necessarily include all factors found in the field. To assess whether active *C. fallax* infestation where propagules were exposed to full sunlight differed from those under the canopy four samples were taken in an area where a mixed *Rhizophora/Avicennia* forest abuts on to an exposed mudflat. Four 36 m transects were established at random such that they ran approximately at right angles to the edge of the forest. Each transect extended 15 m into the *Rhizophora* zone, where canopy cover was high, through a 6 m transition zone and 15 m out on to the mudflat with no canopy cover. Each sample was taken by collecting the first twenty propagules seen on the transect in the 'full sunlight' zone and the 'shade' zone, excluding the transition zone. The transition zone was defined as the first three metres either side of the nominal edge of the forest. This was to exclude propagules that may have been exposed to sunlight in areas where the canopy cover was incomplete. Sampling was carried out in the third week of February.

The eight samples (n=20 propagules per sample), four from in the shade and four from exposed areas were spread out in the laboratory and assessed for infestation. Sampling was repeated one month later. Interpretation of results from this collection (see discussion) take into account the number of confounding factors which have the potential to influence *C. fallax* numbers.

The site for this collection (the northern end of the Cairns Esplanade, see chapter 3) is unusual in that it is kept clear of *Rhizophora* seedlings and saplings by physical removal of all seedlings in October to December of each year (Bird 1972). This makes it an ideal site for this collection, as it has a proven record of recruitment of *Rhizophora* propagules, but does not have the changes in conditions (light levels, humidity, substrate temperature, substrate moisture) which growth of the seedlings and subsequent canopy shading would bring.

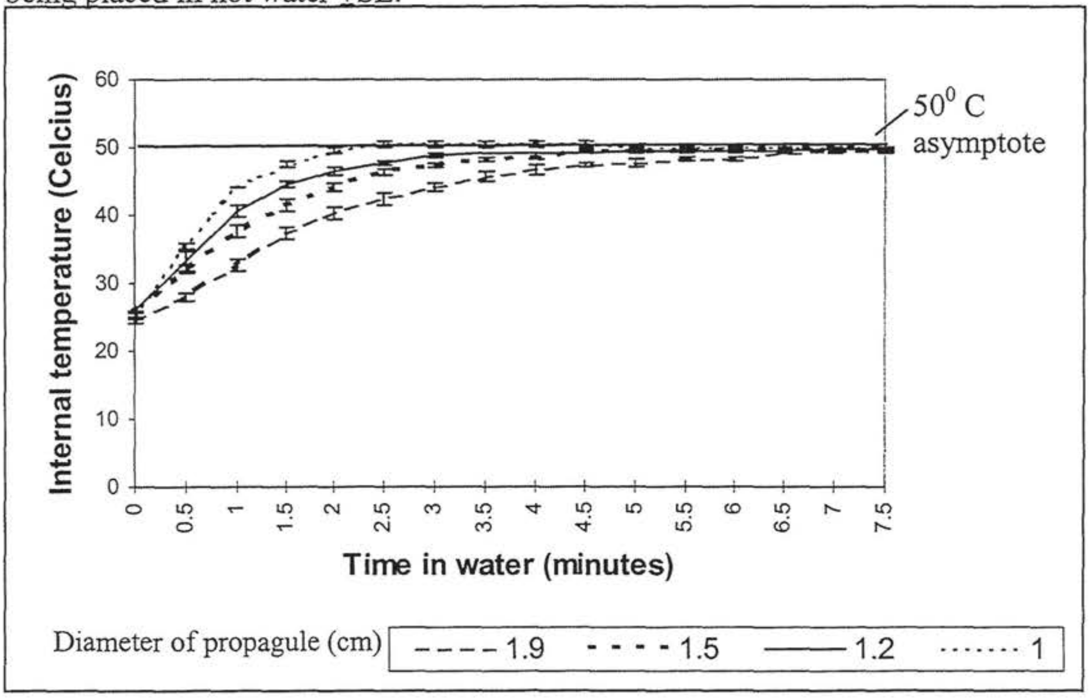
6.3 *Results*

6.3.1 Time taken for internal tissues to approach external temperatures.

Temperature levels within the propagule showed rapid approach to equilibrium with the external temperature. For all external temperature levels used, the mean internal temperature was within one degree of the outside temperature within 6 minutes, with actual attainment of equilibrium effective within 7 minutes (Figure 6-2). The variation in initial rate of change of temperature over the first three minutes (calculated as T_3-T_0 divided by 3) is negatively correlated with diameter of the propagule (Pearson Correlation coefficient = -0.95, n=12 , p= 0.01). Narrow propagules (with diameter of 1.0cm measured at the widest point) reached equilibrium with the external medium within 3 minutes, while thicker propagules (diameter 1.9cm) took nearly 7 minutes to reach equilibrium.

Figure 6-2 Time taken for internal temperature in propagule tissue to approach that of the external environment.

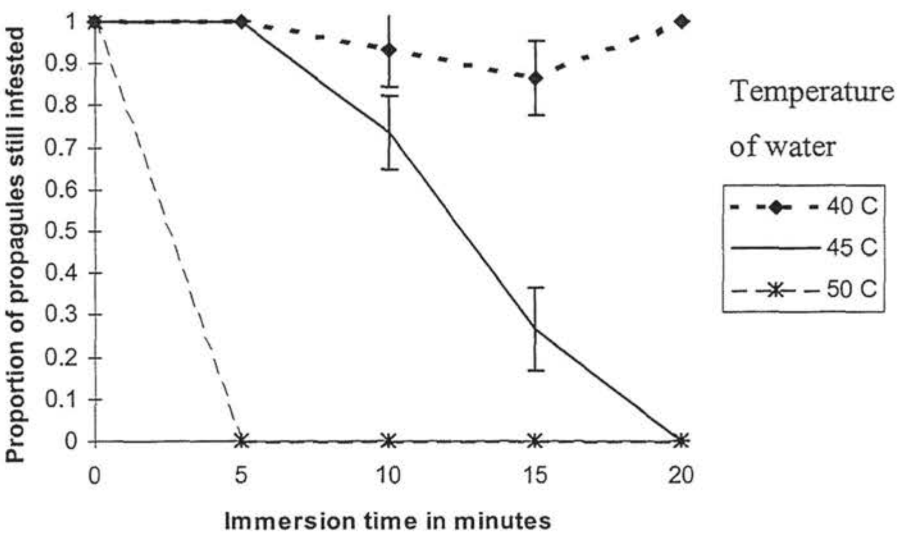
Lines show the mean temperature for propagules of that diameter at given time after being placed in hot water ±SE.



6.3.2 Effect of treatment on the survival of *C. fallax* in *R. stylosa* propagules

Time of immersion and temperature of water both affected survival of scolytids infesting propagules immersed in hot water (Figure 6-3). All times at 50 °C resulted in 100% mortality of the scolytid. Mortality at 40 °C was always low. There was a significant interaction between time and temperature ($F = 12.234$; $df = 6,36$; $p = 0.001$), at 45 °C the mortality increased as the time of immersion increased (Figure 6-3).

Figure 6-3 Proportion of propagules still infested following immersion in hot water for various temperature*time combinations.



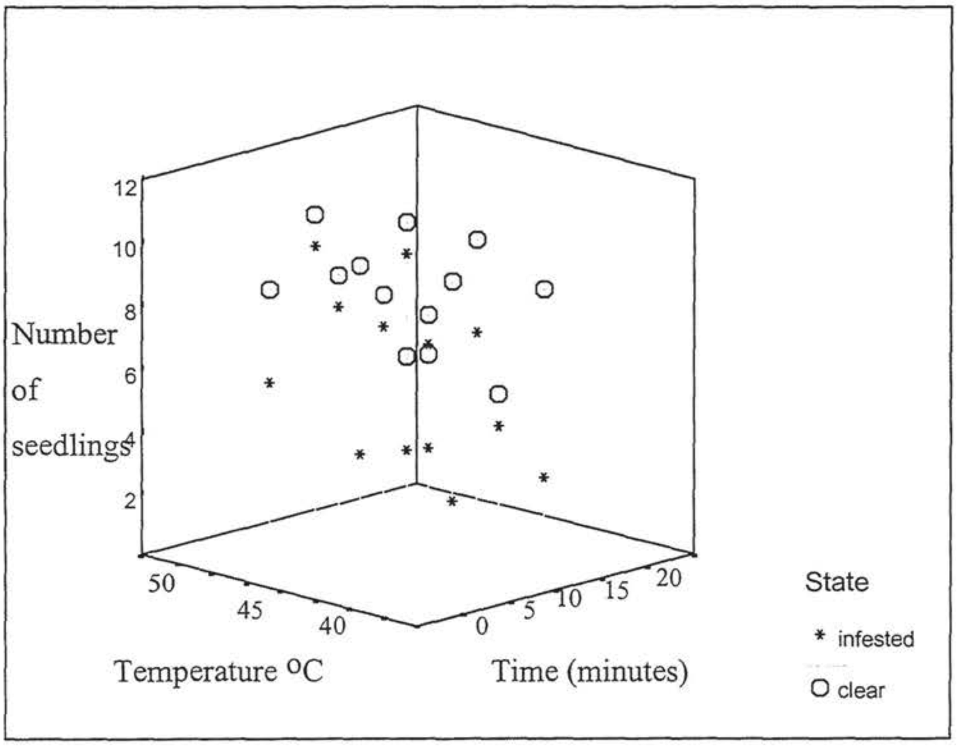
Data points show mean ±standard error

6.3.3 Effect of hot water immersion on recruitment and survival of *R. stylosa* propagules

There was a significant interaction between state (infested or clear), temperature and time ($F = 2.69$; $df = 6, 233$; $p = 0.015$) on the recruitment of seedlings treated with hot water immersion. Comparing recruitment of clear vs. infested propagules showed that there was no effect of temperature or time of immersion on clear propagules. There was a significant temperature*time interaction for recruitment of infested propagules (F=2.98; df =6,116; p = 0.01).

Figure 6.4 shows that clear propagules recruited at a greater rate than infested propagules. The lower recruitment rates for infested propagules are especially noticeable at temperature*time interactions which the previous section showed did not kill the infesting scolytid.

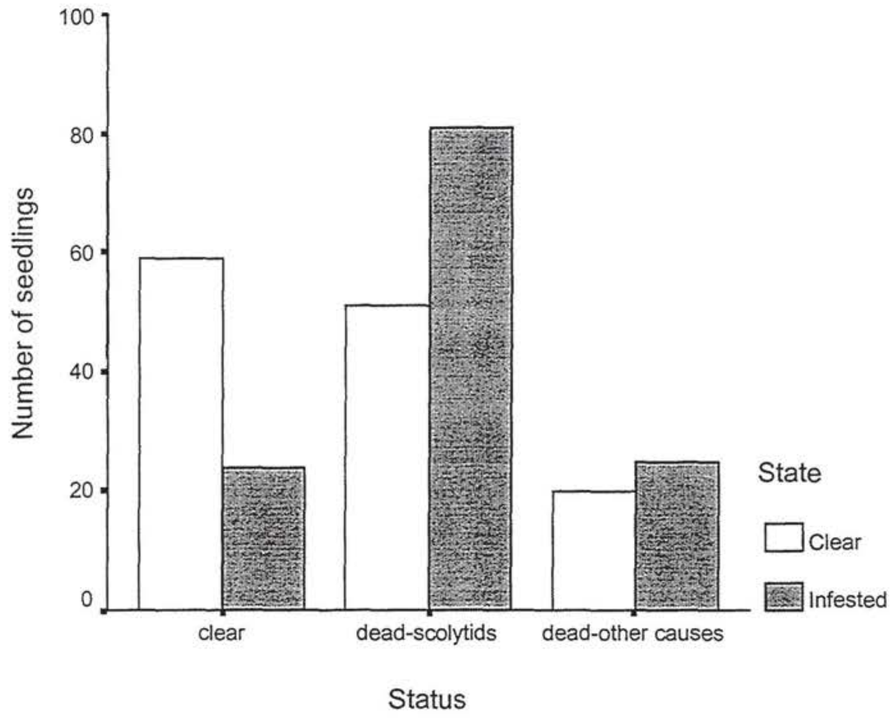
Figure 6-4 Three dimensional scattergram showing levels of recruitment of propagules treated with differing temperature*time combinations.



6.3.4 Effect of immersion in hot water on survival of *R. stylosa* propagules as seedlings in the field.

Many of the propagules became infested in the field after plant out. At the end of 8 months many of the seedlings had died (Figure 6-5). Examination of the hypocotyl of many of these dead seedlings indicated this was the result of scolytid infestation. Approximately 20% of seedlings died from other causes eg. herbivory . The seedlings still alive were all clear of infestation by scolytids. The classifications 'clear' and infested in this graph refer to the status of the propagules prior to immersion in hot water and did not reflect their status when planted. The survival of seedlings to 8 months was therefore analysed to see whether the treatments could be pooled to reflect status when planted.

Figure 6-5 Status of seedlings after 8 months.

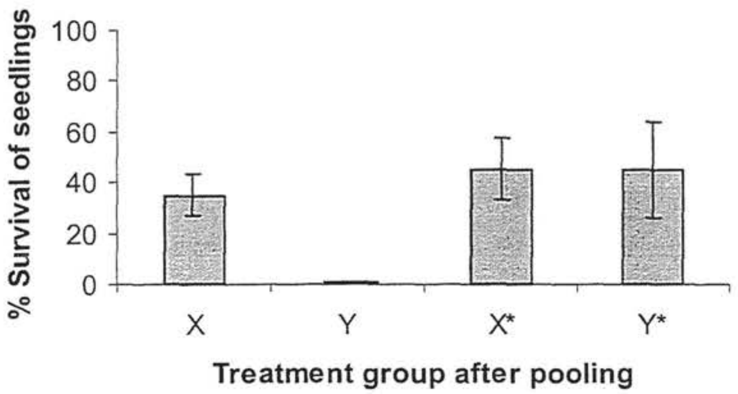


There was no detectable effect of temperature of immersion (F= 0.306; df = 2,57; p = 0.738), time of immersion (F=1.328; df = 3,57; p = 0.274), infestation level (F = 0.022; df = 1,57; p = 0.882) or any significant interaction effects on the survival of propagules for a period of 8 months. The propagules were therefore pooled into two groups, those in which infesting scolytids had been killed (group X) and those in which the infesting scolytid had not been affected by the treatment (Group Y). X* and Y*, had never been infested.

The pooled results showed a significant interaction between state (prior to immersion) and treatment (F=105; df 1,20; p=0.001). This is to be expected as treatment affects whether the propagules will be reassigned into groups X or Y. Comparing just X and Y, ie. the survival of propagules no longer infested with those still infested shows that propagules still infested do not survive at the same rate as those where the scolytids have been killed (F=105; df=1,10; p=0.001Figure 6-6;). Comparison of the survival of the propagules previously infested, now clear (group X), with clear propagules (X* and Y*) shows no difference in survival (F=0, df= 1,p=1). Similarly comparison of survival of the two control groups (X* and Y*) shows that Treatment (immersion in hot water for varying time periods) had no effect on survival of seedlings (F= 0; df = 1,10 p = 1).

Figure 6-6 Survival of infested and clear propagules as seedlings following treatment.

Bar height represents percent mean survival ±SE. '



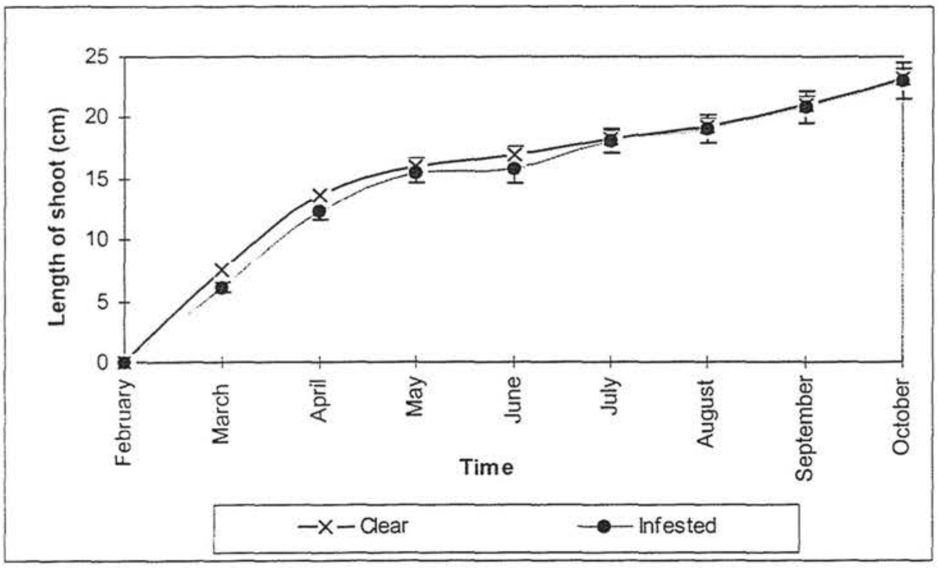
6.3.5 Effect of immersion in hot water on growth of propagules.

Increase in shoot length is a reliable measure of increase in biomass of *R. stylosa* propagules (Smith 1987c). The data were analysed using repeated measures GLM, as length of the seedling shoot was measured 8 times, all propagules starting when planted with shoot length of zero (Figure 6-7). Time since planting was the only significant factor (F=133.8; df = 7,57; p = 0.001). There were no significant effects of temperature of immersion, time of immersion or temperature*time interactions. State (prior to immersion) did not affect shoot length in surviving seedlings (Figure 6-7). Shoot length increased rapidly between February and April. The rate of increase was less during the dry season and rate of increase began increasing again in September and October (Figure 6-7). This graph only reflects growth of seedlings in which infesting scolytids had been killed by immersion in hot water.

Those propagules still infested at planting died as seedlings and were not represented in the group that survived to October.

Figure 6-7 Increase in shoot length of *R. stylosa* propagules planted in the *Rhizophora* zone of the mangrove.

Points (mean ±SE) show that there was no significant difference in growth between clear and infested propagules after immersion in hot water had killed the infesting scolytids.



