THE ROLE OF INSECT LEAF HERBIVORY ON THE MANGROVES *AVICENNIA MARINA* AND *RHIZOPHORA STYLOSA*

Thesis submitted by

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ABSTRACT

This thesis examines insect leaf herbivory and the insect herbivore community on two common mangrove species – *Avicennia marina* and *Rhizophora stylosa,* at two sites near Townsville, northern Queensland. Despite its widely recognised importance in other forested ecosystems, the role of insect herbivory in mangrove ecosystems is often downplayed and remains relatively unexplored. It is generally considered that mangroves lack a diverse and specialised insect herbivore fauna, and are populated with insects from adjoining habitats. It is also commonly believed that mangrove leaves are less palatable and nutritious than leaves of other tree species, and that herbivory levels are less than those found in other forest ecosystems.

Sixty-one insect species were confirmed feeding upon *A. marina* and *R. stylosa* at the study sites, more than doubling the number of published host records for Australian mangroves. Herbivore diversity on the two mangrove species was similar, but only four of the 61 herbivore species were in common between them and the composition of the two faunas was substantially different. The two faunas show a high degree of host-specificity and adaptation to their mangrove hosts and there were substantial similarities between the faunas found in this study and those of other *Avicennia* and *Rhizophora* species elsewhere in the world. The diversity of folivores on these two mangrove species was similar to that of other nearby non-mangrove trees and to that reported for other trees elsewhere in the tropics.

Nearly all mangrove herbivory studies have measured damage on discrete leaf samples collected at one point in time. This approach fails to detect entirely consumed leaves, or partly damaged leaves that have been abscised. These leaves can be accounted for by an alternative long-term method that makes repeated herbivory estimates on tagged leaves. Application of the long-term method in this study found herbivory to be 3-6 times higher than estimated by discrete measurements. *R. stylosa* had only 2-3% loss of leaf area in discrete samples but 7-13% loss in the long-term study. *A. marina* had 6-7% loss of leaf area in discrete samples but 28-36% loss in the long-term study. For both species, most herbivory occurred whilst the leaves were young. Once past the juvenile phase, *R. stylosa* leaves were rarely attacked. In contrast, mature *A. marina* leaves suffered significant insect damage and leaf loss. Herbivory reduced average leaf longevity of all leaves by 4-5% for *R. stylosa* and 12-13% for *A. marina*.

In mangroves, loss of entire leaves is reported to be rare, but in *R. stylosa* and *A. marina* in this study, 4-5% and 19-29% of leaves, respectively, were either entirely consumed, or aborted due to insect damage. For both species, loss of leaf material through premature abscission of damaged leaves was as great as that actually consumed by insects, indicating a role for herbivory in promoting leaf fall.

Destruction of developing leaf buds by insects resulted in greater leaf losses than that suffered by emerged leaves. This was especially important for *R. stylosa,* which can only produce leaves from the apical bud. Damage to *R. stylosa* apical buds was common, frequently resulting in the loss of leaves before they emerged or, where damage resulted in the destruction of the apical bud, cessation of leaf production and death of that shoot. In some cases, new apical buds regenerated from suppressed lateral buds immediately below the destroyed apical bud. Death of existing shoots and regeneration from suppressed laterals are potentially major sources of architectural change to tree growth form. Damage to apical buds also resulted in the loss of developing inflorescences and lateral branches.

The chemical and physical nature of leaves changed significantly as they aged. Young leaves had a higher nutrient and chlorophyll concentration, but lower leaf thickness and leaf mass per unit area. Thus they were more nutritious and less tough for herbivores. These young leaves were especially prone to premature leaf fall because of insect damage. Leaves re-translocated over half of their nutrients prior to senescence but consumption or premature abscission of leaves before this process is complete may increase nutrient loss from the trees to microbial and detrital food chains on the forest floor. Thus herbivore-mediated leaf fall may also impact upon nutrient dynamics in mangrove forests.

This thesis demonstrates that: mangroves support a diverse and distinctive insect herbivore community; leaf herbivory is much higher than previously reported; there are additional mechanisms (eg, apical bud damage) by which herbivores affect leaf loss and other aspects of tree performance; and insects significantly affect leaf longevity, the timing of leaf fall and the quality of leaf litter. These results indicate that the role of herbivorous insects in mangrove ecosystems is more important than previously thought and that its evaluation needs to go well beyond simple static measures of leaf area missing from mature leaves.

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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.

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CHAPTER 1 - INTRODUCTION

1.1 Introduction

Herbivorous insects are widely accepted as playing a significant role in the ecology of forest ecosystems, especially in the tropics. Nonetheless, despite being a tropical forest habitat dominated by medium-sized trees, the role of herbivorous insects in the ecology of mangrove ecosystems has been little studied. Studies examining insect herbivory in mangroves have focused more on herbivory levels on leaves than on the role of insect herbivores in the ecology of mangroves, chiefly because insect herbivory is not thought to play a significant role. This thesis addresses this issue by exploring insect herbivore diversity in mangroves, re-evaluating insect herbivory levels by using alternative methods of assessment, and examining some other mechanisms by which insect herbivores influence the ecology of mangrove trees.

1.2 Mangrove Ecosystems

Mangroves occur in tropical and subtropical latitudes along coastal intertidal areas. Seventy plant species are recognised as mangroves (Duke *et al.* 1998a), although other species may occasionally occur there. Mangroves are distinguishable for a variety of reasons, most notably their adaptations to living in an intertidal environment. One of the main features of mangrove ecosystems is their general floristic simplicity. The total number of species occurring in any given mangrove stand is small compared to other tropical forests, and many mangrove forests are dominated by *Avicennia* spp. (the only genus in the family Avicenniaceae) or various members of the Rhizophoraceae. Most mangrove forests consist of tree species occurring in monocultural stands, or mixtures of a few tree species. Very rarely are there any understorey plants and even the canopy of existing trees has limited vertical stratification. This further simplifies the structural and floristic diversity of mangrove ecosystems. Of additional importance for herbivorous insects is the regular tidal inundation of most mangroves. This has implications for insects living in the lower canopy which may be inundated at high tide, movement of non-flying insects (mostly larvae) between trees, and for species that pupate in the soil. The saline mangrove environment probably has limitations for insects but there is little specific evidence for this. Interestingly, Murphy (1990) records observations of several insect species that live in the intertidal zone of Singapore mangroves and Lever (1952) records a mangrove caterpillar as surviving immersion in tidal water for four and half hours.

Mangrove plant species have specialised adaptations to living in intertidal areas (eg, mechanisms for excluding, translocating and excreting salts) and most mangrove species do not occur in other habitats. Because of their tidal influence, mangrove systems are usually considered to be marine. However, they are defined by, and dominated by, trees that are essentially terrestrial, but which have adapted to tidal inundation. Thus, many similarities between mangrove forests and other types of tropical forests can be expected, especially in relation to the canopy. Despite this, many conceptual and methodological developments in terrestrial forest entomology have not been widely adopted in studies of mangrove forests.

1.3 Importance of Herbivory in Forest Ecosystems

In virtually all forest ecosystems, herbivorous insects have a significant impact on tree growth, form, survivorship, reproductive output and forest ecology (Schowalter *et al.* 1986, Crawley 1989). In a review of herbivory in tropical savannas, Andersen and Lonsdale (1990, p.438) suggest that insect folivores are “..almost universally more important than mammalian folivores” and that insect herbivores are at least as important as vertebrate herbivores in African grassland savannas and more important in Australian savannas. Janzen (1988) claims that caterpillars alone consume more living leaves in tropical forests than all other animals combined. Insects have even been shown to affect the growth of very large (up to 100m tall) trees (Mazanec 1967, 1968). Such effects are usually associated with occasional large outbreaks of particular herbivorous species, but

Morrow and LaMarche (1978) showed that even continual low-levels of damage reduces growth of large subalpine eucalypt trees.

1.4 Status of Herbivory in Mangrove Ecosystems

Despite the important role of herbivory in other forest ecosystems, the role of herbivorous insects in mangroves is commonly considered to be minimal (Heald 1971, Odum and Heald 1975a, Huffaker *et al.* 1984, Tomlinson 1986, Robertson and Duke 1987, Lee 1991, Robertson 1991, Robertson *et al.* 1992). Mangrove researchers have often emphasised the marine, rather than the terrestrial, aspects of mangrove ecosystems, thus overlooking the potential role of herbivorous insects. Central to the notion that insect herbivores are relatively unimportant in mangroves is the perception that the diversity and degree of specialisation of mangrove insects, is less than in other forest ecosystems. However, no studies have addressed the comparative diversity of insect herbivores in mangroves and adjacent habitats.