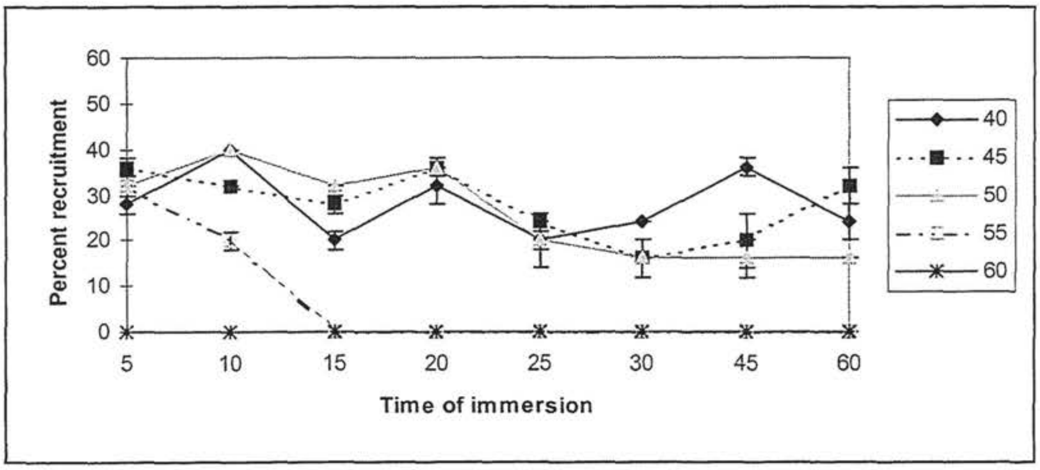
6.3.6 Effect of treatment of propagules at temperature*time combinations greater than those studied in the previous section.

Exposure of propagules to immersion in hot water for periods of more than 20 minutes at temperatures exceeding 50^0C significantly affected the numbers of propagules which recruited (F=2.819, df=15, p=0.007). The interaction of increased temperature and time of immersion decreased recruitment of propagules. Recruitment following immersion in hot water at 40 and 45 degrees for extended periods does not show any trend (Figure 6-8). However, correlation of the proportion of propagules recruiting against time of immersion at 50°C was significant (F=10.688, df=1,14 p=0.006), with lower recruitment after longer periods of immersion at 50 ° C.

Immersion at 55 °C for 15 minutes or more prevented recruitment (Figure 6-8), as did immersion at 60 °C for even 5 minutes. Results for 60 °C are not plotted as they are all zero. The two propagules that recruited following immersion at 55 °C for 10 minutes did not produce healthy normal leaves.

Figure 6-8 Percent recruitment of propagules immersed in hot water at different temperatures for periods of up to one hour and then planted out in the *Rhizophora* zone.

Points represent mean ±SE.



6.3.7 Factors affecting temperature experienced by *R. stylosa* propagules in the field.

Propagules lying in the sun on a dry substrate are up to 10 degrees hotter than any others. Propagules speared in to either wet or dry substrates, or lying on a wet substrate in the sun get hotter than do those in the shade. Propagules speared into or lying on a wet or dry substrate in the shade were essentially at ambient air temperature (Figure 6-9).

The temperature in the propagule was significantly affected by the interaction of time of day with

moisture content of the substrate ($F = 4.804$, $df = 8,18$ $p = 0.003$),

position (lying down or speared in) $F=3.212$, $df = 8,18$ $p = 0.019$ and

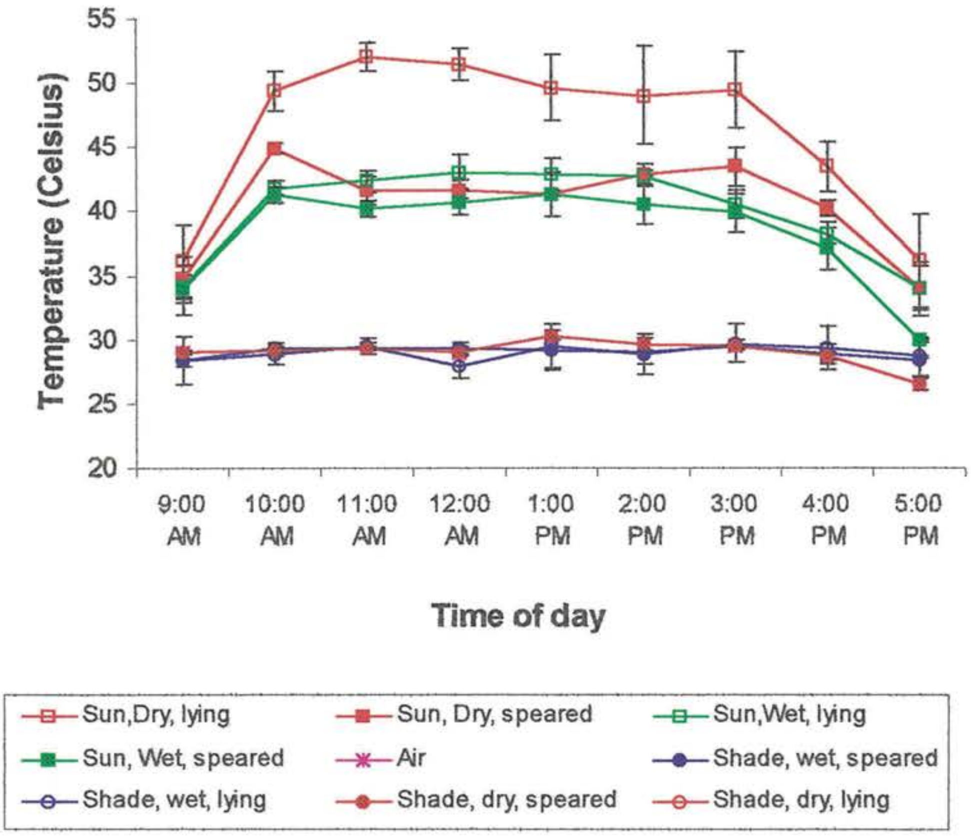
light (under the canopy or in a light gap) ($F= 6.300$, $df = 8,18$ $p = 0.001$)

For any particular group of propagules, time of day significantly affected temperature of the propagules ($F=29.857$; $df =8,18$; $p=0.001$). All propagules started the day at ambient air temperature prior to exposure to direct sunlight. The temperature of propagules in the sun increased between 9 and 10 am, stayed high until after 2.00 p.m. and then fell slowly until shadows covered the propagules between 4.30 and 5.30 p.m.

Propagules exposed to full sunlight for a full day lying on a dry surface began to change colour from green to brown. If left out for a second day they were shrivelled and the green colour on the exposed surface had changed to a dark brown to black colour. Temperatures in propagules speared in to either a wet or dry substrate, or lying on a wet substrate all had temperatures in the 40 to 45 °C range (Figure 6-9). There was no noticeable change in appearance of these propagules after one day.

Figure 6-9 Changes in internal temperature of propagules speared into or lying on either wet or dry mud, in a light gap or under the canopy.

Points indicate mean temperature ±SE. Temperatures of propagules in the shade are marked with a ' λ ', those in the sun with a '□'.

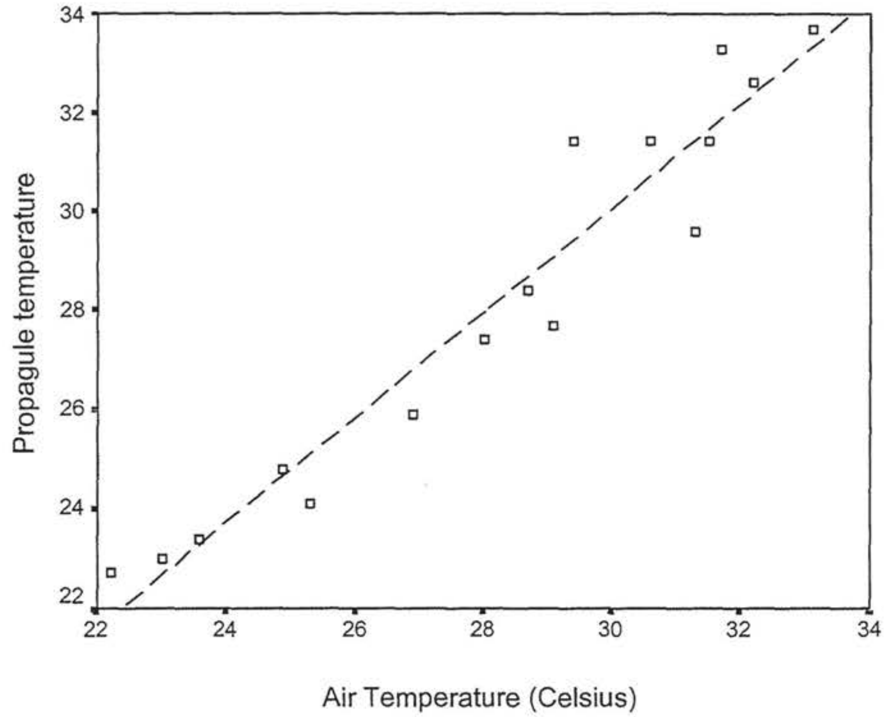


The effect of shade on temperatures inside propagules.

Temperatures of propagules speared into, or lying on, wet or dry substrates in the shade were not significantly different from one another nor from ambient air temperature ($F= 0.048$; $df = 1,10$; $p = 0.834$; Figure 6-9). Despite differences in microclimate, temperatures experienced by propagules under the canopy can be predicted using published climatic data (Figure 6-10). Temperatures of propagules in the shade were compared with minimum, maximum, 9am and 3pm temperatures from Cairns Meteorological office (for the same day and time) and were not significantly different. (F = 192.47, df =1,14; p = 0.001)

Figure 6-10 Correlation of air temperature (Cairns Weather Station) with temperature of propagules in the shade in the *Rhizophora* zone of adjoining mangroves.

Dotted line is line of best fit. (Pearson's correlation coefficient 0.966, p=0.01,



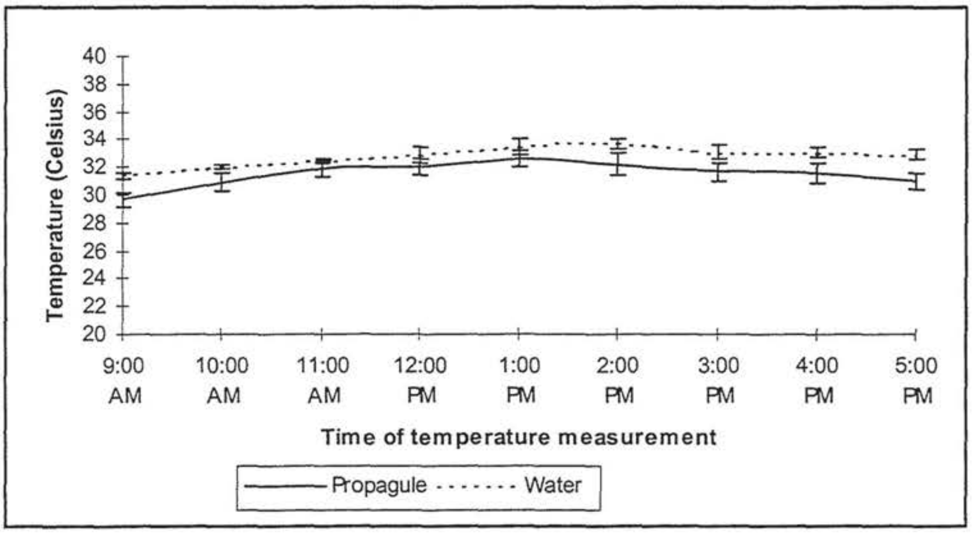
N=16)

6.3.8 Temperature experienced by propagules floating in water in full sunlight.

The mean temperature of propagules floating in water was not significantly different to that of the surrounding water (F=3.40, df=1,10; p=0.139 Figure 6-11).

Figure 6-11 Temperature of propagules floating in water and temperature of water 0.5 cm below the surface.

Points show mean temperature ± SE.



6.3.9 Time taken for sunlight to affect the internal temperature of a propagule.

When propagules were initially shaded, then moved into the sunlight they heated up quickly. 'Speared in' propagule temperature increased from an average 32 °C to 41 °C in an average 11.7 minutes, a mean rate of change of 0.77 °C/min (SE=0.03) on days when air temperature during the experiment was 32 °C ± 1 °C (Figure 6-12). Propagules lying on the sand heated up more slowly. They increased at a rate of 0.52 °C/min (SE =0.03) and took an average of 24 minutes to reach 46 °C. During the day the substrate began to dry in the heat . On these days air temperatures were 34 °C ± 1 °C (Figure 6-13). Under these conditions a propagule under a break in the canopy that resulted in a propagule being in full sunlight for only one hour could reach temperature*time combinations lethal to infesting scolytids.

Figure 6-12 Response in internal temperature of propagules in the 'speared ' position to sun and shade conditions.

Darkened rectangles indicate those time periods when one of the propagules in its container was shaded (100% shade). Dotted line indicates temperature of propagules left in the sun all day.

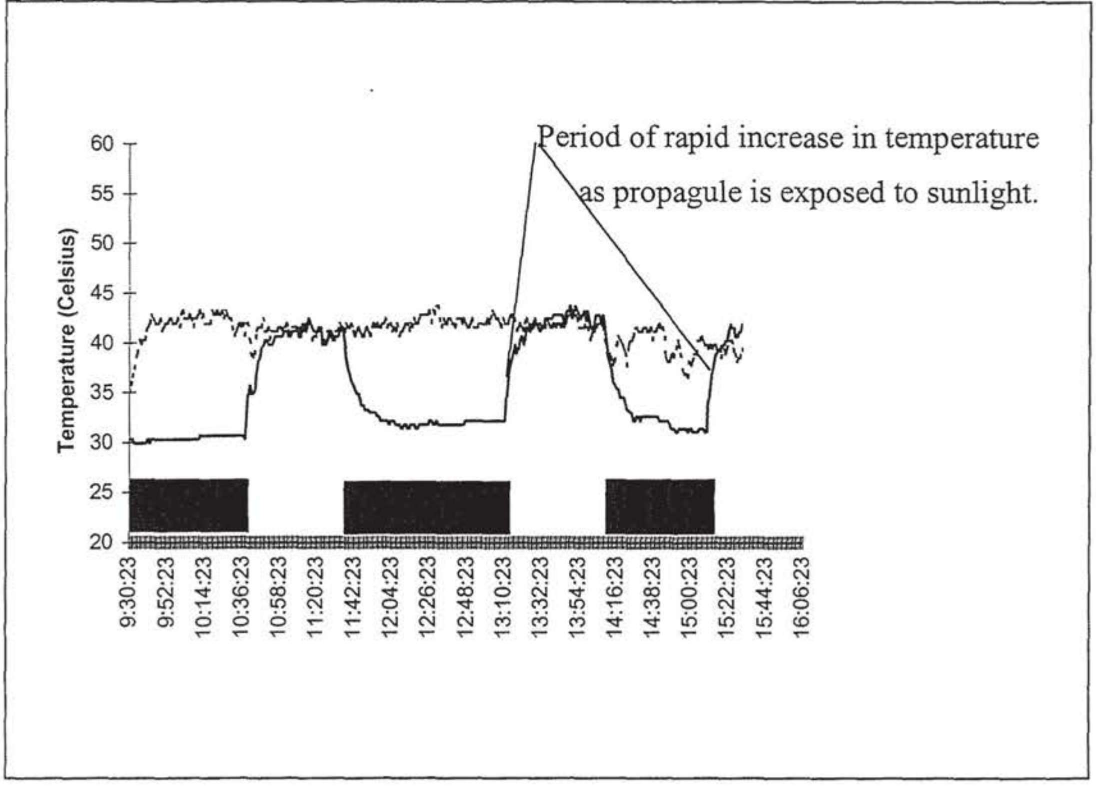
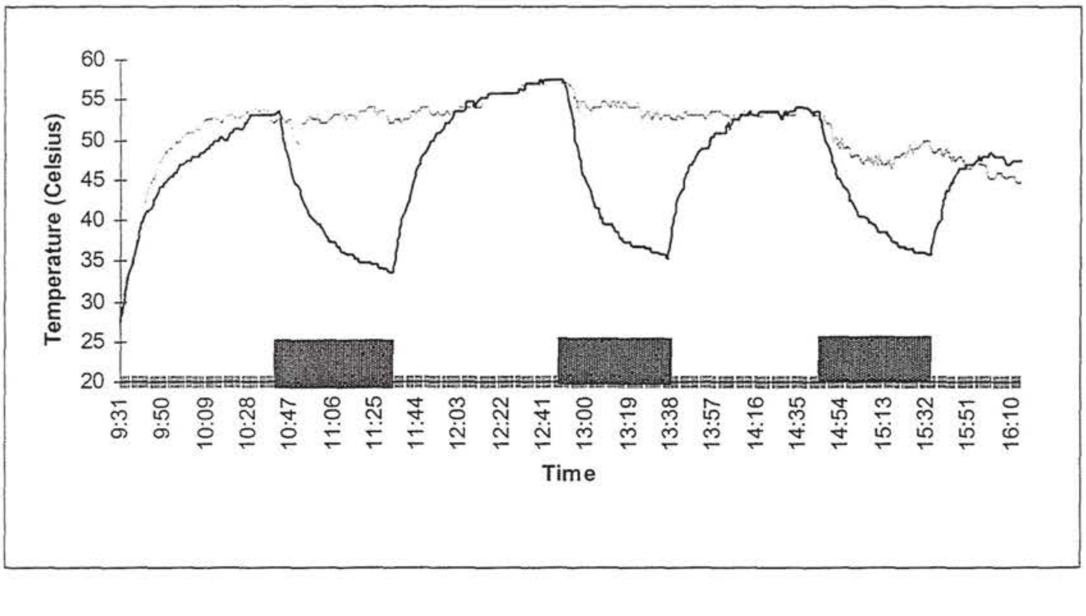


Figure 6-13 Response in internal temperature of propagules in the prone position to sun and shade conditions.

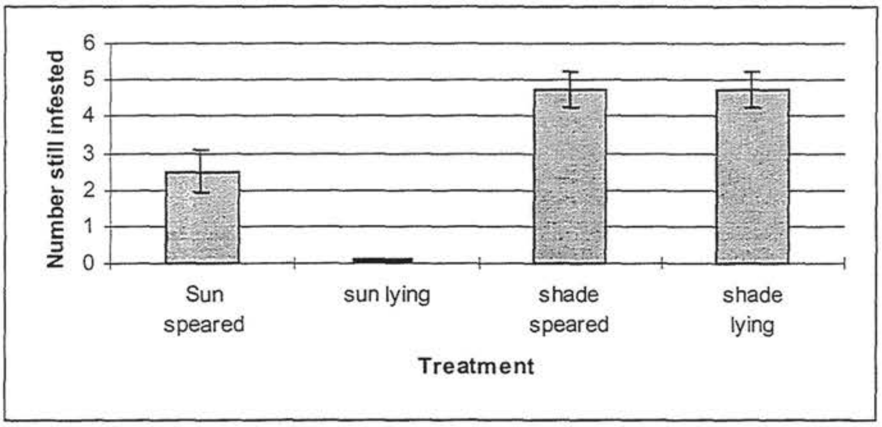


6.3.10 Effect of different light levels and position of infested propagules on continuing infestation by *C. fallax*.

Propagules 'speared in' in the sun had a greater proportion of scolytids surviving after one day exposure to sunlight than propagules lying in the sun ($F = 30$; $df = 1,12$; $p = 0.001$). Mortality of scolytids in propagules placed in the sun was much greater than in propagules under the canopy ($F = 235.2$; $df = 1,12$; $p = 0.000$). There was a significant interaction between light and position with effectively zero mortality of scolytids in propagules under the canopy (either position), 50% mortality 'speared in' in the sun and 100% mortality lying in the sun (Figure 6-14).

Figure 6-14 Number of propagules with active infestation after exposure to the sun for one day.

Sample size in each case was 5 infested propagules.



6.3.11 Effect of exposure to sunlight on recruitment of the propagule.

The effect on the recruitment of the propagules to exposure to sunlight on a damp surface for a period of three days (sufficient to ensure 100% mortality in propagules in either the speared or lying position) was not significantly different to those left under the canopy for the same period. There was no interaction effect ($F = 0.59$; $df = 1,79$; $p = 0.444$) nor was there an effect of position ($F = 0.01$; $df = 1,79$; $p = 0.904$) or light level ($F = 1.85$; $df = 1,79$; $p = 0.178$). Approximately 60 % of all propagules planted out following treatment recruited successfully.

6.3.12 Difference in level of *C. fallax* infestation in *R. stylosa* propagules under the canopy and in a light gap.

Groups of 20 *Rhizophora* propagules, collected from under the canopy, had active infestations of *C. fallax*, with mean percent infested of 53.74% (SE=3.75; n=4) and 79.06% (SE=3.20; n=4) respectively on the sampling dates one month apart. Propagules collected from the adjacent mud flat had zero levels of infestation on both sampling dates ie. mean = 0, SE =0.

6.4 Discussion

Temperatures experienced by propagules exposed to sunlight in the field affect the survival of infesting scolytids. Active infestation of *R. stylosa* propagules by *C. fallax* was always reduced by temperatures of the propagule greater than 40 °C, whether this increase was by way of immersion in hot water or exposure to increased levels of insolation in a light gap. The same level of exposure to increased temperature did not affect the recruitment of *R. stylosa* propagules, which appears to have a greater temperature tolerance than the infesting scolytid.

Conduction of heat through the hypocotyl tissue was fairly rapid, with diameter of the propagule influencing the rate at which heat reached the middle of the propagule. *C. fallax* tunnels vary in shape and this would affect the amount of hypocotyl tissue between the feeding area and the epidermis. This in turn would affect the time taken for the scolytids to become exposed to the higher temperature. Further research would be required to test the hypothesis that some of the variability in the mortality rates of *C. fallax* in propagules exposed at 45 °C for short periods to the actual level of exposure of the scolytids to the elevated temperatures.

Both diameter of the propagule at the position of the feeding scolytids and position of the tunnel within the propagule are factors that may influence temperature to which scolytids are exposed and the duration of exposure. In propagules with above average maximum diameters, where the scolytid tunnel is located in this thicker part of the propagule, the temperature may not reach 45 °C for the critical length of time required for 100% mortality when immersion times are short. This relationship between thickness of the propagule at the location of the infestation, and survival was observed after treatments involving short periods of immersion.

Infested propagules, treated with hot water to kill the scolytids, showed no significant difference in survival and growth at the end of a year. Robertson et al (1990) found that scolytid infestation did not significantly affect the survival and subsequent growth of *R. stylosa* seedlings. The results of this study suggest that the scolytids infesting the propagules in Robertson's study were killed or removed, either by exposure to heat at some stage or to predators (ants).

Propagules in which the scolytids have been killed appear to have no long-term effects from the early infestation, displaying survival and growth rates no different to seedlings from propagules that were never infested. This is consistent with the findings of Wier (1999) that *R. mangle* seedling hypocotyls respond to wounding by developing a layer of tissue within 17 days to separate healthy tissue from necrotic tissue. He also found that vascular tissue proliferated near the wound. This would counteract the effect of scolytid tissue consumption in the hypocotyl and explain why, once the infesting scolytids are killed, survival of previously infested seedlings is not significantly different to that of seedlings which were never infested. Ongoing scolytid infestation is likely to consume any growth of tissue by the hypocotyl and result in the eventual death of the seedling. This may follow as a direct result of consumption of tissue, cutting xylem flow to the shoot, or as a result of stress making the seedling more vulnerable to other stresses. Depletion of the stored resources of the hypocotyl, used up in response to the ongoing wound being inflicted by the scolytids, would decrease the competitiveness of infested seedlings.

6.4.1 Effect of heat on scolytid populations in the natural environment.

In the shade, ie. in the *Rhizophora* zone, where *Rhizophora* seedlings would need to recruit to replace mature trees as they die, the temperature did not exceed the average daily air temperature. Air temperatures in the Cairns region seldom exceeds 40° C (Bureau of Meteorology 1999) and propagules on the forest floor in the shade would seldom experience temperatures that would affect the survival of *C. fallax*. In the shade, therefore, *C. fallax* infestation of a propagules would mean the eventual death of the seedling.

Periods of elevated temperatures do occur. In February 1994, Cairns experienced a period of two days when the temperature during the day did not drop below 38.5°C and peaked at various sites at between 42 and 43° C. Following this period, scolytid infestation levels at all sites dropped, with infestation at Barr Creek dropping to zero. It remained zero for the rest of the season and that year *Rhizophora* propagules recruited in large numbers (Chapter 5 section 5.3.3).

This was an exceptional occurrence for this region, and was compounded by the fact that as the creek mouth at Barr Creek was closed, normal tidal inundation was restricted and the mud surface of the forest floor dried up, reducing evaporative cooling within the mangrove. The temperatures measured in propagules in the shade were not significantly different to the air temperatures measured at the local Bureau of Meteorology recording station. The temperature to which scolytids infesting propagules would be exposed in any particular region could, therefore, be estimated by referral to published climatic data for the region. Where air temperatures are reported in the 40 to 45 ^{0}C range, scolytid numbers are likely to be reduced. It is predicted the effect of *C. fallax* infestation on *Rhizophora* propagules in regions with regular occurrence of temperatures of 40^{0}C or more, for even a few days a year, would be less than in the Cairns region where this study was carried out.

Air temperature and exposure to sunlight are not the only ways in which a propagule can heat up. Propagules in the field may also be subject to immersion in heated water. This could occur as the incoming tidal water moves across the (heated) substrate of the intertidal zone after the surface had been exposed to sunlight during the day. MacMillan (1971) reports on this occurring in Florida and affecting the survival of *A. germinans* propagules and their ability to recruit. The heated water, depending on the topography of the mangrove may quarantine large or small areas of forest. This effect would be site specific.

In most cases however, the volume of water and the high specific heat of water (4.2joules/g^{0}C) mean that water provides a moderating influence. Surface sea water temperatures seldom rise above 33^{0}C (Bureau of Meteorology 1999). Temperature in propagules floating in full sunlight did not increase above the temperature of surrounding water. The dispersal of *C. fallax* to new locations through water dispersal of infested propagules is thus not affected by the lack of shade during the period of dispersal. This is in agreement with the identification of *C. fallax* infested *R. stylosa* propagules in several island locations off the Queensland coast. As *Coccotrypes* spp do not fly far to find their host propagules (Browne 1961), the ability to infest *Rhizophora* forests which have colonised new habitats depends on the ability of the scolytid to survive in the propagule during dispersal.

This study has shown that although propagules may be exposed to sunlight during dispersal by water, the propagule will remain at the temperature of the water. Theoretically any *Rhizophora* forest established through natural (water borne) dispersal of propagules potentially would become infested by *C. fallax* at a later stage. If the initial propagule reaching a new mudflat is infested, the infesting scolytids will be killed when the propagule is stranded and is exposed to the heat of the sun without the moderating influence of water. Infestation by *C. fallax* should not therefore affect the colonising ability of *Rhizophora* propagules.

In north Queensland, propagules stranded on exposed intertidal surfaces that remain damp will have any infesting scolytids killed but will not themselves reach temperatures likely to affect recruitment of the propagules. Propagules lying on a damp substrate did not exceed temperatures of 45°C. In hot water immersion trials, this level of temperature did not affect survival and recruitment of propagules. If the substrate is suitable in other respects (wave action, depth and duration of immersion, salinity etc) recruitment should not be affected. Survival will not be affected by scolytid attack as provided the recruiting propagule is exposed to sunlight it is quarantined against scolytid attack. Seedlings are not susceptible to infestation by *C. fallax* (Chapter 5) so dispersal of *C. fallax* into seedlings during the cooler months of the year is not likely to occur as by this time of the year propagules have established as seedlings.

Propagules stranded (horizontally) on surfaces that dry out during the day are likely to reach temperatures that affect the ability of the propagule to recruit. Propagules lying on a dry substrate reached temperatures in excess of 50°C, the temperature at which immersion in hot water trials produced a temperature*time interaction which resulted in lower recruitment rates. Propagules in the speared in (vertical) position did not exceed 45°C,(when exposed between 8am and 5 pm) a temperature which did not affect survival of seedlings planted out after immersion trials. Recruitment in the high intertidal zone may thus depend on the position in which propagules make contact with the substrate as well as climatic conditions at the time (rainfall, cloud cover), suitability of substrate and shade/sun cover.

While *Rhizophora* is not described as having a disjunct distribution many examples of transects show *Rhizophora* in the low intertidal and high intertidal, separated by *Bruguiera* and *Ceriops* spp forests (Wells 1982, Kenneally 1982, Smith 1982). The recruitment of *R. stylosa* in the high intertidal, where sunlight on dry substrate may quarantine speared in propagules against *C. fallax* infestation and yet still permit survival of the propagule, is not ruled out by the results of the temperatures measured in these tests.

The importance of the water content in the substrate can be attributed to its relatively high specific heat. Water absorbs large quantities of energy for relatively small increases in temperature. Propagules in contact with water either in the substrate or when floating will lose heat to the surrounding water if their temperature rises above the temperature of the surrounding medium. Evaporative cooling may also contribute to lower temperatures of moist surfaces than dry ones. Water is also a good conductor of heat. Propagules on a dry substrate would have reduced ability to lose heat. The dry substrate is more likely to heat up (no evaporative cooling) therefore the temperature differential will be less and conduction of heat away from the propagule to the substrate will be slower.

The effect of substrate and position of the propagule was seen in the experiment to see how quickly *Rhizophora* propagules heated up when exposed to sunlight. The speared in propagule both heated up and cooled down more quickly than did the propagule lying on the substrate (Figure 6-12 and Figure 6-13). The rate of increase in propagules in the speared position was rapid and the internal temperature reached levels that would be lethal to scolytids within 20 minutes. Propagules self elevate when recruiting so this is the position most would achieve in a suitable habitat.

In tests on the survival of *C. fallax* in propagules speared in to a damp substrate, fifty percent of propagules were cleared of *C. fallax* in just one day. No actively infested propagules were found on the mudflats exposed to sunlight despite the levels of infestation for that stage of the season indicating that *C. fallax* levels under the adjoining canopy would reach 100% the following month. The lack of active infestation on the exposed mudflat is confounded by distance effects and density effects both of which have been shown to be associated with decrease in predation levels (Connell 1971; Janzen 1971). The quarantining effect of high light levels are, however, likely to have a synergistic effect on decreases in predation levels associated with density and distance effects.

Density of infested propagules would be reduced under full light conditions. Even when infested propagules are dispersed onto the exposed area, the scolytids are predicted to be killed within one day (lying down) or three days (speared in) thus preventing a build up of infested propagules as sources of infestation for neighbouring propagules.

In this chapter I have provided evidence to support the hypothesis that heat moderates the effect of *C. fallax* on the survival of *R. stylosa* seedlings experienced by propagules. The energy transferred to the propagules by the higher level of insolation increased the temperature of the propagules to a level that is sufficient to kill the scolytid. It was demonstrated that *C. fallax* infestation levels propagules found in areas exposed to full sunlight were minimal and that any infesting scolytids would be killed when propagules recruit in areas exposed to direct sunlight. This low level of infestation has to potential to result in higher levels of recruitment of propagules.

CHAPTER 7

DISCUSSION

7.1 Implications for interpreting mangrove zonation patterns.

The focus of this study was to illustrate the potential that seed predation has to influence the structure of forests under the different conditions that exist under the canopy and in light gaps. Existing attempts to explain forest structure (zonation) in mangroves have traditionally relied on examining biotic and abiotic factors and looking for relationships between these and the existing forest structure (Chapter 2). More recently predation on *Avicennia* by grapsid crabs has been identified as having the potential to contribute to forest structure.

The infestation of *Rhizophora* propagules by *C. fallax* has been shown to have the potential to remove *Rhizophora* from the seedling bank (Chapter 5). *Ceriops* and *Bruguiera*, were not infested (Chapter 4) and therefore have the potential to dominate the *Rhizophora* under-story and colonise any light gaps which appear late in the season. Information on timing of infestation and levels of infestation early in the season (Chapter 4) highlight the importance of timing of the appearance of any light gap.

Cyclones are a seasonal hazard in North Queensland (Beach Protection Authority, Queensland 1984). The strong winds accompanying a cyclone have the potential to cause large breaks in the canopy of the mangroves (Smith *et al* 1994b). The cyclone season extends from December to April, a period that overlaps the time when propagules of *Bruguiera*, *Ceriops* and *Rhizophora* can be found recruiting on the forest floor. The majority of gaps are, however, caused by lightning strikes (Duke 2001) and are smaller events, resulting in patches of patches of approximately 50 m in diameter. In these patches, the trees are left standing for several years, losing their leaves and allowing sunlight to penetrate to the forest floor.(Duke 2001).

Light gaps created by a cyclone or lightning strike which occur early in the season (December/ January in the Cairns region), would be colonised by propagules as they arrived. *Rhizophora* propagules under these conditions would not be negatively affected by *C. fallax* infestation, as the conditions in the light gap would quarantine propagules against infestation. *Bruguiera*, *Ceriops* and *Rhizophora* propagules would compete with all other propagules and seeds dispersing onto the substrate at this time and with any light suppressed seedlings and saplings from previous years. On the other hand, a storm causing light gaps later in the season (April) would probably result in a different outcome. *C. fallax* infestation has the potential to have infested and killed the majority of *Rhizophora* seedlings by April. If *Rhizophora* seedlings are not represented in the seedling bank at this time, they will not be represented in the adult community. Thus two incidences of an event that resulted in the formation of a canopy gap, occurring in a single forest could result in a different late succession community depending on the timing of the events. Years later this would be seen as zonation within the adult community by researchers and could not be explained in terms of existing biotic or abiotic factors.

C. fallax infestation of *R. stylosa* and the effect on recruitment and survival may be restricted to relatively few mangroves in North Queensland. Further studies would be required to demonstrate that it was important in mangroves in other regions. What is important is that this study highlights the need to study both biotic interactions (predation by scolytids) and abiotic interactions (effect of high levels of insolation on the internal temperature of the propagules) and their interaction (the effect of high temperatures on survival of scolytids in propagules).

7.2 Theoretical implications

The effects of seed predation on community structure have been investigated and examples can be found in the literature (Janzen 1970; Connell 1971; Hubbell 1980; Connell 1975; Hubbell 1980). If herbivores are to have an effect on a plant community structure, their influence is most likely to be felt during the plant's recruitment (Crawley and Pacala 1991). The survival rate of seedlings is significant in determining forest structure (Harper and White 1971) and it has been demonstrated that in the case of *C. fallax* in *Rhizophora* propagules, infestation has a significant effect on seedling survival <u>under the canopy.</u> The relationship between *C. fallax* and *Rhizophora* propagules demonstrates both high levels of selectivity and mortality of the selected host, to the point that the question must be asked, how can such high levels continue?

The stability of this type of system depends on spatial heterogeneity of the habitat (Birch 1971). A system in which the host plants were subject to heavy recruitment pressure across all areas of the habitat would be unstable (Stenseth 1980). There are two necessary conditions for stability, hiding places (patches) must exist where the host can 'hide' from the predator and dispersal between patches must take place (Stenseth 1980). These patches can be portions of the habitat with abiotic (or biotic) factors that minimise predator numbers and therefore are available as refuges for prey organisms (Connell 1975). Both conditions for system stability are met in *C. fallax* infestation of *R. stylosa*. Propagules are dispersed by water, with the majority of the dispersing propagules moving out from the *Rhizophora* zone before infestation takes place (Chapter 4), ie. movement between patches can occur. *Rhizophora* escape infestation in any exposed area where solar energy heats propagule tissue to levels that exceed those tolerated by the scolytid (Chapter 6). Thus although *C. fallax* affected *Rhizophora* seedling survival significantly in north Queensland mangrove forests, *Rhizophora* propagules and seedlings in light gaps were not affected by the scolytid.

Connell (1975) proposes a model of the mechanisms determining which 'dominants' (large plants or sessile aquatic animals) will fill a gap. Connell and Slatyer (1977) discuss mechanisms of succession in natural communities and their role in community stability and organisation. In this they suggest that in addition to the competitive interactions between plants or sessile animals, interactions with herbivores, predators and pathogens are of critical importance to the course of succession. They also discuss three alternate models of mechanisms producing the sequence of species in succession. In Model 1 (facultative), the early succession species modify the environment so it is more suitable for later succession species to invade and grow to maturity. In Model 2, any changes wrought on the environment by the earlier colonists do not affect the rates of recruitment and growth of later colonists. In Model 3 (inhibition) the early colonists inhibit the rates of recruitment and growth of later colonists (Connell and Slatyer 1977).

These mechanisms may operate on newly exposed surfaces in which primary succession is occurring, or in areas in which some perturbation has caused the death of dominant organisms and released resources for recolonisation (secondary succession).

The effects of *C. fallax* on survival of *R. stylosa* seedlings and the existence of refuges from attack in the form of light gaps can be used in conjunction with Connell and Slatyers' model to explain the origins of some of the variations in community structure in the intertidal zone.