Given the lack of emphasis on detailed insect research in mangroves, it is perhaps ironic that mangroves are popularly thought to be insect-infested swamps, though this is based on their reputation as habitat for mosquitos and sandflies, not herbivorous insects. Major texts and reviews on the ecology of most forest ecosystems often have entire chapters (eg, Coley 1982, Landsberg and Cork 1997), even entire books, devoted to the role of insect herbivory in the ecology of these systems. In contrast, mangrove texts make little reference to herbivorous insects. In their 388-page textbook, Hutchings and Saenger (1987) were only able to devote one page to herbivorous insects (plus seven to mosquito’s, sandflies and ants), with no reference to the ecological role or function of insects. Even more recently, thorough reviews such as Kathiresan and Bingham (2001) include only a few pages on herbivorous insects with some minor references to ecological function. This does not reflect any bias by the authors but rather the lack of available information on the role of insect herbivory in mangroves. Some authors have been very explicit in downplaying the potential role of insects; for example, in a seminal mangrove text, Tomlinson (1986) suggested that co-evolutionary processes that lead to close animal-plant interactions do not occur in mangroves.

It is also a commonly held belief that mangroves are depauperate in insects and the herbivory level on mangrove leaves is low, because the leaves are so high in anti-herbivore compounds, such as tannins, that they are largely inedible by insects (Janzen 1974, Huffaker *et al.* 1984). Other mechanisms such as the high salinities encountered in mangroves (de Lacerda *et al.* 1986) and the supposedly low nutrititive value of mangrove leaves (Robertson and Duke 1987), have also been suggested to limit diversity and specialisation of insect herbivores in mangroves. Several researchers have suggested that mangroves do not support a distinct insect fauna and that many of the insects found in mangroves come from adjoining terrestrial vegetation (Chapman 1976, Berjak *et al.* 1977, Veenakumari *et al.* 1997, Kathiresan and Bingham 2001).

Mangrove ecosystems are not the only vegetation type where insect herbivores have been thought to be of minor importance. Other plant groups such as ferns and saltmarshes have also previously been considered to have a depauperate insect fauna and to suffer less insect damage than other plant types. Early workers described the resistance of ferns to insect attack and some suggested that because ferns are an ancient plant group that evolved before insects, and that as the major insect radiation occurred in concert with the radiation of the angiosperms, they had less diverse insect faunas (these arguments are reviewed in Hendrix 1980). Although Hendrix (1980) demonstrated that the under-utilisation of ferns by insect herbivores was real, this could be attributed to a number of factors, principally the simplistic architecture of ferns which reduces the number of niches available for insects to exploit. On the basis of the plant architecture hypothesis, Auerbach and Hendrix (1980) suggested that fern and angiosperm plant parts of similar structure should support equally diverse insect faunas, and they demonstrated this with a comparison of leaf-feeding Lepidoptera on ferns and herbaceous angiosperms. Geographic range is also important with the one fern that has been extensively studied – bracken, *Pteridium aquilinum* – being shown to have as diverse a fauna as angiosperms with a similar geographic range in Great Britain (Lawton 1976, Strong and Levin 1979).

Balick *et al.* (1978) and Hendrix and Marquis (1983) have further demonstrated that the level of herbivore damage on ferns is similar to that on angiosperms.

Saltmarsh grasses have also popularly been thought to have low herbivory and limited energy transferred through the grazing pathway (Smalley 1960, Marples 1966). However, more recent research has shown that insect herbivores can regulate saltmarsh growth, reproduction and standing biomass (Bertness *et al.* 1987, Daehler and Strong 1994, Silliman and Zieman 2001). Similarly, the role played by herbivorous insects in grasslands worldwide and termites in savanna areas was not well recognised until in-depth research was conducted (see Andersen and Lonsdale 1990 for a review). In contrast, the role of herbivory can also be overstated in some cases. It has been suggested that Australian eucalypts have unusually high levels of insect herbivory (Fox and Morrow 1983, 1986) but a review of the evidence suggests this is not the case (Ohmart 1984, Landsberg and Ohmart 1989). Thus popularly accepted and seemingly well-established paradigms about the role and importance of herbivorous insects are sometimes shown to be incorrect when appropriate research is done.

Research into plant-animal interactions in mangrove forests (principally leaf-eating crabs) has revealed that they play a major role in population, community and ecosystem-level processes (reviewed in Robertson 1991, Robertson *et al.* 1992). However, prior to the research on crab-plant relationships, the importance of this pathway was also underrated. The arguments for downplaying the role of herbivorous insects in mangrove ecosystems are based on limited observation or investigation and, as was the case for leaf-eating crabs, appropriate research should evaluate the actual role they play.

1.5 Studies of Herbivory Level in Mangroves

Several studies have examined herbivory levels in mangroves (reviewed in Chapter 4) with most concluding that it is low. Heald (1971) appears to have been the first to popularise the notion that insect herbivory was relatively unimportant in mangroves, though his conclusion was only based on a single sample of 50 leaves. Later, in two influential papers, Roberston and Duke (1987) stated that insect herbivory in mangroves is less than that found in other forest ecosystems and Robertson *et al*. (1992) concluded that insect herbivory was of minor importance in mangrove carbon budgets, although they considered their effects on seedlings were likely to be significant. These conclusions, and similar views expressed by other authors (eg, Kathiresan and Bingham 2001), were based on the analysis of discrete herbivory studies whose merits are assessed in this thesis. In addition, the impacts of herbivory on 'greenfall' of pre-senescent leaves (see Lee 1990, Murphy 1990), destruction and suppression of new leaf production, and modification of the quality of leaves and timing of leaf fall, may also have important effects that are as yet either not quantified or unreported in mangrove forests. The inclusion of such factors, and more appropriate methods of estimating herbivory, may alter current views on the role played by insect herbivores in mangroves.

Numerous instances of major outbreaks of insect herbivores in mangrove canopies are known (eg, Kalshoven 1953, Chaiglom 1975, Piyakarnchana 1981, Intari 1984, West and Thorogood 1985, Whitten and Damanik 1986, McKillup and McKillup 1997) though most are treated as curiosities and are usually only reported anecdotally. Three exceptions are from Ecuador (Gara 1990), Hong Kong (Anderson and Lee 1995) and Gladstone, Queensland (Duke 2002), with the latter two including detailed studies of defoliation 'events' that lasted several years. Duke (2002) proposed that such events be considered as a potentially important ecological process and studied in more detail. Apart from these events, herbivory is generally considered to be of relatively little importance in mangroves, though a few recent papers have begun to demonstrate the potential diversity and importance of insect herbivores (eg, Murphy 1990, Feller 1995, Feller and Mathis 1997, Elster *et al.* 1999).

1.6 Measuring Herbivory

Quantification of leaf material lost to insect herbivores is probably the most common type of study of insect-plant interactions. In the mangrove literature, the majority of such studies have relied on measurement of leaf area from discrete samples of leaves collected at one point in time. This method has been applied frequently and involves taking a sample of leaves and measuring the amount of leaf area missing or damaged by insects. For most tree species studied, this method usually provides estimates ranging from 3-10% of leaf area missing (Landsberg and Ohmart 1989). It is a rapid and cheap technique that allows for comparison between samples. However, it may underestimate the true level of herbivory because it does not account for leaves that are entirely consumed or that are prematurely abscised from the tree because of excessive herbivore damage. Most discrete studies have deliberately sampled older leaves on the basis that they have had a longer time to accumulate a greater level of herbivory and are believed to represent herbivory over the lifespan of the leaf. This assumes that damaged leaves are not prematurely abscised, a notion tested in Chapters 4 and 5.

An alternative method involves tagging newly emerged leaves and repeatedly assessing them over a long time period in order to account for leaves that are prematurely lost or entirely eaten. This long-term method involves a considerable increase in sampling effort and complexity and has rarely been undertaken. In most cases where the long-term method has been compared to the discrete method, the former has produced substantially higher herbivory estimates (see Chapter 4).

1.7 Types of Herbivore Damage

In general, the study of insect-plant relationships in mangrove ecosystems is in its infancy and, thus far, has not taken on-board many of the concepts developed from other tropical forests. This is especially so in considering the variety of mechanisms through which insect herbivores act upon plants and influence ecosystems. In addition to consumption of expanded leaf area – the most commonly studied form of herbivory – leaves may be damaged by grazing of the lamina surface, sap-feeding causing necrosis, gall-formation, leaf-mining, leaf deformation and stunting. Most herbivory studies (in mangroves and other ecosystems) have only examined leaf area missing. In the mangrove literature, only one paper (Farnsworth and Ellison 1991) that assessed loss of leaf area also accounted for leaf mines and necrotic damage due to sap-feeding and none has accounted for gall formation.

In addition to direct damage to leaves, herbivores also cause loss of leaves through indirect means such as destruction of growing tips and branches. As in all forests, there are many species of wood-boring insects that tunnel longitudinally downwards through live mangrove branches, resulting in the death of all leaves proximal to the site of tunnelling. This type of damage is destructive, though patchy in its distribution, and can account for a significant proportion of lost leaf area. Feller and Mathis (1997) found that the leaf area lost to wood-boring insects was equal to or greater than that lost by direct consumption of leaf material by leaf-feeding insects. Even more significant might be the impact that destruction of the branch and its apical meristem has on restricting future leaf production. Destruction of growing tips, where new leaves are being produced, often goes unnoticed but can be a major source of mortality of young, developing leaves. Only Onuf *et al.* (1977) and Feller (1995) have examined this form of damage, with both concluding it to be a dominant form of herbivory on the mangrove *R. mangle* in Florida.

Thus, leaf area losses to insects may be underestimated because of both methodological considerations and the failure to include other mechanisms of herbivore damage. Moreover, loss of leaf material through other mechanisms that have rarely been examined (eg, wood-boring and feeding on apical shoot tips) could be even more significant than that lost through these more noticeable means (eg, leaf area missing).

1.8 Aims and Organization of This Thesis

The goal of this thesis is to re-evaluate the level and importance of insect folivory in mangrove ecosystems. To do this, it was necessary to (i) evaluate true herbivory levels by comparing methods for assessing such damage; (ii) examine other means by which insect herbivores act upon leaf area production; and (iii) examine the community of insect herbivores present, their adaptations to living in mangroves and how they might influence mangrove ecology.

Specifically, the aims of this study are to:

1) assess herbivory levels on *Avicennia marina* and *Rhizophora stylosa* by comparing the discrete and long-term methods;
2) examine how herbivory and leaf quality varies with leaf age;
3) determine effects of herbivory on leaf longevity and premature leaf drop;
4) identify the dominant herbivores on *A. marina* and *R. stylosa;*
5) examine insect herbivore diversity and the natural history of insect herbivores on the mangrove *A. marina* and *R. stylosa*; and
6) identify alternative mechanisms through which herbivorous insects impact upon the ecology of mangrove trees and ecosystems.

Following this introductory chapter, Chapter 2 describes the study sites and the two mangrove tree species (*Avicennia marina* and *Rhizophora stylosa*) studied in this thesis. Chapter 3 examines the diversity and distinctiveness of the folivorous insect fauna on these two species. Chapter 4 assesses the level of leaf herbivory on these two mangrove species and compares results from discrete and long-term methods. Chapter 5 looks at the influence of herbivorous insects on leaf longevity and patterns of leaf loss. Chapter 6 looks specifically at tip and apical bud damage as an alternative mechanism by which herbivory results in significant leaf loss. Chapter 7 examines changes in the physical and chemical nature of leaves as they age, to explain differential age-based vulnerability to herbivory and to determine how premature leaf drop due to herbivory may influence the quality of leaf litter as a resource for benthic detritivores. Chapter 8 provides a general discussion of the significance of the research findings in this thesis. Appendix A provides notes on the natural history of some of the more prominent herbivores identified in this study.

CHAPTER TWO – STUDY SITES AND SPECIES

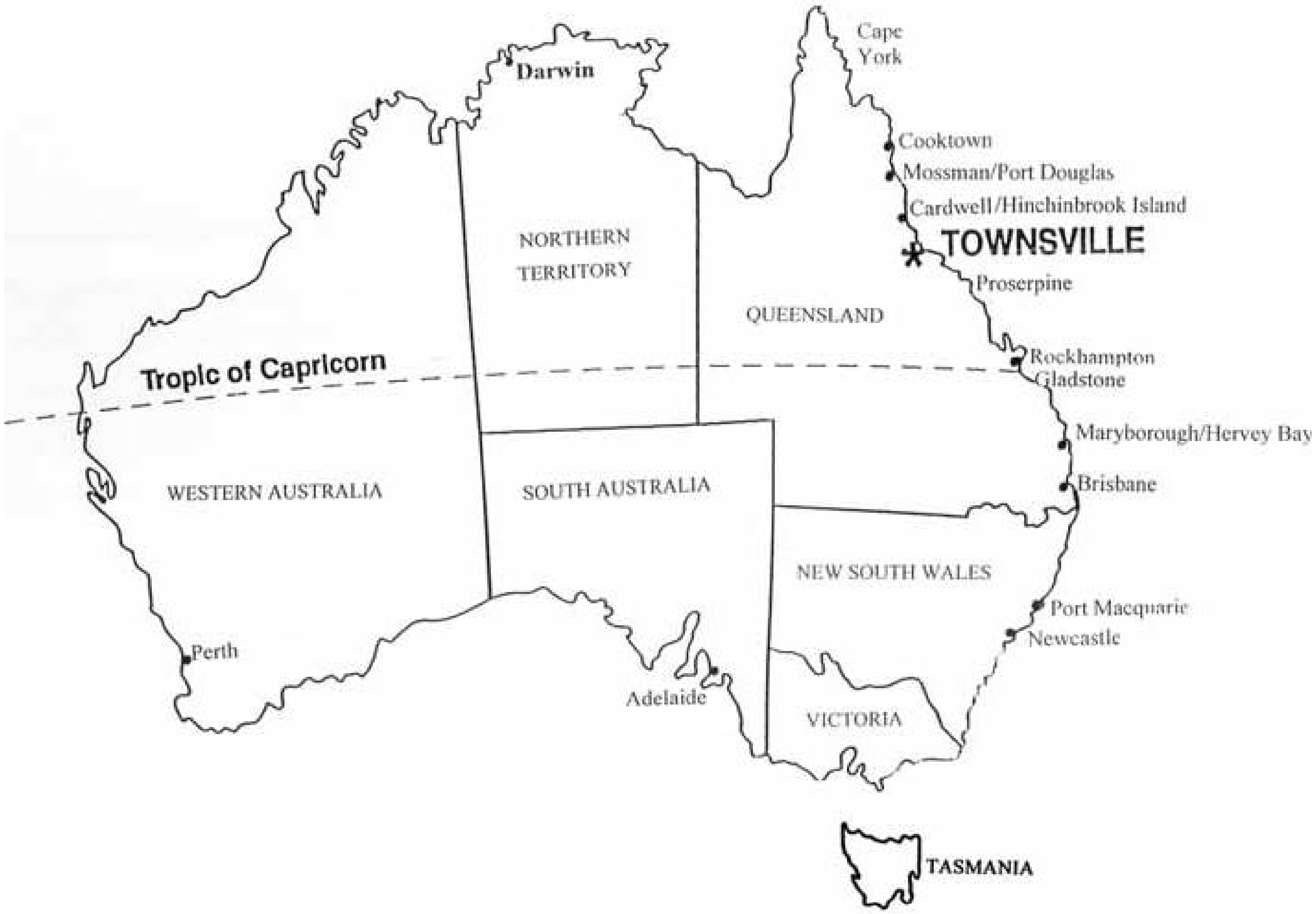
This chapter provides a general review of mangrove habitats and plant associations as well as descriptions of the study sites and general methods. More specific methods can be found within each chapter.

2.1 Mangrove Habitat

Mangrove vegetation is found in intertidal habitats around tropical and subtropical estuaries and coastlines of the world. Mangrove plant species diversity decreases with increasing latitude. Vegetative diversity is very low compared to other tropical habitats. A total of 70 plant species from 28 genera inhabit mangroves and the Australasian region is one of the most diverse in the world, with 47 species from 21 genera present (Duke *et al.* 1998a). Most mangrove plants are trees and shrubs, although a single species of a palm, three ferns and a mistletoe are also recognised as mangrove plants (Duke *et al.* 1998a). Canopy structure in mangroves is less complex than other forest types and there is often little or no understorey development (Janzen 1985, Snedaker and Lahmann 1988). Many plant lineages have adapted to living in mangrove environments with species coming from 20 plant families, of which only two occur exclusively in mangrove habitat (Duke *et al.* 1998a). Even in the Rhizophoraceae, which has the greatest number of mangrove genera and species, and is considered to be the typical mangrove group, only 4 of its 16 genera inhabit mangroves, with most of the others occurring in tropical rainforests (Duke *et al.* 1998a). Thus mangroves represent an ecological, not a genetic community with most members deriving from, and having relatives in, other habitats.