In areas where accretion of substrate is occurring, the level of substrate approaches that at which *Avicennia* spp can become established (Bird 1972). The pneumatophores of these first colonists slow down the rate of water movement and increase the rate of deposition in the immediate location. The level of substrate within the intertidal zone thus reaches the height at which *R. stylosa* can become established (Bird 1972). Up to this stage Model 1 (facultative) is operative. *C. fallax* do not affect recruitment at this stage. This may be associated with low levels of infestation associated with distance and density effects or because light levels under the *Avicennia* canopy assist in quarantining the propagules.

Once *Rhizophora* becomes established, the canopy density increases to the point where *C. fallax* are no longer affected by direct sunlight, and density of propagules on the forest floor allows high levels of *C. fallax* infestation. This results in selective reduction of the levels of recruitment and survival of *Rhizophora* seedlings. *Bruguiera* and *Ceriops* spp. are not affected by *C. fallax* and persist in the seedling and sapling stages. Growth of any seedlings is reduced by the shade canopy provided by *Rhizophora* adults (Ellison and Farnsworth 1996). At this stage, Model 3 (inhibition) is operative. In mild conditions where there are no serious perturbations, dominant *Rhizophora* adults become senescent and die. This is likely to leave a small canopy gap that would be rapidly closed by *Bruguiera* and *Ceriops* whose seedlings are described as shade tolerant and which would thus survive longer under the canopy in low light conditions (Tomlinson 1994; Hogarth 1999).

Under more extreme conditions, tropical storms or human activities may clear large areas. This could be classed as secondary succession as the preceding colonists have already modified the substrate to some extent. Within a large gap, the effect of the scolytid in reducing the competitiveness of *Rhizophora* propagules is not operative, the sunlight effectively quarantining the propagules. In this case succession is more likely to be opportunistic, with season, adjoining community structure and prevailing surface currents determining propagule supply and hence recruitment and survival.

In this model, mortality induced by scolytids and size and frequency of formation of light gaps is important in determining the community structure. Duke et al. (1998) reviewed the factors influencing biodiversity and distributional gradients in mangroves worldwide. These act over a range of scales. The model described in this study is unlikely to be appropriate over the whole range. Care must be taken in extrapolating data from this location to other regions in the world where different predator regimes, different flora and different environmental factors may act to produce different results.

What can be applied globally is the fact that this study highlights the need to take into effect both the history of light gaps in the area and the potential for insect predators to selectively affect recruitment and subsequent survival of seedlings in interpreting community structure.

7.3 Light gaps and zonation patterns in mangroves

Light gaps in terrestrial forests are the subject of numerous investigations into the impact they have on forest dynamics and community structure (Poulson and Platt 1989; Spies 1989; Smith 1992a; Ellison and Farnsworth 1993a; Clarke 1995a; Myers 1985; Spies and Franklin Jerry F. 1989; Smith 1992b; Ellison and Farnsworth 1993b; Clarke 1995b; Myers 1935). In mangroves, seedlings have been classified as preferring sun or shade, and some work has been done on growth rates of seedlings and competitive exclusion of species. McKee (1995a) looked at seedling response to light and nutrient availability and found that at higher nutrient or light availability the species studied differed in relative growth rates and leaf production. At lower levels of light or nutrients, species differences were greatly minimised. She also found that the sympatric species studied varied greatly in their susceptibility to herbivores. Studies on seed predation and the effect on seed viability and growth showed that seed predation by insects must be considered along with factors such as salinity, competition for light, degree of tidal inundation, pore water salinity and predation by crabs (Robertson *et al* 1990). This study on the effect of *C. fallax* infestation in *Rhizophora* propagules demonstrated that survival of *R. stylosa* seedlings was affected under the canopy where levels of infestation by the scolytid were high. No propagules with active infestation were found in light gaps.

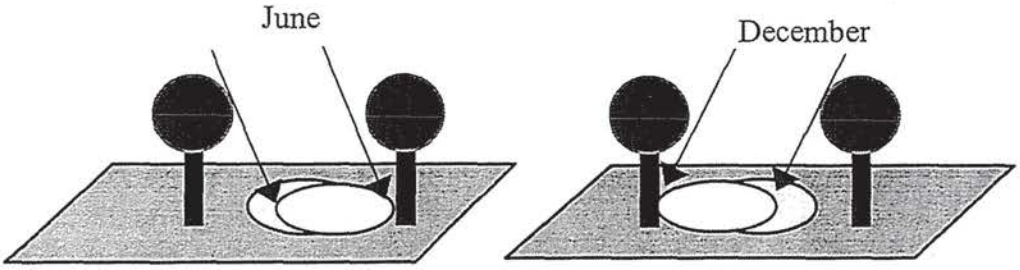
Light gaps may occur for a variety of reasons. A break may form in the canopy as a result of death of a tree or trees as a result of age, disease or predation. Gaps may also form as the result of lightning strike, fire or storm (Boose *et al* 1994; Lugo and Snedaker 1975a; Smith *et al* 1994b; Lugo and Snedaker 1975b; Smith *et al* 1994a; Lugo and Snedaker 1975b). In mangroves, light gaps occur on the banks of rivers and other areas where sediment accumulates, providing emerging substrate for colonisation by mangrove species (Davis 1940; Lugo 1980). Gaps result in locally elevated light levels and these increases in light appear necessary for almost all tree species to attain canopy status (Poulson and Platt 1989).

Regeneration in a light gap is determined by the interplay of probabilities of arrival and survival (Schupp *et al* 1989). Recruitment and growth in light gaps is therefore dependent on both differential dispersal of seeds (or propagules) into light gaps (Howe and Smallwood 1982) and differential predation on the seeds within the gaps (Bowman 1917). Osborne et al. (1990) investigated differential predation on mangrove propagules in open and closed forest habitats and found that 'shade intolerance' in *Aegiceras corniculatum* and *Avicennia marina* may actually reflect an escape from predators that is successful when the seeds are dispersed into light gaps.

The area of the forest floor, in the vicinity of a light gap, that is exposed to direct sunlight shifts on the east-west axis daily and on the north west axis seasonally (Figure 7-1). The distance the patch of light moves will be proportional to canopy height. Any work on light levels and propagule recruitment and growth needs to take into account these shifts in the areas that are subject to high levels of insolation.

The angle of incidence of solar rays varies by 47 degrees along the north south axis between mid summer, when propagule numbers on the ground are high, and mid winter, when seedling numbers are high. Light measurements taken in one season may not reflect the insolation experienced by propagules during the critical recruitment period (Figure 7-1).

Figure 7-1 Effect of season, latitude and canopy height on displacement of light gap under the canopy.



Area under the canopy
Area directly under the gap in the canopy
Area exposed to high levels of insolation
Angle at which sunlight reaches the substrate

Similarly it would be expected that recruitment under a canopy gap would show variation between the north-south and east-west axis of the gap, with east west axis elongated and north-south axis shifted towards the equator.

Light gaps provide a habitat in which *Rhizophora* spp. propagules can escape predation by *C. fallax*. *Rhizophora* seedling numbers under the canopy in the *Rhizophora* zone reflect the heavy mortality caused by *C. fallax* infestation. Where infestation is low, supply and other factors determine seedling numbers. The effect of *C. fallax* on *Rhizophora* species propagules may thus be one of the factors why *Rhizophora* are known as a pioneer species. As a pioneer, *Rhizophora* propagules on exposed land in the intertidal will escape from the effects of *C. fallax* infestation that affect recruitment under the canopy in north Queensland.

7.4 *Parasite Host co-evolution- speculation on the role of* C. fallax *in exerting selection pressure on Family* Rhizophoraceae *over time.*

The infestation of propagules by scolytids may be an example of a predator/prey co-evolution. There are two scolytids that have been identified as infesting propagules of mangroves. In the Atlantic East Pacific Region, Rhizophora spp are attacked by *C. rhizophorae*, whereas in the Indo West Pacific *Rhizophora* spp are attacked by *C. fallax* with the results identified in this thesis. The two regions are separated by two barriers which appear to have been reasonable effective during recent geological time, namely the African Euro-Asian continents and the Pacific Ocean (Duke 1992).

Duke (1995) suggests that mangrove species and their habitat, evolved and diversified following the break up of Gondwanaland over 100 million years ago. Disruption of gene flow within family Rhizophoraceae, would coincide with disruption of gene flow within the mangrove species of genus *Coccotrypes*, the scolytid relying on propagule dispersal for long distance dispersal (Wood 1960; Browne 1961). It seems reasonable to assume therefore that the *Coccotrypes*/ propagule relationship has existed since the period when the initial dispersal of the ancestral *Rhizophora* occurred.

If the scolytid had been transported by man, it is unlikely that speciation between old world and new world would have occurred in the brief time since intercontinental transfer of materials has become common. Supporting this is the widespread occurrence of *C. fallax*, and the lack of speciation within the Indo-Pacific region (Duke 1995).

Rhizophora pollen appeared in the late Eocene. In current classification systems, *Rhizophora Bruguiera* and *Ceriops* are grouped as belonging to family Rhizophoraceae, the implication being that they all evolved from a common ancestor (Duke 1995). It is interesting to speculate whether *Coccotrypes* infestation may have been one of the selection pressures that assisted in the development of the new species. *Ceriops* propagules are very much smaller than those of *Rhizophora*, and quantitative work is likely to support the hypothesis that a single *Ceriops* propagule does not meet the minimum nutritional requirements of a *C. fallax* brood of normal size. Similarly, the propagules of *Bruguiera* spp are not infested by *C. fallax*.

B. parviflora and *B exaristata* are also 'small' propagules and may not meet the nutritional requirements of *C. fallax* larvae. *B. gymnorhiza* on the other hand is in the same size range (with respect to mass) as the *Rhizophora* spp infested by *C. fallax*. A chemical deterrent within *B. gymnorhiza* is most likely the protective mechanism, perhaps working in conjunction with a physical mechanism, for example a higher moisture level within the propagule capable of flooding the chambers of *C. fallax*. It has been demonstrated that sibling species may develop different mechanisms to counter attack by predators.

One can take this speculation one stage further and hypothesise that the evolution of vivipary in members of the mangrove Rhizophoraceae is a mechanism to minimise the period when the reproductive unit is at risk of attack by *Coccotrypes* spp. Flooding of tunnels is reported as a means of protection against scolytid attack, as is the defensive strategy employed by scolytids infesting twigs of ring barking the twig below the area of infestation to prevent flooding of the tunnels (Wood 1960; Browne 1961; Crowson 1981). During the period of development of the propagule on the tree the adult tree has the potential to pump fluid into the propagule and hence flood any scolytid tunnels. The well-developed propagule is capable of establishing roots rapidly and hence flooding new tunnels. By reducing the period of dormancy, the period when the embryonic tissue is not protected is reduced. The 'window of opportunity' for successful infestation of propagules by the scolytid is thus short.

Hammond and Brown (1999) discuss the 'race' between scolytid attack of the seed of *Chlorocardium rodiei* (a large seeded Neotropical tree) and seed germination. In *C. rodiei*, the chance of losing the 'race' was increased because of its prolonged dormancy (Hammond et al, 1999). Vivipary, with no dormancy period and rapid recruitment, should therefore decrease the odds of propagules losing the 'race'.

Successful infestation, which is not cut short by exposure to heat or other factors that result in death of the scolytid, usually results in death of the propagule. The selection pressure for reproductive units that resist scolytid infestation would therefore be high. Juncosa (1982) makes the observation that vivipary is a consequence of the normal torpedo stage of embryo development by the extended growth of the hypocotyl. The temporary cessation of intercalary growth that occurs in seed dormancy in nonviviparous plants is absent and this gives the advantage of immediate germination tidal habitats. Juncosa's hypothesis, while not accounting for vivipary in direct adaptive terms answers the question 'Why vivipary' with the response "Why not?" (Tomlinson 1994). I suggest that in the case of the mangrove Rhizophoraceae, vivipary may have evolved to shorten the time when propagules are susceptible to *Coccotrypes* spp attack. Similarly, *Bruguiera* and *Ceriops* speciation, in particular the differences in propagule size, may reflect adaptations that reduce the success of scolytid infestation, and hence scolytid attack, on these propagules.

7.5 *Directions for further research*

7.5.1 Influence of differences in predator assemblages on the importance of *C. fallax* infestation of *Rhizophora* propagules as a factor in seedling survival.

The composition of the suite of predators on propagules varies between continents (Smith *et al* 1989). The degree to which scolytid infestation affects regeneration needs to be examined under a range of predator assemblages. In an area in which the majority of propagules are consumed by crabs or other large predators, whether or not they are infested by scolytids may be irrelevant. Removal of infested propagules through crab predation may have the effect of reducing scolytid infestation in the remaining propagules. Studies on levels of infestation and survival of seedlings in areas with different assemblages of predators would clarify whether the mechanism affecting recruitment outlined in this study had broad applications.

Similarly any predator on *C. fallax* may influence *C. fallax* numbers and hence the effect on *Rhizophora* recruitment. The mangrove ant, *Polyrachis sokolova* is found in the *Rhizophora* zone and consumes insects and larvae {Clay & Anderson 1996 #4130}. Ants of various species were observed carrying off *C. fallax* larvae in both laboratory and greenhouse conditions. Predation by *P. sokolova* may reduce *C. fallax* infestation to the level where it does not affect *Rhizophora* seedling survival. This requires further investigation.

7.5.2 Effects of differing environmental conditions.

C. fallax are susceptible to increased temperature levels. The 'unusually high' temperatures in Cairns, which resulted in scolytid death in propagules under the canopy, were on days when the published temperature at the local weather station was between 37 ^{0}C and 40 ^{0}C all day. This heatwave resulted in decreased infestation of propagules and increased survival of seedlings at the end of the season. Regions which regularly experience temperatures in this range may find *C.*

fallax populations are normally kept low, with 'outbreaks' occurring only in years with lower than average maximum daily temperatures.

This would require a long-term study of infestation levels and more detailed knowledge of the temperature*time combinations that affect *C. fallax* infesting *Rhizophora* propagules. In this study, scolytids were not affected by short-term (20 minutes) exposure to 40^0 C. Controlled temperature cabinet studies of the effect of prolonged exposure to temperatures in the range 35 to 45^0 C on both the infesting *C. fallax* and the ability of the propagule to recruit and grow are needed. This would assist in predicting environmental conditions in which *C. fallax* are likely to affect survival of seedlings.

7.5.3 Host selection

The evidence suggests that *C. fallax* are able to distinguish between propagules of the three genera of mangrove Rhizophoraceae. Propagules of all three Australian genera are found in close proximity, but only *Rhizophora* are infested. The mechanism of host selection needs further investigation.
Do *C. fallax* use chemical or visual clues or a combination of both for initial host location?
Is final selection based on host size, chemical or physical properties of the propagule

7.6 Implications for forestry research and mangrove regeneration programs

Many countries utilise mangroves as renewable forest and have developed guidelines for wood production, harvest techniques etc (Hamilton and Snedekar 1984; FAO, 1985; FAO, 1985). In several countries harvesting occurs in strip clear cuts that vary between 30 and 50 m wide, and extend inland from the river at right angles (Hartshorn 1989; Hamilton and Snedekar 1984; FAO, 1985; Hamilton and Snedekar 1984; FAO, 1985). Seed trees of specified size and number per hectare are required to be left to allow for natural regeneration of the site (Chan and Nasir 1985; Hamilton and Snedekar 1984; Hamilton and Snedekar 1984).

When natural regeneration fails, hand planting is required (Chan 1988). Insect damage, specifically scolytid damage is known to affect regeneration (Lapis and San-Valentin 1982; San Valentin 1986). Desiccation and overheating of the propagule have also been implicated (Elster *et al* 1999; Blanchard and Prado 1995). The cost of supplementary planting of propagules in areas in which natural regeneration has failed varies with the method used. Planting established seedlings has a higher success rate than planting propagules, but at a higher cost per hectare (Chan 1988). Any strategies to improve the rate of natural regeneration and success rate when planting propagules has the potential to save money.

7.6.1 Maximising natural regeneration after harvesting.

Regeneration of clear felled areas after harvesting is sometimes poor and hand planting in required. This is labour intensive and expensive. *C. fallax* have been implicated in failure of natural regeneration and following planting (Lapis and San-Valentin 1982; San Valentin 1986).

It is possible that the direction of the long axis of the strip (north-south or east-west) may affect the hours of sunshine experienced by individual propagules. A north-south axis would provide a wider 'footprint' of ground exposed to direct sunlight (and hence quarantined against *C. fallax* infestation). Studies on moderating propagule temperature in regeneration areas through provision of shade trees or orientation of harvesting strips may result in guidelines that increase natural regeneration and reduce the need for hand planting.

Where natural regeneration fails and hand planting is required, losses due to insect predation are costly (Lapis and San-Valentin 1982; Chan 1988; Rau and Murphy 1990; Chan 1988; Rau and Murphy 1990). A method of quarantining propagules prior to plant out would be an advantage. Research on applying the laboratory methods used in this study to field conditions may have economic benefits.

7.7 Conclusion

This study illustrates the need to consider both abiotic and biotic factors when looking at the mechanisms determining community structure. *C. fallax* predation has been shown to affect *Rhizophora* propagule recruitment and survival in one portion of the habitat, the established *Rhizophora* zone. *Bruguiera* and *Ceriops* are not infested by *C. fallax* and have the potential to replace *Rhizophora* as a result of the differential predation pressures experienced by the different species through scolytid infestation.

This study also explains the references to 'shade intolerance' of *Rhizophora* and the frequent description of *Rhizophora* as a pioneer species. *C. fallax* does not affect *Rhizophora* recruitment in survival in light gaps. By linking the temperature tolerance limits of the infesting scolytid to temperatures experienced by propagules in light gaps and under the canopy it has been possible to identify heat as the mechanism that causes death of the scolytid. This explains why predation by *C. fallax* is important under the canopy but does not occur in light gaps.

Light gaps, disturbance and patch dynamics are increasingly seen as important in understanding the community structure of terrestrial forests. The interlocking dynamics of shade intolerance, ability of seedlings to respond to formation of canopy gaps, predation and canopy gap formation are all factors in recruitment and survival of seedlings. This study highlights the need to consider these in the context of mangrove community structure.

8 Bibliography

1. Andrews TJ, Clough BF, Muller GJ. 1984. Photosynthetic gas exchange properties and carbon isotope ratios of some mangroves in North Queensland Teas HJ, Editor. Physiology and management of mangroves. Volume 9. The Hague: Dr W. Junk Publishers. Chapter Tasks for Vegetation Science. p 15-23.