The flora which comprise mangrove forests has a wide range of specialised physiological, developmental, phenological and structural adaptations for living in intertidal environments that make this a unique association with little overlap of plant species between mangroves and adjacent communities. Compared to their low vegetative diversity, mangroves have a much greater animal diversity and most species are mangrove dependent and equally adapted to life in mangrove environments. Due to the strong demarcation between mangrove and non-mangrove habitats, and the dependence on mangrove plants to create mangrove habitat, animal

Figure 2. Map of Australia Showing Locations Mentioned in the Text



associations within mangrove communities are particularly strong. This has been investigated and established for a wide variety of animal groups such as fish, crabs, gastropods, other marine invertebrates and even birds, of which many are mangrove-dependent (Ford 1982). However, little effort has been expended on investigating the insect community of mangroves (reviewed in Chapter 3).

2.2 General Study Location

This study was carried out at two sites near Townsville along the northern coast of Queensland. At latitude 19°15’S Townsville is located in a dry tropical region of Australia (Figure 2.1). Mean annual rainfall is 1,143mm/yr with two-thirds of that falling during the summer months January-March (Bureau of Metereology 2002). During the remainder of the year, rainfall is low and evaporation is high, producing dry and hot conditions. Due to the lower rainfall and river runoff, mangrove communities around Townsville are noticeably shorter and of lower plant diversity than those further northwards in the Wet Tropics. Though many mangroves across the world are found in higher rainfall areas, their occurrence in drier climates is also quite common. The seasonally wet, but otherwise predominantly hot and dry, climatic conditions of the Townsville area, create mangrove communities that are representative of a large proportion of mangrove communities in northern Australia.

There are 12 species of mangrove commonly found around Townsville (Table 2.1), though some less common species may also be present. Most mangrove stands in the area are formed by *A. marina*, *R. stylosa* or *Ceriops tagal*, *Bruguieria gymnorrhiza*, *Aegialitis annulata* and *Aegiceras corniculatum* are also common at most sites. Extensive salt marshes and saltpans adjoin the landward margins of most mangrove stands in the area.

Table 2.1 Mangrove Species Occurring Around Townsville
(list compiled from pers. obs. and N. Duke pers. comm.)

Avicenniaceae
Avicennia marina
Combretaceae
Lumnitzera racemosa
Euphorbiaceae
Excoecaria agallocha
Melicaeae
Xylocarpus mekongensis
Myrsinaceae
Aegiceras corniculatum
Myrtaceae
Osbornia octodonta
Plumbaginaceae
Aegialitis annulata
Rhizophoraceae
Bruguiera exaristata
Bruguiera gymnorrhiza
Bruguiera parviflora
Ceriops australis
Ceriops tagal
Rhizophora apiculata
Rhizophora stylosa
Rhizophora x *lamarckii*
Sonneratiaceae
Sonneratia alba

2.2.2 Study Sites

Two study sites were selected, Gordon Creek and Saunders Beach. Gordon Creek is located on the south side of Townsville and is a tributary of Ross River, which flows through the city (Figure 2.2). It is a riverine-based mangrove system, with mangroves occurring along the banks and overflow areas of a meandering creek. Saunders Beach is a dune-based mangrove system 25 km NE of Townsville (Figure 2.3) consisting of a single block of mangroves behind the shorefront sand dune. These mangroves are flooded at high tide by an adjoining creek (Althaus Creek).

Figure 2.2 Map of Townsville and Ross River Estuary Showing Location of Gordon Creek Study Site (within square). Scale 1cm=350m

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Figure 2.3 Map Showing Location of Saunders Beach Study Site (within square), 25km NE of Townsville. Scale 1cm=250m

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Mangrove species are usually distributed in distinct zones that reflect their position along the intertidal profile. Mangrove zonation is a well-known phenomenon, usually considered to be comparable across different locations. However, recent research questions the generality of mangrove zonation, finding species distributions along intertidal profiles to be variable and unpredictable (Bunt 1996) and that other factors such as animal predation on propagules (Smith 1992), propagule dispersal (Rabinowitz 1978) and complex plant interactions (Osborne and Smith 1990) also affect the occurrence of species along the intertidal profile.

At Gordon Creek, varying bank heights along the creek means that tidal penetration into forests is more often via a complex network of shallow gullies that snake through the forest, rather than overbank flooding. This creates a complex zonation pattern that generally results in either very narrow zones or close associations of various tree species. In several locations, channels of *R. stylosa* meander through extensive fields of saltmarsh grasses (Figure 2.4). Additionally, there is a road which dissects the site (Figure 2.4). Most commonly, the creek is fringed by either *A. marina* or *R. stylosa*, although where the banks are higher, this may be *Ceriops tagal* or even saltmarshes lining the creek edge. These other associations generally occur in areas where the bank is high and few channels are present, or in some cases, through bank erosion. *A. marina* does not form monospecific zones at this locality, although it is dominant in some places and is also common among the saltmarsh (Figure 2.6). Other species such as *B. gymnorrhiza*, *X. mekongensis*, *A. annulata* and *E. agallocha* are also common at this site.

At Saunders Beach, the mangrove community behind the large foreshore sand dune (Figure 2.5) is somewhat rectangular in shape due to residential development of the leeward margins. In contrast to the Gordon Creek site, the relatively simple topography of this forest enables high tides to penetrate in an even and orderly fashion across the site. The site is dominated by a large stand of *R. stylosa*. *A. marina* occurs as isolated trees in the lee areas of the stand but is more common on beach margins at the front of the stand and as canopy emergents among *R. stylosa* (Figure 2.5). *Ceriops tagal* and *B. gymnorrhiza* are the only other species at this site in any abundance.

Figure 2.4 Images of Mangroves at the Gordon Creek Study Site

R. stylosa and *A. marina* along tidal gutter through salt marsh paddock

Abandoned road through Gordon Creek site, lined by *A. marina*

A. marina (light colour) and *R. stylosa* (dark colour) along creek bank

Figure 2.5 Images of Mangroves at the Saunders Beach Study Site

Mangroves behind foreshore sand dune, looking toward estuary

A. marina growing at sand dune/estuarine mud interface

Typical scene of *R. stylosa* with canopy emergent *A. marina*

The intention in this study is to determine, via examination of two assessment methods, whether herbivory has been underestimated, and also to investigate some alternative mechanisms through which herbivory may affect mangrove plants. It is not the intention in this study to investigate variability of herbivory between locations, across intertidal locations or within the canopy. As such, trees selected for this study were distributed across a wide variety of locations at both sites in order to obtain a general result for each mangrove forest.

2.2.3 Plant Species Studied

Avicennia marina (Forssk.) Vierh. and *Rhizophora stylosa* Griff. were chosen for study as they are the most common mangrove trees in Australia, occupy a wide variety of habitats within mangrove forests and have very large geographic ranges. Various members of *Rhizophora* and *Avicennia* are also the most common trees in many other mangrove forests around the world. This therefore increases the relevance and general applicability of the results.

Avicennia species are the most widely distributed of any mangrove (Tomlinson 1986) and also grow in a wide range of salinities and intertidal positions covering all the major tropical and subtropical coastlines in the world (Duke 1991). *Avicennia* was formerly in the family Verbenaceae, but as it has no close relatives there (Mukherjee and Chanda 1973, Tomlinson 1986), it is now recognised as the only genus in the family Avicenniaceae, and comprises a group of eight obligate-mangrove tree species (Duke 1991).

Two species of *Avicennia* occur in Australia. *A. integra* occurs only in 15 estuaries of the Northern Territory but *A. marina* occurs around most of mainland Australia, including Victoria, Adelaide and south of Perth (Duke 1991). This species also occurs from eastern Africa through the Persian Gulf, India, SE Asia, China, Japan, Philippines, western Pacific Islands and New Zealand (Duke 1991). Within Australia, three varieties are recognised (after Duke 1991): var. *australasica* (formerly known as var. *resinifera*) ranges from Rockhampton down to Adelaide and also in New Zealand and New Caledonia; var. *marina* ranging from Bunbury, south of Perth, to the southern Kimberley, is referable to the Asian and Arabian forms of *A. marina*; and the variety

Figure 2.6 *Avicennia marina* var. *eucalyptifolia* Tree Among Salt Grass at Gordon Creek

Figure 2.7 Typical Image of *Rhizophora stylosa* Trees about 3m high

found at the Townsville study sites – var. *eucalyptifolia* (previously elevated to species status eg, Moldenke 1960) – ranges across northern Australia from Mackay to the Kimberley, as well as southern New Guinea and the Solomon Islands. Zones of overlap and intergradation do occur between the three varieties (Duke 1991, Duke *et al.* 1998b).

As is typical of the genus, *Avicennia marina* has a spreading canopy (Figure 2.6). It may grow to 30m high but is generally 5-10m (Duke 1991). Smaller heights are attained under less favourable environmental conditions (eg, in cold or dry climates). Most trees around Townsville are <5m high. The leaves are greyish-green on the upper surface and a pale grey on the underside. Leaf size and shape is highly variable, reflecting regional (eg, temperature, rainfall) and local (eg, intertidal position) environmental and developmental factors (Duke 1990a). *Avicennia* spp. excrete salt from their leaves, leaving visible salt crystals on their surface. Around Townsville, *A. marina* produces new leaves and abscises old leaves, year-round but with a distinct seasonal peak of leaf production and leaf loss from March-August.

With 19 species/hybrids from four genera, the family Rhizophoraceae is the most diverse within mangrove habitats and is often referred to as the true mangrove family, even though 12 other genera within the family do not occur within mangroves (Duke *et al.* 1998a). Within the genus *Rhizophora*, there are six species and three hybrids (Duke *et al.* 1998a). Three *Rhizophora* species and one hybrid are known from Australia, with *R. stylosa* being the most common and widely distributed of these. *R. stylosa* occurs from northern New South Wales to the tip of Cape York and the Torres Strait Islands (Duke and Bunt 1979). It grows to 30m high, though most trees around Townsville are not more than 5 m high (Figure 2.7). *Rhizophora* species have large, thick, leathery leaves that are dark-green in colour. These do not excrete salt at their surface but may accumulate salt within their thick leaves. Around Townsville, *R. stylosa* produces new leaves and abscises old leaves, year-round but with a distinct seasonal peak of production from November-May.

CHAPTER 3 – FOLIVOROUS INSECT DIVERSITY AND DISTINCTIVENESS

3.1 Introduction

3.1.1 Status of Insect Herbivores in Mangroves

The studies described in this chapter evaluate the common assumptions of low insect diversity and distinctiveness in mangrove habitats (Chapman 1976, Feller and Mathis 1997, Veenakumari *et al.* 1997, Hogarth 1999, Kathiresan and Bingham 2001). Sand-flies and ants are thought of as the dominant insect groups in mangroves (Hutchings and Saenger 1987, Clay and Andersen 1996). The belief that insect herbivory is much lower in mangrove forests compared to adjacent or similar terrestrial ecosystems (Huffaker *et al.* 1984, Robertson and Duke 1987) has further fuelled the idea that faunal diversity and distinctiveness is low (Kathiresan and Bingham 2001). Tomlinson (1986) summarised the known literature as suggesting that co-evolutionary processes that give rise to close plant-animal relationships do not occur in mangroves.

The partly marine habit of mangroves might inhibit some aspects of their faunal development compared to other tropical forests. However, folivorous (leaf-feeding) canopy insects, which are the focus of this study, are not subject to tidal inundation (unless in the lower canopy) and the trees themselves provide a buffer against the marine environment by excluding and/or removing excess salt. Mangrove trees have evolved from terrestrial or freshwater species which would have had a suite of insect herbivores upon them. As the trees adapted and evolved to the intertidal environment, their insect fauna would be expected to adapt with them. Some species that have part of their life-cycle on the ground (eg, species with root-feeding larvae or that pupate in soil) may not have adapted to the mangrove environment, although such factors are not always inhibitory. For instance, Murphy (1990) describes how several insect species, including caterpillars, live on the intertidal floor of mangroves, feeding on algal and other detritus, retreating to sealed burrows or cocoons during high tide. He also describes how root-feeding bugs and beetle larvae survive tidal immersion. Lever (1952) recorded a leaf-tying caterpillar feeding on mangroves, surviving over four and a half hours submerged in tidal water. Mangroves also support a diverse ground-dwelling ant fauna (Clay and Andersen 1996), including mangrove-specialist species that retreat to sealed burrows during tidal inundation (Nielsen 1987a,b). During the current study, it was observed that many species feeding within lower strata of mangrove canopies also readily survived tidal inundation (see Appendix A).

Appreciating the diversity and habits of the insects present is central to properly evaluating their role in the ecology of mangroves. In contrast to other tropical forests (especially rainforests), the insect diversity of mangroves is relatively unexplored. Entomological studies in other tropical forests have described vast diversity and demonstrated the diverse ways in which herbivorous insects affect plant ecology in these ecosystems. More is known about insect communities in saltmarshes than in mangroves and insects are considered to be important in that ecosystem (Strong *et al.* 1984, Bertness *et al.* 1987, Daehler and Strong 1995, Silliman and Zieman 2001), even though salinity influences are more extreme there. Herbivorous insects might well have pivotal roles in mangrove ecology, just as, for example, herbivorous crabs have been shown to be much more significant in mangroves than was initially thought (Robertson 1986, Robertson and Daniel 1989, Robertson *et al.* 1992, Lee 1998).

3.1.2 Diversity of Mangrove Insect Fauna

There are many factors which influence insect herbivore diversity and it can be viewed at several scales. At the whole ecosystem level, insect herbivore diversity is affected by the variety of the vegetation types present whilst the diversity of insects attacking individual tree species depends on factors such as the trees' geographic range, their architecture, their chemical and physical defence mechanisms and the number of their nearby conspecifics. Because of their limited floristic and structural diversity, mangrove forests may have fewer insect species in total than other forest ecosystems (Abe 1988), but the insect diversity on individual tree species may match that of similarly sized and structured trees in other habitats. Because of their aquatic dispersal capabilities, most mangrove species, especially *Avicennia marina* and *Rhizophora stylosa*, have large geographic ranges, thereby increasing the available pool of insect herbivores. Whilst *A. marina* is one of only eight species in the monogeneric family Avicenniaceae, the family Rhizophoraceae contains 19 species from four genera (Duke *et al.* 1998a). Most mangrove stands in northern Queensland contain at least three genera of Rhizophoraceae but *A. marina* is the only Avicenniaceae species present in the region. This should create a higher degree of specialisation of herbivores on *Avicennia* whereas it would be expected that many of the insects feeding on *Rhizophora* would also feed on other members of the Rhizophoraceae.

In a classic experiment, Simberloff and Wilson (1969) and Wilson and Simberloff (1969), described the terrestrial arthropod fauna of seven mangrove (*R. mangle*) islands in the Florida Keys by defaunating them and monitoring their recolonisation. They estimated that the seven islands housed 75 arboreal insect and 15 arboreal spider species and that, at any one time, each island (11-18m diameter and with no terrestrial benthos) supported 20-40 arboreal insect and 2-10 arboreal spider species out of an estimated total pool of 500 insect and 125 spider species. The proportion that were herbivores was not presented and none were explicitly recorded as feeding on *R. mangle,* though it was the only plant present on most islands. The islands were selected specifically because of their small size and isolation and were essentially permanently inundated. Because the study was focused on testing island biogeography theory, they only sampled atypically small mangrove stands and did not explore the ecology or distinctiveness of the insect community. Thus, this widely cited work did not allow evaluation of the ecology of the insect assemblage.

Murphy (1980, 1990) and Murphy and Tan (1980), working in Singapore mangroves, were the first to demonstrate the extent and diversity of the mangrove folivorous insect fauna. More importantly, they demonstrated that many of the faunal elements were distinctive and well adapted to living in mangrove forests. Since then, several authors have published information on the hosts of mangrove insects but few have determined the ecological role of the insects encountered. The recent studies of Elster *et al.* (1999) on impacts on seedlings, and Feller and Mathis (1997), Feller and McKee (1999) and Feller (2002) on wood-boring insects in mangroves, provide rare exceptions.

Outside Australia, several studies have documented insect herbivore communities in mangroves. Farnsworth and Ellison (1991) claimed to recognise 66 different folivore species from mangroves in Belize but did not list them. Murphy (1980) and Murphy and Tan (1980) recognised over 300 insect species from Singapore but did not provide a list or specify their role. Murphy (1990) provided descriptive notes for 102 species of herbivorous insects from Singapore mangroves. Rau and Murphy (1990) reported 37 species, 33 of which were folivorous, from Thailand mangroves. Veenakumari *et al.* (1997) reported 128 folivorous species from the Andaman and Nicobar Islands of India, along with 69 non-folivorous herbivores, 43 species of Hymenoptera parasites and 36 predatory insect species. Only Murphy (1990) and Veenakumari *et al.* (1997) provided sufficient information for comparative faunal analysis with other studies.