2. Asquith NM, Wright SJ, Clauss MJ. 1997. Does mammal community composition control recruitment in neotropical forests? Evidence from Panama. Ecology 78(3): 941.

3. Attiwill PM, Clough BF. 1980. Carbon dioxide and water vapour exchange in the white mangrove. Photosynthetica 14:40-7.

4. Ball MC. 1988a. Ecophysiology of mangroves. Trees 2:129-42.

5. Ball MC, Cowan IR, Farquhar GD. 1988c. Maintenance of leaf temperature and the optimization of carbon gain in relation to water loss in a tropical mangrove forest. Australian Journal of Plant Physiology 15:263-76.

6. Banus MD, Kolehmainen SE. 1975. Floating, rooting and growth of Red Mangrove (*Rhizophora Mangle* L.) seedlings: effect on expansion of mangroves in southwestern Puerto Rico. in : Walsh GE, Snedaker SC, Teas HJ, Editors. Proceedings of the International Symposium on Biology and Management of Mangroves. Volume 1. Gainesville, Florida: Institute of Food and Agricultural Sciences, University of Florida. p 370-84.

7. Beach Protection Authority, Queensland. 1984. Mulgrave Shire Northern Beaches. Brisbane: Government Printer, Queensland.

8. Bernays EA, Chapman RF. 1994. Host-plant selection by phytophagous insects. London: Chapman and Hall.

9. Birch LC. 1971. The role of environmental heterogeneity in determining distribution and abundance. in: den Boer PJ, Gradwell GR, Editors.

Dynamics of Populations. Wageningen: Centre for Agricultural Publishing and Documentation. p 109-28.

10. Bird ECF. 1972a. Mangroves and coastal morphology in Cairns Bay, North Queensland. Journal of Tropical Geography 35:11-6.

11. Blanchard, Prado. 1995. Natural regeneration of *Rhizophora mangle* in Strip clearcuts in Northwest Ecuador. Biotropica 27(2):160-7.

12. Blasco F. 1984. Climatic Factors and the biology of mangrove plants. in: Snedaker SC, Snedaker JG, Editors. The mangrove ecosystem: research methods. Paris: UNESCO. p 19-35.

13. Boose ER, Foster DR, Fluet M. 1994. Hurricane impacts to tropical and temperate forest landscapes. Ecological Monographs 64(4):369-91.

14. Boto KG. 1982. Nutrient and Organic fluxes in Mangroves. Clough BF, Editor. Mangrove ecosystems in Australia. Canberra: Australian Institute of Marine Science. p 239-57.

15. Boto KG, Wellington JT. 1983. Phosphorous and nitrogen nutritional status of a northern Australian mangrove forest. Marine Ecology Progress Series 19:63-9.

16. Boto KG, Wellington JT. 1984. Soil characteristics and nutrient status in a northern Australian mangrove forest. Estuaries 7:61-9.

17. Bowman HHM. 1917. Ecology and physiology of the red mangrove. Proceedings of the American Philosophical Society 56:589-672.

18. Bridgewater PB. Mangrove Vegetation of the Southern and Western Australian Coastline. Clough BF, Editor. Mangrove Ecosystems in Australia. Canberra: Australian Institute of Marine Science. p 111 to 120.

19. Briggs JC. 1974. Marine Zoogeography. New York: McGraw-Hill.

20. Browne FG. 1961. The biology of Malayan Scolytidae and Platypodidae. Malayan For. Rec. 22:89-100.

21. Bunt JS, Williams WT. 1981a. Studies in the analysis of data from Australian tidal forests ('mangroves') 1, Vegetational sequences and their graphical representation. Australian Journal of Ecology 5:385-90.

22. Bunt JS, Williams W.T., Clay HJ. 1982a. River water salinity and the distribution of mangroves species along several rivers in north Queensland. Australian Journal of Botany 30:401-12.

23. Bunt JS, Williams WT, Duke NC. 1982b. Mangrove distributions in north-east Australia. Journal of Biogeography 9:111-20.

24. Bunt JS, Williams WT, Hunter JF, Clay HJ. 1991. Mangrove sequencing: analysis of zonation in a complete river system. Marine Ecology Progress Series 72:289-94.

25. Bunt JS. 1996. Mangrove Zonation: An examination of Data from Seventeen Riverine Estuaries in Tropical Australia. Annals of Botany 78:333-41.

26. Bunt SJ, Williams WT. 1981b. Vegetational Relationships in the Mangroves of Tropical Australia. Marine Ecology Progress Series 4:349-59.

27. Bureau of Meteorology. 1971. Climatic Survey: Northern Region 16, Queensland. Canberra: Department of the Interior.

28. Bureau of Meteorology . 1999. Climate Averages [Web Page]. Located at: www.bom.gov.au/climate/averages/. Accessed 2001-01-20.

29. Carlson PR, Yarbro LA, Zimmerman CF, Montgomery JR. 1983. Pore water chemistry of an overwash mangrove island. Florida Scientist 46:239-49.

30. Chan HD, Razini U, Putz FE. 1984. A preliminary study on planting of *Rhizophora* species in an *Avicennia* forest at the Matang Mangroves. Soemodihardjo S. et al, Editors. Prosiding Seminar II Ekosistem Jakarta Indonesia: Lembagu Ilmu Pentetahuan.

31. Chan HT. 1988. Rehabilitation of logged over mangrove areas using wildings of Rhizophora apiculata. Journal of Tropical Forest Science. 1(2):187-8.

32. Chan HT, Nasir H. 1985. Propagule dispersal, establishment and survival of *Rhizophora mucronata*. Malaysian Forester 48:3-4 324-329.

33. Chapman VJ. 1976. Mangrove Vegetation. Vaduz: J. Cramer.

34. Chapman VJ. 1984. Mangrove biogeography. in : Dov Por F, Dor I, Editors. Hydrobiology of the Mangal. Volume Developments in Hydrobiology. The Hague: Dr W. Junk Publishers. Chapter 20.

35. Christensen B, Wium-Anderson S. 1977. Season growth of mangrove trees in southern Thailand. I The phenology of *Rhizophora apiculata* Bl. Aquatic Botany (3):281-6.

36. Clarke LD, Hannon NJ. 1967. The mangrove and salt marsh communities of the Sydney district. 1 Vegetation, soils and climate. Journal of Ecology 55:753-71.

37. Clarke LD, Hannon N.J. 1970. The mangrove and salt marsh communities of the Sydney district. III. Plant Growth in relation to salinity and waterlogging. Journal of Ecology 58:351-69.

38. Clarke LD, Hannon NJ. 1971. The mangrove and salt marsh communities of the Sydney district. IV. The significance of species interaction. Journal of Ecology 59:535-53.

39. Clarke LD, Hannon NJ. 1969. The mangrove and salt marsh communities of the Sydney district, II The holoceonotic complex with particular reference to physiography. Journal of Ecology 57:213-34.

40. Clarke PJ. 1995a. The population dynamics of the mangrove *Avicennia Marina*; demographic synthesis and predictive modeling. Hydrobiologia 295:83-8.

41. Clay RE, Anderson AN. 1996. Ant fauna of a mangrove community in the Australian seasonal tropics, with particular reference to zonation. Australian Journal of Zoology 44:521-33.

42. Connell JH. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rainforests. in: den Boer PJ, Gradwell G.R., editors. Dynamics of Populations. Wageningen: Centre for Agricultural Publishing and Documentation.

43. Connell JH. 1975a. Some mechanisms producing structure in natural communities; a model and evidence from field experiments. in : Cody ML, Diamond J. M. editors. Ecology and Evolution of Communities. Cambridge, Mass.: Harvard University Press. p 460-90.

44. Connell JH, Slatyer RO. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist 111:1119-44.

45. Crawley MJ, Pacala SW. 1991. Herbivores, Plant Parasites, and plant diversity. in: Toft CA, Aeschlimann A, Bolis L, Editors. Parasite-Host Associations. Oxford: Oxford University Press. p 157-73.

46. Crowson RA. 1981. The Biology of the Coleoptera. Sydney: Academic Press.

47. Curtis AH. 1888. How the mangroves form islands. Garden and Forest 1:100.

48. Davis JHJ. 1940a. The ecology and geologic role of mangroves in Florida. Papers From the Tortugas Lab. 32(Carnegie Institute Washington Pub. no. 517):303-412.

49. Dowling RM, McDonald TJ. 1982. Mangrove Communities of Queensland. in: Clough BF, Editor. Mangrove Ecosystems in Australia. Australian Institute of Marine Science.

50. Duke NC. 1992. Mangrove Floristics and Biogeography. in : Robertson AI, Alongi DM, Editors. Tropical Mangrove Ecosystems. Volume Coastal and Estuarine Studies. Washington DC: American Geophysical Union. Chapter 41.

51. Duke NC. 1995. Genetic diversity, distributional barriers and rafting continents- more thoughts on the evolution of mangroves. Hydrobiologia 295:167-281.

52. Duke NC, Bunt JS. 1979. The genus *Rhizophora* (Rhizophoraceae) in North Eastern Australia. Australian Journal of Botany 27:657-78.

53. Duke NC, Bunt JS, Williams WT. 1984. Observations on the floral and vegetative phenologies of north eastern Australian mangroves. Australian Journal of Botany 32:87-99.

54. Duke, N.C. and Pinzon, Z.S. 1992. Aging Rhizophora seedlings from leaf scar nodes: a technique for studying recruitment and growth in mangrove forests. Biotropica, 24: 173-186

55. Duke NC, Ball M.C., Ellison JC. 1998. Factors influencing biodiversity and distributional gradients in mangroves. Global Ecology and Biogeograph Letters 7:27-47.

56. Duke, N.C., Pinzon, Z.S. and Prada, M. C. 1999. Recovery of tropical mangrove forests following a major oil spill: a study of recruitment and growth and the benefits of planting. In A. Yanez-Arancibia and A.L. Lara-Dominguez (eds) Mangrove Ecosystems in Tropical America. Chapter 15, pp231-254. Instituto De Ecologia A.C. Mexico, UICN/ORMA Costa Rica, and NOAA/NMFS Silver Spring MD USA.

57. Duke, N.C. 2001. Gap creation and regerative processes driving diversity and structure of mangrove ecosystems. Wetlands Ecology and Management, 9: 257-269.

58. Edney EB. 1961. The water and heat relationships of fiddler crabs (*Uca* spp.). Transactions of the Royal Society of South Africa. (36):71-91.

59. Egler FA. 1950. Southeast saline Everglades vegetation, Florida, and its management. Vegetatio 3:213-65.

60. Egler FE. 1948. The dispersal and establishment of red mangrove, *Rhizophora*, in Florida. Caribbean Forester (9):229-320.

61. Ellison AM, Farnsworth EJ. 1993a. Seedling survivorship, growth and response to disturbance in Belizean mangal. American Journal of Botany 80(10):1137-45.

62. Ellison AM, Farnsworth EJ. 1996. Spatial and temporal variability in growth of Rhizophora mangle saplings on coral cays: links with variation in insolation, herbivory, and local sedimentation rate. The Journal of Ecology 84(5):717-31.

63. Elster C, Perdomo L, Schnetter ML. 1999. Impact of ecological factors on the regeneration of Mangrove in the Cienaga Grande de Santa Marta, Colombia. Hydrobiologia 413:35-46.

64. Environment Australia. 1997. Australian Geographic Place Names (Gazeteer) [Web Page]. Located at: http://www.erin.gov.au/database/MAN200R.html. Accessed 2000.

65. Evans GC. 1972. The quantitative analysis of plant growth. Volume 1. Oxford: Blackwell Scientific Publications; (Studies in Ecology.

66. FAO. 1985. Mangrove management in Thailand, Malaysia and Indonesia. Rome: Food and Agricultural Organization of the United Nations.; (FAO Environment Paper: 4).

67. Farnsworth EJ, Ellison AM. 1997. Global patterns of pre-dispersal propagule predation in mangrove forests. Biotropica (3):318-30.

68. Frith DW. 1977. A selected bibliography of mangrove literature. Research Bulletin No. 19 ed. Thailand: Phuket Marine Biological Center.

69. Galloway RW. 1982. Distribution and physiographic patterns of Australian mangroves. in: Clough BF, Editor. Mangrove ecosystems in Australia: structure, function and management. Canberra: ANU Press. p 31-54.

70. Giglioli MEC, Thornton I. 1965. The mangrove swamps of Keneba, lower Gambia River basin. 1 Descriptive notes on the climate, the mangrove swamps, and the physical condition of their soils. Journal of Applied Ecology 2:81-103.

71. Gullan PJ, Cranston PS. 1994. The Insects; an outline of entomology. London: Chapman and Hall.

72. Gunn CR, Dennis JV. 1973. Tropical and temperate stranded seeds and fruit from the Gulf of Mexico. Contributions in Marine Science 17:111-21.

73. Hallman GJ, Sharp JL. 1990. Hot water immersion quarantine treatment for Carambolas infested with fruit fly (Diptera, Tephritidae). Journal of Economic Entomology 8(4):1471-.

74. Hamilton LS, Snedekar SC, Editors. 1984. Handbook for Mangrove Area Management. By a writing team of the Environment and Policy Institute East West Centre. Hawaii: East West Centre, Environment and Policy Institute.

75. Hammond DS, Brown VK, Zagt R. 1999. Spatial and temporal patterns of seed attack and germination in a large-seeded neotropical tree species. Oecologica 119(2):208-18.

76. Hara AH, Hata TY, Hu BKS, Tenbrink VL. 1993. Hot water Immersion as a Potential Quarantine treatment against *Pseudaulacaspis cockerilli* (Homoptera: Diaspididae). Journal of Economic Entomology 86(4):1167-70.

77. Harper JL. 1977. Population biology of plants. London: Academic Press. Harper JL, White J. 1971. The dynamics of plant populations. in: den Boer PJ, Gradwell GR, Editors. Dynamics of Populations. Wageningen: Centre for Agricultural Publishing and Documentation.

78. Hartshorn GS. 1989. Application of gap theory to tropical forest management: natural regeneration on strip clear-cuts in the Peruvian Amazon. Ecology 70(3):567-9.

79. Hogarth PJ. 1999. The Biology of Mangroves. Oxford: Oxford University Press; (Biology of Habitats).

80. Holmes JC, Price PW. 1986. Communities of Parasites. in: Kikkawa J, Anderson DJ, Editors. Community Ecology: Pattern and Process. Melbourne: Blackwell Scientific Publications.

81. Howe HF, Smallwood J. 1982. Ecology of seed dispersal. Annual Review of Ecology and Systematics (13):201-28.

82. Hubbell SP. 1980. Seed predation and the coexistence of tree species in tropical forests. OIKOS 35(2):214-29.

83. Hutchings P, Saenger P. 1987a. Ecology of Mangroves. St Lucia: University of Queensland Press.

84. Janzen DH. 1970. Herbivores and the number of tree species in tropical forests. American Naturalist 104:501-28.

85. Janzen DH. 1971. Escape of *Cassia Grandis* L beans from predators in time and space. Ecology 52:964-79.

86. Jimenez JA, Sauter K. 1991. Structure and dynamics of mangrove forests along a flooding gradient. Estuaries 14:49-56.

87. Johnstone IM. 1983a. Succession in zoned mangrove communities: where is the climax? in: Teas HJ, editor. Biology and ecology of mangroves. The Hague: Dr W. Junk Publishers. p 131-9.

88. Jolivet P. 1998. Interrelationships between insects and plants. London: CRC Press. p 309.

89. Jones WT. 1971. The field identification and distribution of mangroves in Eastern Queensland. Queensland Naturalist 20(1-3):35-51.

90. 88. Juncosa AM. 1982. Developmental morphology of the embryo and seedling of *Rhizophora Mangle* L. (Rhizophoraceae). American Journal of Botany (71):170-9.

91. Kenneally KF. 1982. Mangroves of Western Australia Clough BF, Editor. Mangrove Ecosystems in Australia. Canberra: Australian Institute of Marine Science. p 95-110.

92. Kirkendall LW. 1993. Ecology and Evolution of Biased Sex Ratios in Bark and Ambrosia Beetles [in]Wrensch DL, Ebbert MA, Editors. Evolution and Diversity of Sex Ratio in Insects and Mites. London: Chapman and Hall. p 235-345.

93. Komiyama A, Chimchome V, Kongsangchai J. 1992. Dispersal patterns of mangrove propagules. A preliminary study on *Rhizophora mucronata*. Research Bulletin of the Faculty of Agriculture, Gifu University. (57):27-34.

94. Krebs CJ. 1994a. Ecology: The Experimental Analysis of Distribution and Abundance. Fourth ed. New York: Harper Collins College Publishers.

95. Lapis ER, San-Valentin HO. 1982. Protection of *Rhizophora mucronata* seedlings against *Poecillips Fallax* Eggers (Coleoptera: scolytidae) by cultural methods. Sylvatrop 7:3-4, 171-6.

96. LaRue CD, Muzik T.J. 1951. Does the mangrove really plant its own seedlings? Science (114):661-2.

97. Lear R, Turner T. 1977. Mangroves of Australia. Brisbane: University of Queensland Press.

98. Louda SM. 1995. The effect of seed predation on plant regeneration: evidence from Pacific Basin Mediterranean scrub communities. in: Arroyo

MTK, Zedler PH, Fox MD, Editors. Ecology and Biogeography of Mediterranean Ecosystems in Chile, California and Australia. New York: Springer -Verlag. p 331-44.

99. Lovelock C. 1993. Field guide to the Mangroves of Queensland. Townsville: Australian Institute of Marine Science.

100. Lugo AE. 1980a. Mangrove ecosystems, successional or steady state? Biotropica 12(Supplement 2):65-72.

101. Lugo AE. 1980b. Mangrove ecosystems, successional or steady state? Biotropica 12(Supplement 2):65-72.

102. Lugo AE, Snedaker SC. 1974. The Ecology of Mangroves. Annual Review of Ecology and Systematics 5:39-64.

103. Lugo AE, Snedaker SC. 1975a. Properties of a Mangrove forest in Southern Florida. in: Walsh GE, Snedaker SC, Teas HJ, Editors. Proceedings of the international Symposium on Biology and Management of Mangroves. Volume 1. Gainsville, Florida: Institute of Food and Agricultural Sciences. p 170-212.

104. Macnae W. 1966. Mangroves in Eastern and Southern Australia. Australian Journal of Botany 15:67-104.

105. Macnae W. 1967. Zonation within mangroves associated with estuaries in North Queensland. in: Lauff GH, Editor. Estuaries. American Association for the Advancement of Science. Chapter Publ. 83. p 432-41.