In Australia there have been no comprehensive surveys of mangrove insects, though some brief surveys have been conducted. For mangrove forests at Cairns, Hegerl and Davie (1977) recorded 30 insect species from 19 families during incidental field collecting, and from mangrove forests in Sydney, Hutchings and Recher (1974) found museum records for 41 species from 17 families. Derrington (1993) used canopy fogging, sweep netting and visual surveys to collect insects from 83 families at one mangrove stand near Townsville. Meades *et al.* (2002) used intercept traps and canopy fogging on two occasions to capture 252 arboreal insect species from a temperate mangrove community near Wollongong, south of Sydney. In all of these cases, most of the insects recorded were not herbivores, and with the exception of two species in Hutchings and Recher (1974), no host associations were made. Hockey and de Baar (1991) provided host records for 19 herbivorous Lepidoptera from Queensland mangroves, though only six actually fed on leaves, with the remainder feeding on either wood or fruit. Hockey and De Baar (1988) provided host records for 30 Coleoptera species from Queensland mangroves but all fed on wood or fruit, not leaves. Numerous individual host records exist, although they are biased towards certain groups such as butterflies and moths. A literature search revealed more than 80 herbivorous insect species recorded as feeding on Australian mangroves, though only 30 of these were recorded as feeding on leaves (Table 3.1). By comparison, over 450 insect herbivores, including 282 feeding on leaves, have been recorded from the paperbark tree, *Melaleuca quinquenervia* in Queensland (Balciunas and Burrows 1995). This species occurs in coastal freshwater swamps, often directly adjacent to mangroves. It took approximately five years of search effort to compile that list, but it serves to indicate the level of diversity that can be expected in comprehensive surveys.

Table 3.1 Literature Records for Folivorous Insects From Mangroves in Australia.

Herbivore Species or Taxa	Sites in Australia	Feeding Habit	Mangrove Hosts	Notes	Reference
DIPTERA **Agromyzidae**					
Melanagromyza avicenniae	Sydney[1]	Shoot-feeder	*A. marina*	Restricted to *A. marina*	Hutchings and Saenger 1987
Cecidomyiidae					
Actilasioptera coronata	Brisbane	Leaf gall-former	*A. marina*	Restricted to *A. marina*	Gagne and Law 1998
Actilasioptera pustulata	Brisbane	Leaf gall-former	*A. marina*	Restricted to *A. marina*	Gagne and Law 1998
Actilasioptera subfolium	Brisbane	Leaf gall-former	*A. marina*	Restricted to *A. marina*	Gagne and Law 1998
Actilasioptera tuberculata	Brisbane	Leaf gall-former	*A. marina*	Restricted to *A. marina*	Gagne and Law 1998
Actilasioptera tumidifolium	Brisbane, Townsville	Leaf gall-former	*A. marina*	Restricted to *A. marina*	Gagne and Law 1998
HOMOPTERA **Diaspididae**					
Aulacaspis australis	Brisbane	Leaf sap-feeder	*B. gymnorhiza*		Brimblecombe 1959
Pseudococcidae					
Pseudococcus hypergaeus	Port Augusta, Sth Australia	Leaf sap-feeder	*A. marina*	Also non-mangrove hosts	Williams 1985
LEPIDOPTERA **Geometridae**					
Anisozyga sp.	Brisbane	Leaf-feeder	*A. corniculatum*		Hockey and de Baar 1991
Limacodidae					
Doratifera stenora	Gladstone	Leaf-feeder	*R. stylosa*		Duke 2002
Doratifera quadriguttata[2]	Maryborough	Leaf-feeder	*R. stylosa*		Hockey and de Baar 1991
	Australia, PNG	Leaf-feeder		Non-mangrove hosts	Common 1990, Robinson *et al.*2001
Lycaenidae					
Hypochrysops apelles apelles	Maryborough, Urangan	Leaf-feeder	*A. marina, C. tagal*		Manski 1960
	Gold Coast		*R. stylosa, C. tagal, B. gymnorhiza*		Smales and Ledward 1942,
	Darwin		*L. racemosa*		Meyer 1996
	Northern NSW to Cape York			Also non-mangrove hosts	Hutchings and Saenger 1987, summarised in Braby 2000
Hypochrysops epicurus	Port Macquarie to Maryborough	Leaf-feeder	*A. marina*	Apparently restricted to *A. marina*	Smales and Ledward 1942, de Baar and Hockey 1987, Sands1999
Hypochrysops narcissus	Port Douglas	Leaf-feeder	*A. corniculatum, C. tagal*		Valentine and Johnson 1988
	Innisfail to Cooktown	Leaf-feeder	*A. marina, L. racemosa, R. stylosa, B. exaristata*		Muller 1998
	Townsville to Cape York			Also non-mangrove hosts	Summarised in Braby 2000
Hypolycaena phorbas phorbas	Gladstone to Cape York	Leaf-feeder	*A. corniculatum, L. racemosa, C. tagal, O. octodonta, R. stylosa*	Also non-mangrove hosts	Valentine and Johnson 1988, Moss 1989, Hill 1999, Braby 2000
Nacaduba kurava	Northern NSW to Cape York	Leaf-feeder	*A. corniculatum*	Also non-mangrove hosts	Hutchings and Saenger 1987
Arhopala micale amytis[3]	Cairns	Leaf-feeder	*H. littoralis, H. tiliaceus*	Also non-mangrove hosts	Manski 1960
	Gladstone to Cape York	Leaf-feeder		Non-mangrove hosts	Summarised in Braby 2000 and Robinson *et al.* 2001

Table 3.1 cont'd

Ogyris amaryllis hewitsoni	Maryborough to Cairns	Leaf-feeder	*A. mackayense* (mangrove mistletoe)		Hutchings and Saenger 1987
	Darwin, Arnhem Land	Leaf-feeder	*A. thalassium* ***(mangrove mistletoe)***		Braby 2000
Lymantriidae					
Orgyia australis	Northern NSW to Maryborough and NW Aust.	Leaf-feeder	*A. corniculatum*	Also non-mangrove hosts	Common 1990
Noctuidae					
Achaea janata	Most of Australia	Leaf-feeder	Probably *E. agallocha*[4]	Numerous non-mangrove hosts	Edwards 1978, Robinson *et al.* 2001
	Maryborough		Possibly *A. marina*[5]		Hockey and de Baar 1991
Achaea serva	Gladstone	Leaf-feeder	*E. agallocha*	Also non-mangrove hosts	McKillup and McKillup 1997
Pyralidae					
Undet. Phycitinae sp.	Brisbane, Maryborough	Leaf and fruit-feeder[6]	*A. marina*		Hockey and de Baar 1991
Saturniidae					
Syntherata janetta[7]	Brisbane	Leaf-feeder	*C. tagal*		Manski 1960
	Brisbane	Leaf-feeder	*A. corniculatum*		Hockey and de Baar 1991
	Nthn Australia	Leaf-feeder	*A. corniculatum*		Common 1990
Tineodidae					
Cenoloba obliteralis	NSW	Fruit-feeder[8]	*A. marina*		West *et al.* 1983
Tortricidae					
Isotenes miserana	Victoria to North Qld	Leaf-binder	*A. corniculatum*	Also non-mangrove hosts	Common 1990, Robinson *et al.* 2001
Procalyptis parooptera	Eastern Australia[9]	Leaf-binder	*C. tagal*		Hutchings and Saenger 1987
	Singapore, Thailand	Leaf-binder	*Ceriops spp., Bruguiera spp., Rhizophora spp.*		Robinson *et al.* 2001
Cryptoptila immersana	NSW and eastern Qld	Leaf-binder	*A. speciosum* (mangrove fern)	Also non-mangrove hosts	Common 1990
ORTHOPTERA					
Valanga irregularis	Corio Bay, Qld	Leaf-feeder	Unnamed mangroves		Ellway 1974 in H&S1987

[1] Location not stated by Hutchings and Saenger (1987)

[2] Listed as *D. unicolor* in original publication. Name synonomised by Checklist of Australian Lepidoptera

[3] Listed as *Norathura micale amytis* in original publication. Name synonomised by Checklist of Australian Lepidoptera

[4] Hosts include '..mangroves (probably *Excoecaria agallocha* (L.)' Edwards (1978). Whitten and Damanik (1986) record this species (as *Ophiusa melicerata*) defoliating extensive stands of *E. agallocha* in Sumatra. Veenakumari *et al.* (1997) records *E. agallocha* as a host in the Andaman and Nicobar Islands

[5] Three pupae collected from *A. marina*, but feeding not confirmed

[6] specimens collected feeding on both plant parts appear to be the same species

[7] Listed as *Antheraea janetta* in Manski (1960)

[8] considered to be a fruit-feeder (Hutchings and Saenger 1987, Common 1990, Hockey and de Baar 1991) but reported by West et al. (1983) as defoliating *A. marina*. Hutchings and Recher (1974) report it as feeding on fruit and young shoots of *A. marina* at Careel Bay, Sydney.

[9] Specific distribution records in Australia not able to be found but appears to be widespread (Hutchings and Saenger 1987, pers. obs.)

This chapter describes the folivorous insect fauna of *A. marina* and *R. stylosa* from Saunders Beach and Gordon Creek near Townsville. The folivore fauna is then compared to that of other mangrove systems as reported in Murphy (1990) and Veenakumari *et al.* (1997), non-mangrove trees taken from various literature sources, and coastal tree species in northern Queensland using the author's unpublished data from another study.

3.2 Methods

3.2.1 Sampling the Insect Herbivore Community

A variety of methods can be used to sample insects. Fogging tree canopies with insecticides can produce quantitative results and a high diversity of arthropods, and is therefore popular in biodiversity studies (Stork 1987a,b, Bassett 1991b, Majer *et al.* 1994, Erwin 1995, 1997, Novotny and Bassett 2000). It has also been used in several mangrove studies (Simberloff and Wilson 1969, Wilson and Simberloff 1969, Abe 1988, Derrington 1993, Patari 1996, Meades *et al.* 2002). However, it was not utilised in this study because the focus was on leaf herbivores only, not the entire fauna, and it was necessary to capture insects live to determine their feeding habits and rear the juvenile stages to adult for identification. Neither is possible with insecticidal fogging, which is lethal, and the insects are collected in sheets below the tree, so their host status or habit cannot be ascertained. Sweep-netting is popular and effective in grasslands and other open habitats but not useful in dense mangrove habitats. Light and other types of aerial traps only attract a fraction of the insect community, and then only the flying stages of species, thus neglecting important non-flying stages such as caterpillars, beetle larvae, gall-larvae and Hemiptera nymphs. They also attract insects from adjacent habitats and provide no indication of the host status of the captured species. Thus, the best remaining methods that provide a reasonable means of capturing the major components of the herbivore fauna whilst observing their habits are visual surveys and direct collection of plant material for laboratory sorting.

The purpose of this part of the study was to compile a list of folivorous herbivores from mangroves at Saunders Beach and Gordon Creek and also to compare folivore diversity with that known from adjacent terrestrial forests. The latter goal relied on collection of plant material for laboratory sorting whilst the former also included visual searching.

From 1991-1996, I was involved in a project to collect insect herbivores from the swamp paperbark tree *Melaleuca quinquenervia*, which is found in coastal habitats from Sydney to Cape York. In northern Queensland, most effort was focused on this species, and several of its close relatives, in coastal habitats between Townsville and Tully. These trees support a diverse and distinctive insect herbivore fauna that significantly influences their growth, productivity and ecology (eg, Balciunas and Burrows 1993, 1995; also see Turner *et al.* 1998 for a review). As well as *M. quinquenervia* and several of its close relatives, similar collections were made from *Callistemon viminalis* and several *Acacia* spp. that occurred in the same habitats. All of these species occur in coastal woodlands, seasonal freshwater swamps or coastal sand dune communities near, or often directly adjacent to, mangroves, thus providing a suitable dataset for comparison of folivore diversity between trees in the two habitats. In order to make a valid comparison, the same methods as that study were utilised in collecting mangrove insects.

Individual collections were made by clipping a large amount of branch material from various areas of a tree and placing it into a plastic bag. By using pole-pruners, the upper tree canopies were able to be sampled. The bag was returned to the laboratory where its contents and lining were searched for all insects present. All herbivorous insects were placed on to fresh plant material to determine if feeding occurred. Insects were reared on appropriate plant material until their host status could be confirmed or until they reached the adult stage. Insects that were reared to adult or that died in the process of rearing and confirming their feeding habits, were preserved by either pinning (for adult specimens) or in alcohol (for larvae/nymphs).

Two samples were collected from each species (*A. marina* and *R. stylosa*) at each site (Gordon Creek and Saunders Beach), every three months, from October 1994 to August 1995, for a total of 32 collections (16 on each species). This enabled comparison with the data from the non-mangrove species, also based on 16 samples for each species taken over the same period.

Whilst such collections provide a basis for comparing faunal diversity, they are an inefficient means of determining total herbivore diversity because insect communities generally consist of a few common species with a very large number of rare species (Majer *et al.* 1997, Novotny and Basset 2000). With a program of random, repeated sampling, the chances of finding new species with each additional collection are slim and considerable effort is expended dealing with species already recorded. More effective means are to directly search plant material in the field by eye. This allows effort to be specifically focused on finding new species. Because this method relies heavily on observer experience, it is not easily quantified and therefore difficult to compare between studies. However, because of its practicality in all environmental conditions and the ability to collect all life stages and to observe the habits and specific collecting sites of insects, it is actually the most common means by which herbivore lists are compiled. All of the insect surveys published for mangroves that have confirmed host records have used this method as the predominant means of compiling their faunal lists.

Thus, in addition to the field collections described above, *A. marina* and *R. stylosa* trees were searched in the field. For each species, 50 separate visual searches (25 at each site), each 30 minutes long, were undertaken at irregular intervals from August 1994 – July 1995. By climbing lower limbs and/or bending long branches, parts of the upper tree canopies were also searched using this method. Many new species were also collected opportunistically whilst undertaking other work.

3.2.2 Comparison to Folivore Diversity Studies in the Literature

Murphy (1990) and Veenakumari *et al.* (1997) provide lists of folivores from mangroves that are useful for comparison with the current study even though both relied entirely upon visual searching, and the amount of searching effort employed is not indicated in either study. However, it is clear that the list of Murphy (1990) was compiled over many years of collecting effort and the survey of Veenakumari *et al.* (1997), whilst more limited in time, involved the efforts of 4-6 people. Both studies appear to represent greater effort than was possible in this study but are the only studies from mangroves available for comparison.

In an attempt to determine how the diversity of folivorous insects collected in this study compares to non-mangrove tree and shrub species, the literature was searched for similar surveys. Despite a large number of studies on insect herbivore diversity in a wide range of forest types, finding directly comparable studies is difficult. Because of the wide variety of sampling methods, levels of effort, sampling conditions, observer experience and the different focus taken (eg, relatively few studies actually investigate host status), direct comparisons with studies from forest trees elsewhere are difficult. Nevertheless, there is sufficient robustness to allow some comparisons to be made with the published literature. To be included for consideration, surveys had to involve trees, or at least large shrubs, in tropical or sub-tropical locations. Because of their strong relationship with increasing numbers of herbivore species, surveys that covered very large geographic areas or that included many years of searching effort were also excluded because they cannot be compared to the dataset in the current study. Thus the remaining literature considered suitable for comparison with the survey undertaken in this study included tropical/subtropical trees or shrubs where surveys were carried out over short-moderate time frames (usually <1 year) and limited geographic ranges. Furthermore, the surveys had to specify the nature of the host association as only folivorous insects were considered in this analysis. Thirteen studies were located that met most of these criteria.

3.3 Results

3.3.1 Diversity of Folivorous Insects Collected in This Study

A total of 61 species of folivorous insects were collected from *A. marina* and *R. stylosa* during this study (Table 3.2). This is more than double the known number of records for insects feeding on mangrove leaves in Australia (Table 3.1). The actual number may be higher as five other morphologically different types of galls, each only located 1-2 times on *A. marina*, were not been included in the faunal lists presented here because of uncertainties over their distinctiveness as new galls (ie, they

Table 3.2 Folivorous Insect Species Collected From *A. marina* and *R. stylosa*. Hosts codes: AM = *A. marina* and RS = *R. stylosa*. Site Codes: GC = Gordon Creek and SB = Saunders Beach. Abundance ratings of Rare, Uncommon, Moderate, Common are based on subjective judgement.