106. Macnae W. 1968. A general account of the fauna and flora of mangrove swamps and forests in the Indo-West Pacific region. Advances in Marine Biology 6:73-270.

107. Martinez-Ramos M, Alvarez-Buylla E, Sarukhan J. 1989. Tree demography and gap dynamics in a tropical rain forest. Ecology 70(3):555-8.

108. Mathews EG, Kitchling RC. 1984. Insect Ecology. St Lucia, Qld: University of Queensland.

109. McKee KL. 1993. Soil physiochemical patterns and mangrove species distribution-reciprocal effects. Journal of Ecology 81(3):477-87.

110. McKee KL. 1994. Mangrove species distribution and propagule predation in Belize: an exception to the Dominance-Predation Hypothesis. Biotropica :334-45.

111. McKee KL. 1995a. Interspecific variation in growth, biomass partitioning and defensive characteristics of neotropical mangrove seedlings: response to light and nutrient availability. American Journal of Botany 82(3):299-307.

112. McKee KL. 1995b. Seedling recruitment patterns in a Belizean mangrove forest;- effects of establishment ability and physico-chemical factors. Oecologia 101:448-60.

113. McMillan C. 1975. Interaction of soil texture with salinity tolerances of black mangrove (*Avicennia*) and white mangrove (*Laguncularia*) from North America Walsh GE, Snedaker SC, Teas HJ, Editors. Proceedings of the International Symposium on the Biology and Management of Mangroves. Volume 2. Gainesville: University of Florida. p 561-6.

114. McMillan C. 1971a. Environmental factors affecting seedling establishment of the black mangrove on the Central Texas Coast. Ecology 52:927-30.

115. McMillan C. 1971b. Environmental factors affecting seedling establishment of the black mangrove on the Central Texas Coast. Ecology 52:927-30.

116. Murphy DH, Meepol W. 1990. Timber Beetles of the Ranong Mangrove Forests. Mangrove Ecosystems Occasional Papers 7:5-7.

117. Myers JG. 1935. Zonation along river courses. Journal of Ecology 23:356-60.

118. New TR. 1986. Associations between insects and plants. Kensington NSW: New South Wales University Press.

119. Nickerson NH, Thibodeau FR. 1985. Association between pore water sulfide concentrations and distributions of mangroves. Biogeochemistry 1:183-92.

120. Onuf CP, Teal JM, Valeila I. 1977. Interactions of nutrients, plant growth and herbivory in a mangrove ecosystem. Ecology 58:514-26.

121. Osborne K. 1988. A distribution study of the mangrove, *Aegiceras corniculatum* (L.) Blanco, in some northern Australian estuaries. Townsville, Australia: James Cook University of North Queensland. 82pp . Batchelor of Science Honors Thesis.

122. Osborne K, Smith TJIII. 1990. Differential predation on mangrove propagules in open and closed canopy forest habitats. Vegatatio 89:1-6.

123. Pimm SL. 1978. An experimental approach to community structure. American Zoologist 18:797-807.

124. Poulson TL, Platt WJ. 1989. Gap light regimes influence canopy tree diversity. Ecology 70(3):553-5.

125. Putz FE, Chan HT. 1986. Tree growth, dynamics and productivity in a mature mangrove forest in Malaysia. Forest Ecology and Management 17(2-3):211-30.

126. Queensland Department of Transport. 1996. Official tide tables and boating safety guide. Brisbane: Queensland Department of Transport.

127. Qureshi T. 1990. Experimental Plantation for rehabilitation on mangrove forests in Pakistan. Mangrove Ecosystems Occasional Papers 4:3-30.

128. Rabinowitz D. 1975. Planting experiments in mangrove swamps of Panama. Walsh GE, Snedaker S.G., Teas H.J., editors. Proceeding of the International Symposium on Biology and Management of Mangroves; 1975; Gainsville, Florida: Institute of Food and Agricultural Sciences, University of Florida. p 385-93.

129. Rabinowitz D. 1977. Effects of a Mangrove Borer *Poecilips rhizophorae* , on propagules of *Rhizophora harrisonii* in Panama. The Florida Entomologist 60(2):129-34.

130. Rabinowitz D. 1978a. Dispersal properties of mangrove propagules.

Biotropica 10(1):47-57.

131. Rabinowitz D. 1978b. Early growth of mangrove seedlings in Panama and an hypothesis concerning the nature and dispersal and zonation. Journal of Biogeography 5:113-33.

132. Rabinowitz D. 1978c. Mortality and initial propagule size in mangrove seedlings in Panama. Journal of Ecology (66):45-51.

133. Rau MT, Murphy DH. 1990. Herbivore attack on mangrove plants at Ranong. Mangrove Ecosystems Occasional Papers 7:25-31.

134. Ricklefs RE, Latham RE. 1993. Global patterns of Diversity in Mangrove Floras. in: Ricklefs RE, Schluter D, Editors. Species Diversity in Ecological Communities. Chicago: University of Chicago Press. p 215-29.

135. Ridd PV, Sam R. 1996. Profiling Groundwater Salt Concentrations in Mangrove Swamps and Tropical Salt Flats. Estuarine, Coastal and Shelf Science 43:627-35.

136. Robertson AI, Giddins R, Smith TJ III. 1990. Seed predation by insects in tropical mangrove forests: extent and effects on seed viability and the growth of seedlings. Oecologia 83:213-9.

137. Rollet B. 1981. Bibliography on mangrove research, 1600-1975. Paris: UNESCO.

138. Saenger P. 1982. Morphological, anatomical and reproductive adaptations of Australian mangroves. in: Clough BF, Editor. Mangrove Ecosystems in Australia. Canberra: Australian Institute of Marine Science. p 153-92.

139. Saenger P, Robson J. 1977. Structural analysis of mangrove communities on the Central Queensland coastline. Marine Research in Indonesia 18:101-18.

140. Saenger P, Specht MM, Specht L, Chapman VJ 1977. Mangal and Coastal Salt-marsh communities in Australasia. in: Chapman VJ, Editor. Wet Coastal Ecosystems. Oxford: Elsevier Scientific Publishing Company. p 293-347.

141. San Valentin HO. 1986. Biology and ecology of *Poecilips fallax* Egger (Coleoptera; scolytidae) infesting *Rhizophora* spp seedlings. Bakawan Newsletter 1 (3):3, 51-2.

142. Scholander PF, Dam LV, Scholander SI. 1955. Gas exchange in the roots of mangroves. American Journal of Botany 42:92-8.

143. Schoonhoven LM, Jermy T, van Loon JJA. 1998. Insect -Plant Biology. Melbourne: Chapman and Hall.

144. Schupp EW, Howe HF, Augspurger CK, Levey DJ. 1989. Arrival and survival in tropical treefall gaps. Ecology 70(3):562-4.

145. Semeniuk V. 1983. Mangrove distribution in northwestern Australia in relationship to regional and local freshwater drainage. Vegetatio 53:11-31.

146. Sherrod CL, Hockaday DL, McMillan C. 1986. Survival of red mangrove, *Rhizophora mangle*, on the Gulf of Mexico coast of Texas. Contributions in Marine Science 29:27-36.

147. Sherrod CL, McMillan C. 1985. The distributional history and ecology of mangrove vegetation along the northern Gulf of Mexico coastal region. Contributions in Marine Science 28:129-40.

148. Smith TJ III. 1987a. Effects of light and intertidal position on seedling survival and growth in tropical tidal forests. Journal of Experimental Marine Biology and Ecology. 110:133-46.

149. Smith TJ III. 1987b. Seed Predation in relation to tree dominance and distribution in mangrove forests. Ecology 68:266-73.

150. Smith TJ III. 1987c. Effects of Seed Predators and Light Level on the Distribution of Avicennia Marina (Forsk.) Vierh. in Tropical Tidal Forests. Estuarine, Coastal and Shelf Science 25:43-51.

151. Smith TJ III. 1988a. The influence of seed predators on structure and succession in tropical tidal forests. Proceedings of the Ecological Society of Australia 15:203-11.

152. Smith TJ III. 1988b. Differential distribution between subspecies of the mangrove *Ceriops tagal*: Competitive interactions along a salinity gradient . Aquatic Botany 32:79-89.

153. Smith TJ III. 1992a. Forest Structure. in: Robertson AI, Alongi DM, Editors. Tropical Mangrove Ecosystems. Volume Coastal and Estuarine Studies. Washington D.C.: American Geophysical Union. Chapter 41. p 101-36.

154. Smith TJ III, Chan HT, Mc Ivor CC, Robblee MB. 1989. Comparisons of seed predation in tropical tidal forests from three continents. Ecology 70:146-51.

155. Smith TJ III, Duke NC. 1987. Physical determinants of inter estuary variation in mangrove species richness around the tropical coastline of Australia. Journal of Biogeography 14:9-19.

156. Smith TJ III, Robblee MB. , Wanless HR, Doyle TW. 1994a. Mangroves, hurricanes and lightning strikes. Bioscience 44(4):256-64.

157. Snedaker SC. 1982. Mangrove species zonation: why? in: Sen DN, Rajpurohit K.S., Editors. Tasks for Vegetation Science. Volume 2. The Hague: D.W. Junk Publishers. p 111-25.

158. Specht RL. 1970. Vegetation. in: Leeper GW, editor. The Australian Environment. 4 ed. Melbourne: CSIRO and Melbourne University Press. p 44--67.

159. Spies TA, Franklin J. F. 1989. Gap characteristics and vegetation response in coniferous forests of the Pacific northwest. Ecology 70(3):543-5.

160. Stenseth NC. 1980. Spatial heterogeneity and population stability: some evolutionary consequences. OIKOS 35(2):165-84.

161. Strong DR. 1984. Exorcising the Ghost of Competition Past: Phytophagous Insects. in: Strong DR, Simberloff D, Abele LG, Thistle AB, Editors. Ecological Communities: Conceptual Issues and the Evidence. Princeton, New Jersey: Princeton University Press. p 28-41.

162. Strong DR. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. Ecology (73):747-54.

163. Thom BG. 1967. Mangrove ecology and deltaic geomorphology: Tabasco, Mexico. Journal of Ecology 55:301-43.

164. Thom BG. 1975. Mangrove Ecology from a Geomorphic viewpoint. in: Walsh GE, Snedaker SC, Teas HJ, Editors. Proceedings of the International Symposium on Biology and Management of Mangroves. Volume 2. Gainesville, Florida: Institute of Food and Agricultural Sciences. p 469-81.

165. Tomlinson PB. 1994. The Botany of Mangroves. Sydney: Cambridge University Press.

166. Valiela I. 1984. Marine ecological processes. New York: Springer.

167. Walsh GE. 1974. Mangroves: A review. in : Reimhold R.J. , Queen WH, Editors. Ecology of Halophytes. New York: Academic Press. p 51-174.

168. Warming E. 1925. Oecology of plants. Oxford: Oxford University Press.

169. Watson JG. 1928. Mangrove forests of the Malay peninsula. Malayan Forest Records 6:1-275.

170. Wells AG. 1982. Mangrove Vegetation of Northern Australia. in: Clough BF, Editor. Mangrove Ecosystems in Australia, Structure Function and Management. Australian Institute of Marine Science.

171. White PS, Pickett STA. 1985. Natural disturbance and Patch Dynamics, an Introduction. in: Pickett STA, White PS, Editors. The Ecology of Natural Disturbance and Patch Dynamics. Sydney: Academic Press, Inc. p 3-13.

172. Wier AM, Schnitzler MA, Tattar TA, Klekowski EJ, Stern AI. 1996. Wound periderm development in red mangrove, *Rhizophora mangle* L. International Journal of Plant Sciences 157(1):63-70.

173. Williams WT, Bunt JS, Clay HJ. 1991. Yet another method of species sequencing. Marine Ecology Progress Series 72:283-7.

174. Wood SL. 1960. Insects of Micronesia Coleoptera: Platypodidae and Scolytidae Volume 18. Honolulu: Bernice P Bishop Museum.

175. Wood SL. 1986. A reclassification of the genera of Scolytidae (Coleoptera). Great Basin Naturalist Mem. 10:1-126.

176. Woodroffe C. 1992. Mangrove Sediments and Geomorphology. in : Robertson AI, Alongi DM, Editors. Tropical Mangrove Ecosystems. Volume Coastal and Estuarine Studies. Washington D.C.: American Geophysical Union. Chapter 41.

177. Woodroffe CD. 1984. Development of mangrove forest from a geological perspective. in: Teas HJ, Editor. Biology and Ecology of Mangroves. Volume 8. The Hague: Dr W Junk Publishers. Chapter Tasks for Vegetation Science. p 1-18.

178. Woodrow RJ, Grace JK. 1998. Laboratory evaluation of high temperatures to control *Cryptotermes brevis* (Isoptera: Kalotermitidae). Journal of Economic Entomology. 91(4):905-9.

179. Woodruff RE. 1970. A mangrove borer, *Poecilips rhizophorae* (Hopkins)(Coleoptera; Scolytidae) . Florida Department Agriculture and Consumer Services, Division of Plant Industries Entomological Circular 98 (Bureau Entomological Control 186):1-2.

180. Yamashiro M. 1961. Ecological study on *Kandelia candel* (L.) Druce, with special reference to the structure and falling of the seedlings. Hikobia 2(3):209-14.

181. Zar JH. 1984. Biostatistical analysis. 2 ed. Sydney: Prentice-Hall

International, Inc.

182. Zimmerman EC. 1992. Australian Weevils (Coleoptera: Curculionoidea) Volume VI. Australia: CSIRO.

Appendices

1 Appendix 1 Key to identifying infested *Rhizophora* propagules

1a	No bore holes in propagules......................	clear
1b	One or more boreholes in propagule.........	go to 2
2a	Frass associated with boreholes.................	infested
2b	No frass associated with boreholes	leave in warm dry place for 24 hours and check for frass, go to 3
3a	Frass associated with boreholes...........	Infested *
3b	Boreholes are present but no frass	Not infested. **

* The temperature in the field may have dropped below that required for activity of the adult,

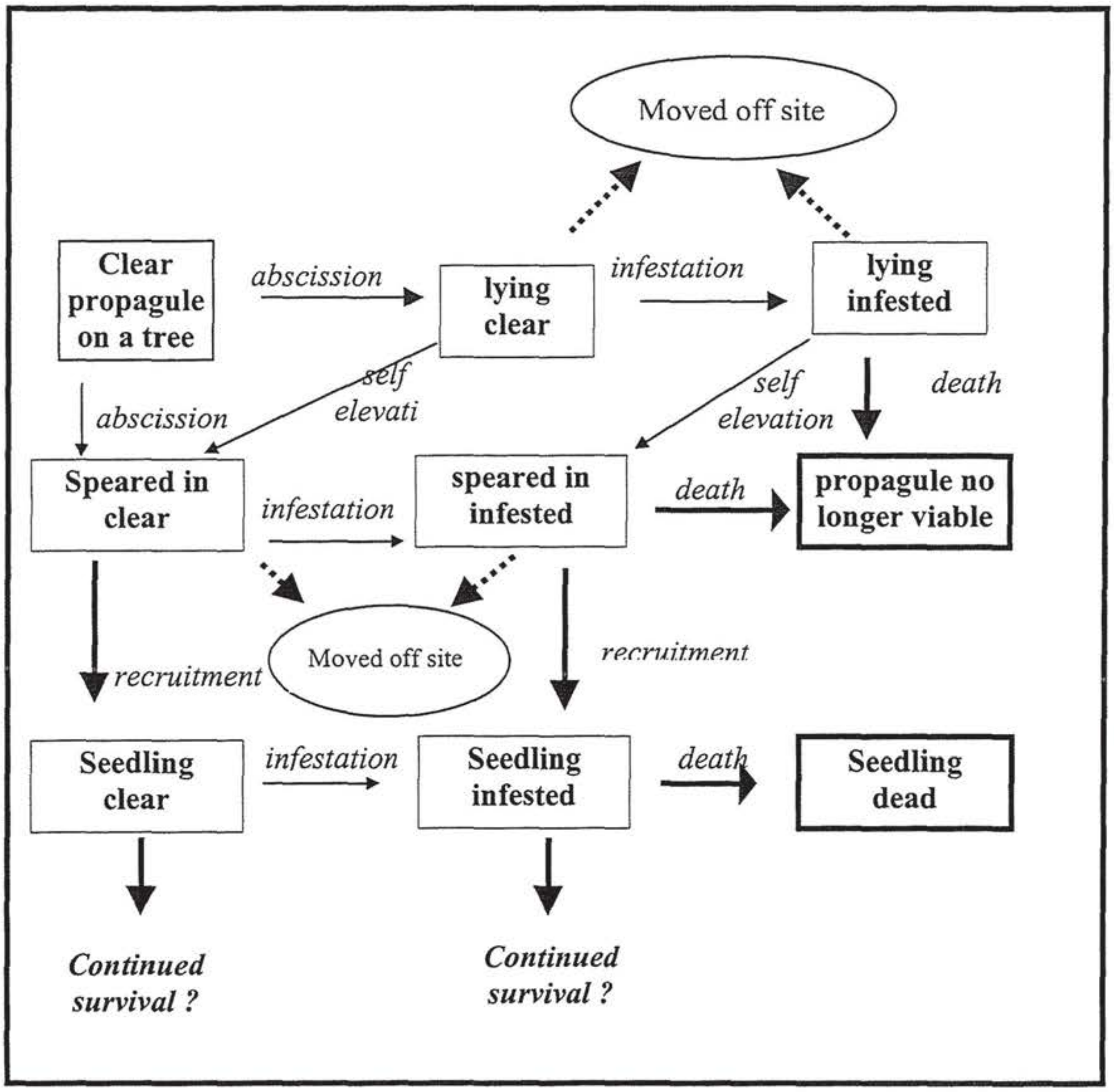
or Frass had been washed away previously by rain or tidal action

** The boreholes were produced by insects other than a scolytid.

or The female abandoned the tunnel

or The scolytids infesting the propagule are dead.

Figure 1 Possible changes to a propagules position, infestation status and health following abscission from the parent tree.



Any interpretation of numbers of propagules, speared or lying, clear or infested, recruited or dead needs to take into account the way in which propagules on the ground may progress through the different stages. Note that this diagram makes no mention of consumption of propagules by crabs, snails or vertebrates.

2 Appendix 2 Statistical tables analyses reported in Chapter 4

2.1 Variability in numbers of propagules at different locations, different years over the season. Tests of Between-Subjects Effects (Section 4.3.5

Dependent Variable: TPROPS = Number of *R. stylosa* propagules on the ground

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	141429.020	50	2828.580	2.414	.001
Intercept	149904.024	1	149904.024	127.918	.000
YEAR2	24768.375	1	24768.375	21.136	.000
LOCATION	3535.801	2	1767.900	1.509	.231
DATE	73182.502	8	9147.813	7.806	.000
YEAR2 * LOCATION	1600.750	2	800.375	.683	.510
YEAR2 * DATE	14676.792	7	2096.685	1.789	.110
LOCATION * DATE	8013.491	16	500.843	.427	.968
YEAR2 * LOCATION * DATE	10183.583	14	727.399	.621	.835
Error	59765.500	51	1171.873		
Total	351615.000	102			
Corrected Total	201194.520	101			

a R Squared = .703 (Adjusted R Squared = .412)

2.2 Effect of Location, season and year on levels of infestation. Section 4.3.6

Tests of Between-Subjects Effects
Dependent Variable: NPINFEST

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Intercept	35.997	1	35.997	33.271	.001
	7.584	7.010	1.082		
YEAR2	.696	2	.348	2.512	.120
YEAR2	.696	2	.348	2.512	.120
	1.806	13.032	.139		
	1.806	13.032	.139		
LOCATION	3.175	2	1.587	20.386	.000
LOCATION	3.175	2	1.587	20.386	.000
	1.106	14.201	7.787E-02		
	1.106	14.201	7.787E-02		
DATE	7.630	7	1.090	7.600	.003
DATE	7.630	7	1.090	7.600	.003
	1.390	9.690	.143		
	1.390	9.690	.143		
YEAR2 * LOCATION	4.796	4	1.199	16.350	.000
YEAR2 * LOCATION	4.796	4	1.199	16.350	.000

	1.919	26.168	7.334E-02		
YEAR2 * DATE	1.805	13	.139	1.892	.081
	1.913	26.066	7.339E-02		
LOCATION * DATE	1.092	14	7.800E-02	1.063	.430
	1.911	26.032	7.341E-02		
YEAR2 * LOCATION * DATE	1.909	26	7.342E-02	1.357	.159
	3.680	68	5.411E-02		

2.2.1 Regression Analysis for proportion of propagules infested against time spent on the ground, for three locations

Airport mangroves

SUMMARY OUTPUT

Regression Statistics	
Multiple R	0.85248
R Square	0.726723
Adjusted R Square	0.719132
Standard Error	0.173844
Observations	38

ANOVA

	df	*SS*	*MS*	*F*	*Significance F*
Regression	1	2.8932	2.893	95.73435	1.11E-11
Residual	36	1.08797	0.030		
Total	37	3.98121			

	Coefficients	*Standard Error*	*t Stat*	*P-value*	*Lower 95%*	*Upper 95%*
Intercept	0.020556	0.0515	0.398	0.692279	-0.08394	0.125048
X Variable 1	0.008828	0.0009	9.784	1.11E-11	0.006998	0.010658

Barr Creek

SUMMARY OUTPUT

Regression Statistics	
Multiple R	0.917751
R Square	0.842266
Adjusted R Square	0.833965
Standard Error	0.131137
Observations	21

ANOVA

	df	*SS*	*MS*	*F*	*Significance F*
Regression	1	1.744732	1.744732	101.4563	4.68E-09
Residual	19	0.326741	0.017197		
Total	20	2.071472			

	Coefficients	*Standard Error*	*t Stat*	*P-value*	*Lower 95%*	*Upper 95%*
Intercept	0.137854	0.051344	2.684	0.014659	0.030389	0.245319
X Variable 1	0.010522	0.001045	10.07	4.68E-09	0.008336	0.012708

Richters Creek

Regression Statistics	
Multiple R	0.900317
R Square	0.810571
Adjusted R Square	0.803555
Standard Error	0.16576
Observations	29

ANOVA

	df	*SS*	*MS*	*F*	*Significance F*
Regression	1	3.17446	3.17446	115.5338	2.95E-11
Residual	27	0.741865	0.027476		
Total	28	3.916325			

	Coefficients	*Standard Error*	*t Stat*	*P-value*	*Lower 95%*	*Upper 95%*
Intercept	0.048641	0.054595	0.890949	0.380827	-0.06338	0.160661
X Variable 1	0.012674	0.001179	10.74866	2.95E-11	0.010254	0.015093

2.2.2 Regression analysis for individual cohorts at Richters Creek

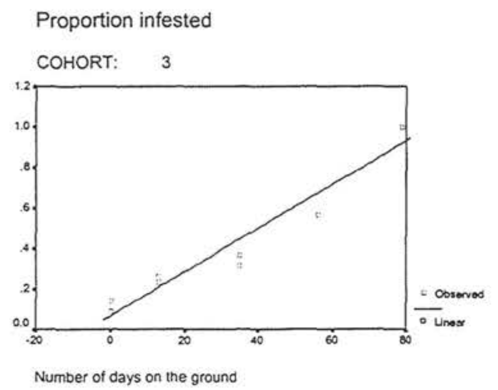
The slopes and intercepts of these regression lines were used in the to pool cohorts (not significantly different) and keep locations separate (significantly different, see analysis end of this section)

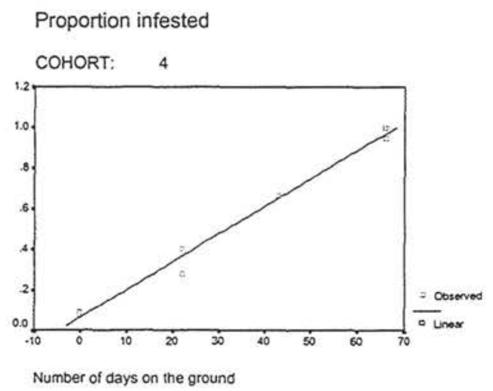
COHORT: 3

Independent: DAYS

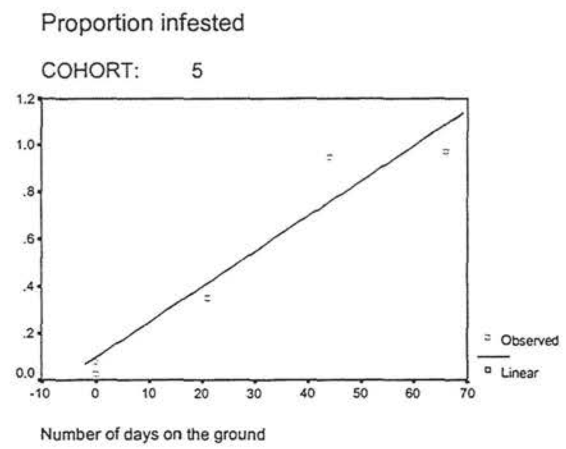
Cohort	Dependent	Mth	Rsq	d.f.	F	Sigf	b0	b1
3	INFEST	LIN	.941	7	112.07	.000	.0694	.0108
4	INFEST	LIN	.988	5	417.68	.000	.0627	.0138
5	INFEST	LIN	.908	5	49.47	.001	.950	.0151
6	INFEST	LIN	.972	4	139.02	.000	.2096	.0183

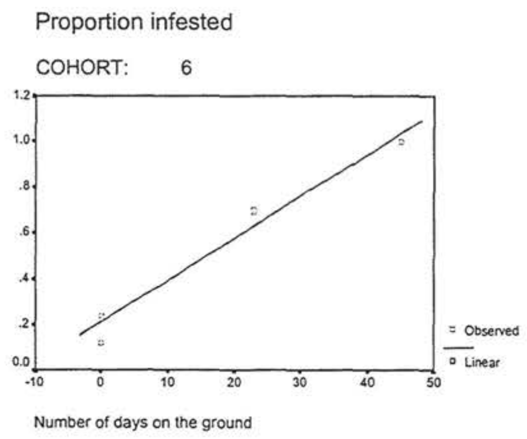
Richters Creek





Richters Creek

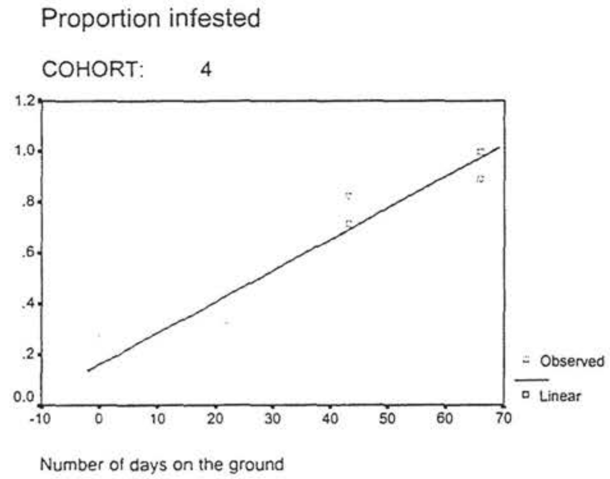


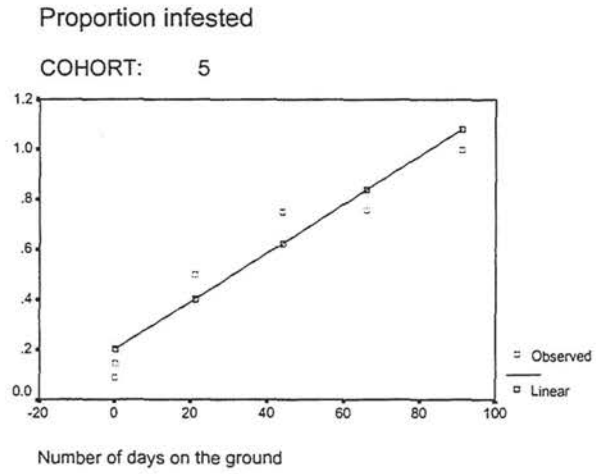


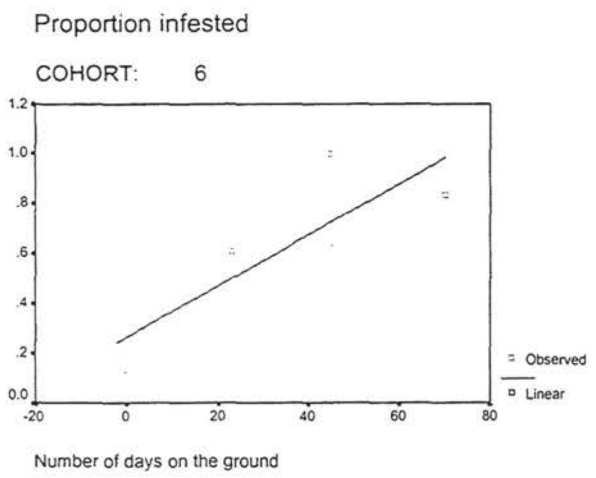
2.2.3 Regression analysis for individual cohorts at Barr Creek

Cohort	Dependent	Mth	Rsq	d.f.	F	Sigf	b0	b1
4	INFEST	LIN	.915	5	53.72	.001	.1586	.0124
5	INFEST	LIN	.906	6	57.55	.000	.2001	.0097
6	INFEST	LIN	.742	4	11.49	028	.2634	.0103

Barr Creek



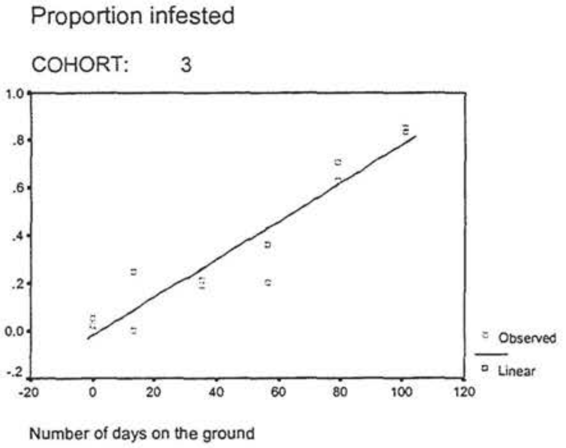


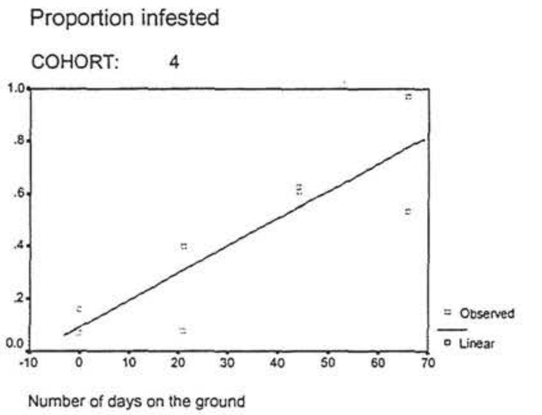


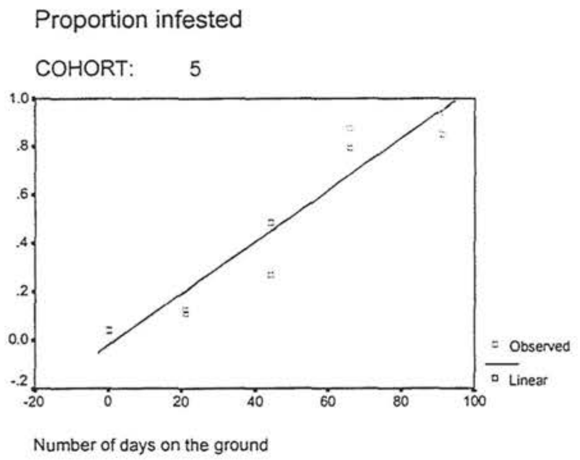
2.2.4 Regression analysis for individual cohorts at Airport

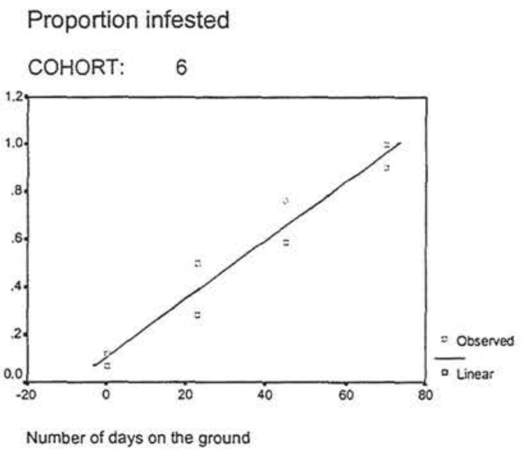
Cohort	Dependent	Mth	Rsq	d.f.	F	Sigf	b0	b1
3	INFEST	LIN	.888	10	79.58	.000	-.0194	.0080
4	INFEST	LIN	.753	6	18.30	.005	.0895	.0104
5	INFEST	LIN	.910	8	81.28	.000	-.0219	.0107
6	INFEST	LIN	.946	6	105.11	.000	.1042	.0123

Airport









2.3 *Analysis of slopes and coefficients to justify pooling of cohorts, locations kept separate.*

Regression coefficients-ANOVA

	Airport	Barr	Richters
1	0.01	0.0108	0.008
2	0.0124	0.0138	0.0104
3	0.0097	0.0151	0.0107
4	0.0103	0.0183	0.0123

Each figure represents the coefficient of x (slope) for the regression line.
each regression line calculated using date and infestation data for cohort from 2 sites at each location.

Anova: Two-Factor Without Replication

SUMMARY	*Count*	*Sum*	*Average*	*Variance*
Row 1	3	0.0288	0.0096	2.08E-06
Row 2	3	0.0366	0.0122	2.92E-06
Row 3	3	0.0355	0.011833	8.25E-06
Row 4	3	0.0409	0.013633	1.73E-05
Column 1	4	0.058	0.0145	9.66E-06
Column 2	4	0.0424	0.0106	1.5E-06
Column 3	4	0.0414	0.01035	3.15E-06

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Rows	2.51E-05	3	8.36E-06	2.810982	0.130162	4.757055
Columns	4.33E-05	2	2.17E-05	7.283153	0.02483	5.143249
Error	1.78E-05	6	2.97E-06			
Total	8.63E-05	11				

ANOVA, value of intercept of regression lines.
Values taken from previous tables were;-

Cohort	Airport	Barr	Richters
1	-0.0194	0.1789	0.0694
2	0.0895	0.1586	0.0627
3	-0.0219	0.2001	0.95
4	0.1042	0.2634	0.2096

Each figure represents the value of the intercept on the y axis of the regression line (mean of 2 sites at each location, three locations, 4 cohorts).

Anova: Two-Factor Without Replication

SUMMARY	*Count*	*Sum*	*Average*	*Variance*
Row 1	3	0.2289	0.0763	0.009866
Row 2	3	0.3108	0.1036	0.002448
Row 3	3	1.1282	0.376067	0.259371
Row 4	3	0.5772	0.1924	0.006558
Column 1	4	1.2917	0.322925	0.179353
Column 2	4	0.801	0.20025	0.002059
Column 3	4	0.1524	0.0381	0.004639

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Rows	0.164956	3	0.054985	0.83905	0.520062	4.757055
Columns	0.163289	2	0.081645	1.245858	0.35275	5.143249
Error	0.393197	6	0.065533			
Total	0.721443	11				

3 Appendix 3 Statistical tables for analyses reported in Chapter 5

3.1 *Correlation of proportion of propagules infested in April, with survival of seedlings to October (Figure 5.2)*

Regression Statistics	
Multiple R	0.805146
R Square	0.64826
Adjusted R Square	0.626277
Standard Error	0.96852
Observations	18

ANOVA

	df	*SS*	*MS*	*F*	*Significance F*
Regression	1	27.66085	27.66085	29.48819	5.55E-05
Residual	16	15.0085	0.938031		
Total	17	42.66934			

	Coefficients	*Standard Error*	*t Stat*	*P-value*	*Lower 95%*	*Upper 95%*
Intercept	3.939115	0.40603	9.701547	4.18E-08	3.078371	4.799859
X Variable 1	-4.62265	0.851269	-5.4303	5.55E-05	-6.42726	-2.81804

3.2 *Analysis of variance, Proportion of newly recruited seedlings infested (5 survey dates) compared to proportion of established seedlings infested on same dates (three sites only with surviving seedlings).*

Anova: Single Factor

SUMMARY

Groups	*Count*	*Sum*	*Average*	*Variance*
Column 1	5	4.32939879	0.86588	0.089044
Column 2	5	0.60297783	0.120596	0.000335

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	1.388621314	1	1.388621	31.0726	0.000526	5.317645

Within Groups	0.357516664	8	0.04469
Total	1.746137978	9	

3.3 *Analysis of variance, survival of seedlings grown from infested and clear propagules, after 8 months.*

Tests of Between-Subjects Effects
Dependent Variable: Survival to 8 months

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	7.200	1	7.200	9.391	.007
Intercept	45.000	1	45.000	58.696	.000
STATE	7.200	1	7.200	9.391	.007
Error	13.800	18	.767		
Total	66.000	20			
Corrected Total	21.000	19			

a R Squared = .343 (Adjusted R Squared = .306)

3.4 *Analysis of Variance, recruitment of seedlings from infested and clear propagules*

Tests of Between-Subjects Effects
Dependent Variable: RECRUIT

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	.450	1	.450	1.976	.177
Intercept	8.450	1	8.450	37.098	.000
STATE	.450	1	.450	1.976	.177
Error	4.100	18	.228		
Total	13.000	20			
Corrected Total	4.550	19			

a R Squared = .099 (Adjusted R Squared = .049)

4 Appendix 4 Statistical tables for the analysis in Chapter 6

4.1.1 Correlation of Change in Temperature in the first three minutes of immersion with diameter of propagule. Section 6.3.2

Correlations

		Diameter	Change after 3 mins
DIAMETER	Pearson Correlation	1.000	-.953
	Sig. (2- tailed)	.	.000
	N	12	12

** Correlation is significant at the 0.01 level (2- tailed)

4.1.2 Effect of temperature on survival of scolytids

Results of tests of Between –Subjects Effects. Dependant Variable: Arcsin transformed mean proportion of propagules in which scolytids survived immersion in hot water.

Source	Type III Sum of Squares	df	F	Sig.
Temperature	16.968	2	168.907	.000
Time	2.056	3	13.644	.000
Temperature*Time interaction	3.687	6	12.234	.000

4.1.3 Post Hoc analysis of survival of Scolytids in propagules immersed in hot water. Chapter 6 section 6.3.2

Multiple Comparisons – Temperature of immersion using Tukey HSD
Dependent Variable: Arcsin transformed means of survival

		Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
(I) Temperature	(J) Temperature				Lower Bound	Upper Bound
40	45	.7841	7.924E-02	.000	.5904	.9777
	50	1.4549	7.924E-02	.000	1.2612	1.6486
45	40	-.7841	7.924E-02	.000	-.9777	-.5904
	50	.6708	7.924E-02	.000	.4772	.8645
50	40	-1.4549	7.924E-02	.000	-1.6486	-1.2612
	45	-.6708	7.924E-02	.000	-.8645	-.4772

Based on observed means.
* The mean difference is significant at the .05 level.

Multiple Comparisons of Immersion time using Tukey HSD
Dependent Variable: Arcsin transformed means of survival

		Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
(I) Immersion time	(J) Immersion time				Lower Bound	Upper Bound
5	10	.3425	9.150E-02	.003	9.609E-02	.5889
	15	.4884	9.150E-02	.000	.2420	.7348
	20	.5236	9.150E-02	.000	.2772	.7700
10	5	-.3425	9.150E-02	.003	-.5889	-9.6090E-02
	15	.1459	9.150E-02	.394	-.1005	.3923
	20	.1811	9.150E-02	.215	-6.5329E-02	.4275
15	5	-.4884	9.150E-02	.000	-.7348	-.2420
	10	-.1459	9.150E-02	.394	-.3923	.1005
	20	3.520E-02	9.150E-02	.980	-.2112	.2816
20	5	-.5236	9.150E-02	.000	-.7700	-.2772
	10	-.1811	9.150E-02	.215	-.4275	6.533E-02
	15	-3.5202E-02	9.150E-02	.980	-.2816	.2112

Based on observed means.
* The mean difference is significant at the .05 level.

4.1.4 Effect of treatment on recruitment of propagules (section 6.3.3)

Tests of Between subjects effects
Dependent variable : Recruitment

Source	Type III Sum of Squares	df	Mean Square	F	Sig
Corrected Model	15.568	25	.624	3.325	.000
Intercept	93.295	1	93.295	497.177	.000
TEMP2	2.028	2	1.014	5.403	.005
TIME	1.764	3	.588	3.134	.026
STATE	5.900	1	5.900	31.440	.000
TEMP2*TIME	1.386	6	.231	1.231	.291
TEMP2*STATE	.217	2	.109	.579	.561
TIME*STATE	.189	3	6.306E-02	.336	.799
TEMP2*TIME*STATE	3.030	6	.505	2.691	.015
Error	43.722	233	.188		
Total	167.000	259			
Corrected Total	59.320	258			

4.1.5 Comparison of effect of treatment on recruitment of infested and clear propagules, section 6.3.3

Tests of Between-Subjects Effects
Dependent Variable: Recruitment State 0= Clear of infestation. 1= Still infested

STATE	Source	Type III Sum of Squares	df	Mean Square	F	Sig.
0	Corrected model	1.892	12	.158	1.008	.446
	Intercept	73.270	1	73.270	468.450	.000
	TEMP2	.467	2	.233	1.492	.229
	TIME	.958	3	.319	2.042	.112
	TEMP2*TIME	.467	6	7.778E-02	.497	.809
	Error	18.300	117	.156		
	Total	105.000	130			
	Corrected Total	20.192	129			
1	Corrected model	6.779	12	.565	2.578	.005
	Intercept	26.061	1	26.061	118.914	.000
	TEMP2	1.767	2	.884	4.032	.020
	TIME	.990	3	.330	1.506	.217
	TEMP2*TIME	3.922	6	.654	2.983	.010
	Error	25.422	116	.219		
	Total	62.000	129			
	Corrected Total	32.202	128			

4.1.6 Re-allocation of propagules on basis of survival of scolytids within the propagule following treatment in different temperature*time combinations.

Each infested propagule was paired with a clear propagule which had received the identical treatment and was then allocated to the same group.

Temperature	**Time**	**No. still infested after treatment/20**	**No. allocated to Group X**	**No. allocated to group Y**
40	5	20	0	20
40	10	18	2	18
40	15	18	2	18
40	20	20	0	20
45	5	20	0	20
45	10	11	9	11
45	15	4	16	4
45	20	0	20	0
50	5	0	20	0
50	10	0	20	0
50	15	0	20	0
50	20	0	20	0
Control (infested)	0	20	0	20
Totals			**129**	**131**

4.1.7 Analysis of Variance of survival and growth of propagules after 8 months in the field following immersion in hot water at different Temperature*Time combinations .

Seedlings which did not survive have shoot length equal to 0.

Multivariate Tests- Repeated measures of length of shoot on seedlings over a period of 8 months.

Effect		Value	F	Hypothesis df	Error df	Sig
TIME9	Pillai's Trace	.949	133.840	8	57	.000
	Wilks' Lamda	.051	133.840	8	57	.000
	Hotelling's Trace	18.785	133.840	8	57	.000
	Roy's Largest Root	18.785	133.840	8	57	.000
TIME9*TEMP	Pillai's Trace	.239	.983	16	116	.480
	Wilks' Lamda	.774	.976	16	114	.487
	Hotelling's Trace	.277	.969	16	112	.495
	Roy's Largest Root	.95	1.412	8	58	.211
TIME9*TIME	Pillai's Trace	.343	.953	24	177	.531
	Wilks' Lamda	.688	.952	24	165.9	.532
	Hotelling's Trace	.410	.950	24	167	.535
	Roy's Largest Root	.257	1.894	8	59	.078
TIME9*TEMP* TIME	Pillai's Trace	.880	1.332	48	372	.077
	Wilks' Lamda	.352	1.402	48	284.5	.050
	Hotelling's Trace	1.270	1.464	48	332	.030
	Roy's Largest Root	.727	5.637	8	62	.000

a) Exact statistic
b) The statistic is an upper bound on F that yields a lower bound on the significance level
c) Design: Intercept + TEMP+TIME+TEMP*TIME Within Subjects Design: TIME9

Mauchly's Test of Sphericity

	Mauchly's W	Approx Chi -square	df	Sig	Epsilon		
Within subjects effect					Greenhouse-Geisser	Huyn-Feldt	Lower-bound
TIME9	.000	481.129	35	.000	.301	.372	.125

Tests the null hypothesis that the error covariance matrix of the orthonormalized transformed dependent variables is proportional to an identity matrix.

a) may be used to adjust the degrees of freedom for the averaged tests of significance. Corrected tests are displayed in the layers (by default) of the Tests of Within Subjects Effects table

b) Design: Intercept +TEMP+ TIME+TEMP*TIME within Subjects Design: TIME9

Tests of Within –Subjects Effects.

Source		Type III Sum of Squares	df	F	Sig.
TIME9	Sphericity Assumed	2293.849	8	513.409	.000
	Greenhouse-Geisser	2293.849	2.409	513.409	.000
	Huyn-Feldt	2293.849	2.980	513.409	.000
	Lower-Bound	2293.849	1.000	513.409	.000
TIME9*TEMP	Sphericity Assumed	116.662	16	1.306	.188
	Greenhouse-Geisser	116.662	4.819	1.306	.266
	Huyn-Feldt	116.662	5.959	1.306	.257
	Lower-Bound	116.662	2.000	1.306	.278
TIME9*TIME	Sphericity Assumed	83.263	24	.621	.920
	Greenhouse-Geisser	83.263	7.228	.621	.743
	Huyn-Feldt	83.263	8.939	.621	.777
	Lower-Bound	83.263	3.000	.621	.604
TIME9*TEMP *TIME	Sphericity Assumed	552.988	48	2.063	.000
	Greenhouse-Geisser	552.988	14.456	2.063	.016
	Huyn-Feldt	552.988	17.878	2.063	.009
	Lower-Bound	552.988	6	2.063	.070
Error (TIME9)	Sphericity Assumed	2859.484	512		
	Greenhouse-Geisser	2859.484	154.201		
	Huyn-Feldt	2859.484	190.702		
	Lower-Bound	2859.484	64		

4.1.8 Regression statistics for levels of recruitment at 50 Celsius with time – Chapter6.3.4

Model Summary

Model	R	R Square	Adjusted R Square	Std . Error of the Estimate
1	.659	.434	.393	.279946

ANOVA

Model		Sum of Squares	df	Mean Square	F	Sig.
1	Regression	.836	1	.836	10.663	.006
	Residual	1.090	14	7.837E-02		
	Total	1.926	15			

Coefficients

		Unstandardised Coefficients		Standardised Coefficients	t	Sig.
Model		B	Std Error	Beta		
1	(Constant)	1.442	.121		11.960	.000
	TIME	-1.445E-02	.004	-.659	-3.265	.006

a) Dependent Variable TRANRAT = arcsine transformed ratio of propagules which recruited following treatment in hot water.

4.1.9 Analysis of Factors affecting temperatures experienced by R. stylosa propagules in the field, section 6.3.7

Multivariate Tests- Source file Sunprops99, Factor1 = time of day

Effect		Value	F	Hypothesis df	Error df	Sig.
FACTOR1	Pillai's Trace	.829	10.924	8	18	.000
	Wilks' Lamda	.171	10.924	8	18	.000
	Hotelling's Trace	4.855	10.924	8	18	.000
	Roy's Largest Root	4.855	10.924	8	18	.000
FACTOR1* SUBSTRAT	Pillai's Trace	.681	4.804	8	18	.003
	Wilks' Lamda	.319	4.804	8	18	.003
	Hotelling's Trace	2.135	4.804	8	18	.003
	Roy's Largest Root	2.135	4.804	8	18	.003
FACTOR1* POSITION	Pillai's Trace	.588	3.212	8	18	.019
	Wilks' Lamda	.412	3.212	8	18	.019
	Hotelling's Trace	1.428	3.212	8	18	.019
	Roy's Largest Root	1.428	3.212	8	18	.019
FACTOR1* LIGHT	Pillai's Trace	.737	6.300	8	18	.001
	Wilks' Lamda	.263	6.300	8	18	.001
	Hotelling's Trace	2.800	6.300	8	18	.001
	Roy's Largest Root	2.800	6.300	8	18	.001

a) Exact statistic
b) Design: Intercept + SUBSTRAT+POS+LIGHT Within Subjects Design: FACTOR1

Mauchly's Test of Sphericity
Measure: MEASURE1

	Mauchly's W	Approx Chi-square	df	Sig.	Epsilon		
Within Subjects Effect					Greenhouse -Geisser	Huyn-Feldt	Lower-bound
FACTOR 1	.000	178.380	35	.000	.323	.407	.125

Tests the null hypothesis that the error covariance matrix of the orthonormalized transformed dependent variables is proportional to an identity matrix.

a) May be used to adjust the degrees of freedom for the averaged tests of significance. Corrected tests are displayed in the layers (by default) of the Tests of Within Subjects Effects table.
b) Design: Intercept+SUBSTRAT+POSI+LIGHT Within Subjects design: FACTOR1

Tests of Within Subject Effects
Measure: MEASURE-1

Source		Type III Sum of Squares	df	Mean Square	F	Sig.
FACTOR1	Sphericity Assumed	820.194	8	102.524	18.174	.000
	Greenhouse-Geisser	820.194	2.584	317.372	18.174	.000
	Huyn-Feldt	820.194	3.254	252.040	18.174	.000
	Lower-Bound	820.194	1.00	820.194	18.174	.000.000
FACTOR1* SUBSTRAT	Sphericity Assumed	443.292	8	55.412	9.823	.000
	Greenhouse-Geisser	443.292	2.584	171.531	9.823	.000
	Huyn-Feldt	443.292	3.254	136.220	9.823	.000
	Lower-Bound	443.292	1.000	443.292	9.823	.004
FACTOR1* POSI	Sphericity Assumed	103.008	8	12.876	2.282	.023
	Greenhouse-Geisser	103.008	2.584	39.859	2.282	.096
	Huyn-Feldt	103.008	3.254	31.654	2.282	.080
	Lower-Bound	103.008	1.000	103.008	2.282	.143
FACTOR1* LIGHT	Sphericity Assumed	635.115	8	81.639	14.472	.000
	Greenhouse-Geisser	635.115	2.584	252.721	14.472	.000
	Huyn-Feldt	635.115	3.254	200.697	14.472	.000
	Lower-Bound	635.115	1.000	635.115	14.472	.001
Error (FACTOR1)	Sphericity Assumed	1128.248	200	5.641		
	Greenhouse-Geisser	1128.248	64.608	17.463		
	Huyn-Feldt	1128.248	81.536	13.868		
	Lower-Bound	1128.248	25.000	45.130		

Tests of Within-Subjects Contrasts

Measure: MEASURE_1

Source	FACTOR1	Type III Sum of Squares	df	Mean Square	F	Sig.
FACTOR1	linear	66.302	1	66.302	7.288	.012
	Quadratic	564.276	1	564.276	28.758	.000
	Cubic	.953	1	.953	.403	.531
	Order 4	155.667	1	155.667	53.419	.000
	Order 5	25.129	1	25.129	3.457	.075
	Order 6	1.214	1	1.214	.493	.489
	Order 7	6.646	1	6.646	9.086	.006
	Order 8	6.334E-03	1	6.334E-03	.009	.923
FACTOR1* SUBSTRAT	linear	27.743	1	27.743	3.050	.093
	Quadratic	330.581	1	330.581	16.848	.000
	Cubic	3.094E-02	1	3.094E-02	.013	.910
	Order 4	56.174	1	56.174	19.277	.000
	Order 5	24.223	1	24.223	3.332	.080
	Order 6	.639	1	.639	.260	.615
	Order 7	3.380	1	3.380	5.235	.031
	Order 8	7.181E-02	1	7.181E-02	.107	.746
FACTOR1* POSI	linear	23.948	1	23.948	2.632	.117
	Quadratic	19.039	1	19.039	.970	.334
	Cubic	1.306	1	1.306	.552	.465
	Order 4	50.638	1	50.638	17.377	.000
	Order 5	4.991E-02	1	4.991E-02	.007	.935
	Order 6	5.466	1	5.466	2.221	.149
	Order 7	2.200	1	2.200	3.007	.095
	Order 8	.362	1	.362	.542	.469
FACTOR1*LIGHT	linear	13.966	1	13.966	1.535	.227
	Quadratic	543.758	1	543.758	27.712	.000
	Cubic	6.718	1	6.718	2.836	.104
	Order 4	54.964	1	54.964	18.682	.000
	Order 5	26.576	1	26.576	3.656	.067
	Order 6	1.91E-03	1	1.91E-03	.000	.983
	Order 7	3.773	1	3.773	5.158	.032
	Order 8	3.358	1	3.358	5.026	.034
Error (FACTOR1)		9.097	25	9.097		
	Quadratic	19.622	25	19.622		
	Cubic	2.367	25	2.367		
	Order 4	2.914	25	2.914		
	Order 5	7.269	25	7.269		
	Order 6	2.461	25	2.461		
	Order 7	.732	25	.732		
	Order 8	.668	25	.668		

Tests of Between –Subjects Effects
Measure:MEASURE _1
Transformed Variable: Average

Source	Type III Sum of Squares	df	F	Sig.
Intercept	53883.575	1	53883.575	.000
SUBSTRAT	2796.284	1	2796.284	.000
POSI	320.419	1	320.419	.097
LIGHT	7523.891	1	7523.891	.000
Error	2700.606	25	108.024	

4.1.10 Correlation of air temperature with temperature of propagules in the shade

		Air Temperature (Celsius)	Propagule temperature
Air Temperature (Celsius)	Pearson Correlation	1.000	.966
	Sig. (2 –tailed)	.	.000
	N	16	16
Propagule Temperature	Pearson Correlation	.966	1.000
	Sig. (2 –tailed)	.000	.
	N	16	16

Correlation is significant at the 0.01 level (2 –tailed)

4.1.11 Analysis of variance table for effect of light and position on survival of *C. fallax* in *R. stylosa* propagules speared into of lying in sun or shade in the mangrove.

Source of Variation	SS	df	F	P-value
Position	6.25	1	30	0.000141
Light	49	1	235.2	3.02E-09
Interaction	6.25	1	30	0.000141
Within	2.5	12		

4.1.12 Analysis of variance of effect of exposure to sunlight and shade on survival of propagules.

Source of Variation	SS	df	F	Sig.
WITHIN+RESIDUAL	90.17	79		
LIGHT	2.11	1	1.85	.178
POSITION	.02	1	.01	.904
LIGHT*POSITION	.68	1	.59	.444
Model	2.72	3	.79	.500
Total	92.89	82		