Order/Family	**Species**	**Host**	**Site**	**Feeding Mode**	**Abundance**
Coleoptera					
Chrysomelidae	*Monolepta sp.* complex[1]	AM, RS	GC, SB	Graze leaf surfaces	Moderate
Curculionidae	*Alcidodes ?bubo*[3]	AM	GC, SB	Graze leaf petioles	Moderate
	undet. sp.	RS	GC	Bore into apical tips	Uncommon
Scarabaeidae	undet. sp.	AM	SB	Graze leaf surfaces	Rare
Hemiptera					
Aleyrodidae	undet. sp.	RS	GC, SB	Leaf sap-feeder	Common
Coccoidae	undet. sp. A	RS	SB	Leaf sap-feeder	Rare
	undet. sp. B	RS	SB	Leaf sap-feeder	Common
	undet. sp. C	AM	SB	Leaf sap-feeder	Rare
	undet. sp. D	AM	GC	Leaf sap-feeder	Rare
Diaspididae	undet. sp. A	RS	SB	Leaf sap-feeder	Common
	undet. sp. B	RS	SB	Leaf and stem sap-feeder	Uncommon
	undet. sp. C	RS	GC, SB	Leaf sap-feeder	Moderate
Flatidae	undet. sp.	AM, RS	GC, SB	Leaf sap-feeder	Common
Auchenorrhyncha	undet. sp. A	AM, RS	GC, SB	Leaf sap-feeder	Moderate
	undet. sp. B	RS	SB	Leaf sap-feeder	Moderate
Pentatomidae	undet. sp. A	RS	GC	Leaf sap-feeder	Moderate
	undet. sp. B	AM	GC	Leaf sap-feeder	Rare
	undet. sp. C	RS	SB	Leaf sap-feeder	Uncommon
Psyllidae	undet. sp.	RS	GC, SB	Leaf sap-feeder	Rare
Ricaniidae	undet. sp.	AM	SB	Leaf sap-feeder	Uncommon
Lepidoptera					
Geometridae	undet. sp.	AM	SB	Consume leaf lamina	Rare
?Gracillariidae	undet. sp.	AM	GC, SB	Forms linear leaf mine[3]	Common
Lycaenidae	*Hypochrysops apelles* [3]	RS	GC, SB	Graze leaf surfaces	Common
	Hypolycaena phorbas	RS	GC	Graze leaf surfaces	Rare
Lymantriidae	undet. sp.	RS	GC	Consume leaf lamina	Uncommon
Oecophoridae	*?Hieromantis* sp.	AM	GC, SB	Leaf-binder	Moderate
Psychidae	undet. sp. A	RS	GC	Consume leaf lamina	Rare
	undet. sp. B	AM	SB	Consume leaf lamina	Rare
Pyralidae	*?Ptyomaxia* sp.	AM	GC, SB	Leaf-binder	Common
Saturniidae	*?Syntherata* sp.	RS	GC, SB	Leaf-feeder	Uncommon
Tortricidae	*Adoxophyes* sp.	RS	GC, SB	Leaf-roller	Common
	Procalyptis parooptera	RS	GC, SB	Leaf-binder	Common
Unknown	undet. sp. A	AM	GC	Leaf-binder	Rare
	undet. sp. B	AM	GC, SB	Leaf-binder	Moderate
	undet. sp. C	RS	GC, SB	Leaf-binder	Moderate
	undet. sp. D	AM	SB	Feeds on galls	Common
	undet. sp. E	RS	SB	Consume leaf lamina	Rare

Table 3.2 cont'd

Leaf-miners	undet. sp.	AM	GC, SB	Worm-trail leaf mine[3]	Uncommon
	undet. sp.	RS	GC, SB	Type A leaf mine[3]	Moderate
	undet. sp.	RS	GC	Type B leaf mine[3]	Rare
	undet. sp.	RS	SB	Type C leaf mine[3]	Rare
	undet. sp.	RS	SB	Type D leaf mine[3]	Rare
Diptera					
Cecidomyiidae	*Actilasioptera tumidifolium*	AM	GC, SB	Bulbous gall[3]	Common
	undet. sp. B[2]	AM	GC, SB	Edge gall[3]	Common
	undet. sp. C[2]	AM	GC, SB	Spike gall[3]	Common
	undet. sp. D[2]	AM	GC, SB	Yellow-lump gall[3]	Uncommon
	undet. sp. E[2]	AM	GC, SB	Cabbage gall[3]	Moderate
	undet. sp. F[2]	AM	GC, SB	Marble gall[3]	Moderate
	undet. sp. G[2]	AM	GC, SB	Acne gall[3]	Moderate
	undet. sp. H[2]	AM	GC, SB	Pimple gall[3]	Common
	undet. sp. I[2]	AM	GC, SB	Mid-vein gall[3]	Moderate
Orthoptera					
Tettigoniidae	undet. sp. A	RS	GC	Consume leaf lamina	Rare
	undet. sp. B	RS	SB	Consume leaf lamina	Rare
	undet. sp. C	RS	SB	Consume leaf lamina	Rare
	undet. sp. D	AM	GC	Consume leaf lamina	Rare
Gryllidae	undet. sp.	AM, RS	GC, SB	Consume leaf lamina	Uncommon
Unknown					
	Causative agent not known	AM	GC, SB	Raised pit gall[3]	Moderate
	Causative agent not known	AM	GC, SB	Circular leaf mine-Type B[3]	Common
	Causative agent not known	RS	GC, SB	Type E leaf mine[3]	Uncommon
	Causative agent not known	RS	GC	Type F leaf mine[3]	Rare
	Causative agent not known	RS	GC	Type G leaf mine[3]	Rare

[1] More than one species may be present

[2] Probably *Actilasioptera* spp. (R. Gagne pers. comm.)

[3] Illustrated by photo in Appendix A

may be unusually shaped variants of already known galls). Additionally, the *Monolepta* sp. beetles may represent more than one species but the taxonomy of this large group is complex and unresolved. At least two species of herbivorous *Apion* sp. weevils are abundant on both *A. marina* and *R. stylosa* but as no feeding damage could be found on leaves of either host, they have not been listed in Table 3.2. Of the 61 species listed in Table 3.2, 49 were collected from Saunders Beach and 43 from Gordon Creek with 31 of the 61 species being collected at both sites.

A total of 31 folivorous species were recorded from *A. marina* and 34 from *R. stylosa* (Table 3.3). Despite the individual plants from which collections were made being closely located to each other, only four out of 61 species were collected from both hosts (Table 3.2) and there were major differences in the composition of the folivore fauna between the two mangrove species (Table 3.3). Lepidoptera (both external feeding and leaf-mining moths) were the most diverse group on both species. Dipterous gall-formers were particularly diverse and conspicuous on *A. marina* but entirely absent on *R. stylosa*. More than twice as many sap-feeding bug species were found on *R. stylosa* than on *A. marina*. For both species, beetles were conspicuously low in diversity.

Table 3.3 Number of Folivorous Insect Species Found on *Avicennia marina* and *Rhizophora stylosa* at Gordon Creek and Saunders Beach, Near Townsville.

Insect Group	***Avicennia marina***	***Rhizophora stylosa***
Lepidoptera (moths)	7	9
Coleoptera (beetles)	3	1
Orthoptera (grasshoppers)	2	4
Scale Insects (sap-feeding bugs)	2	6
Other Hemiptera (sap-feeding bugs)	4	7
Leaf-Miners (mostly moths)	3	7
Gall-Formers (mostly flies)	10	0
TOTAL	**31**	**34**

3.3.2 Comparison of Folivore Diversity Between Mangroves

The 61 folivore species collected in this study compares favourably to the 102 species listed by Murphy (1990) and the 128 species recorded by Veenakumari *et al.* (1997). All three studies covered relatively limited geographical areas but the latter two involved greater searching effort and surveyed all the mangrove species present rather than just two species, as was the case in this study. From just the *Avicennia* and *Rhizophora* species surveyed in each study, Murphy (1990) reported around 50 folivores (exact number could not be determined) and Veenakumari *et al.* (1997) reported 58 folivores.

Table 3.4 provides a summary of the number of folivorous species found only on *Avicennia* and *Rhizophora* species for various insect orders in all three studies. In the current study, with equal searching effort on both species, the number of folivorous herbivore species located on each is similar. Murphy (1990) reports about twice as many species on *Avicennia* as on *Rhizophora* whereas Veenakumari *et al.* (1997) found nearly twice as many on *Rhizophora* as on *Avicennia*. There were four species of *Avicennia* and three species of *Rhizophora* in the study area (Singapore) of Murphy (1990) whereas the study area (Andaman and Nicobar Islands between India and the

Table 3.4 Comparison of Numbers of Folivorous Insect Species in Each Insect Order Found on *Rhizophora* and *Avicennia* Species in Three Studies.

	***Avicennia* spp.**			***Rhizophora* spp.**		
	Murphy (1990)	**Veenakumari *et al.* (1997)**	**This Study**	**Murphy (1990)**	**Veenakumari *et al.* (1997)**	**This Study**
Coleoptera	5	6	3	2	9	1
Diptera	Several	1	9	0	1	0
Hemiptera	7	2	6	9	8	13
Hymenoptera	0	1	0	0	0	0
Lepidoptera	19	12	9	6	20	13
Orthoptera	0	0	2	0	1	4
Unknown	-	-	2	-	-	3
Total	**32+**	**22**	**31**	**17**	**39**	**34**

Malay Peninsula) of Veenakumari *et al.* (1997) had one species of *Avicennia* and two species of *Rhizophora*. The abundance of, and search effort on, each of these species, was not stated in those studies.

In the studies of Murphy (1990) and Veenakumari *et al.* (1997), Lepidoptera dominated the fauna to a much greater degree than in the current study whereas both Diptera and the sap-feeding Hemiptera were more diverse in the current study (Table 3.4). Notably, Murphy (1990) and Veenakumari *et al.* (1997) reported more species of Coleoptera than were found in the current study.

The proportional insect folivore species richness collected from all mangroves by Murphy (1990), Veenakumari *et al.* (1997), in the current study, and the world average for herbivorous insect communities (from Strong *et al.* 1984) is compared in Table 3.5. All three mangrove studies show a higher than average proportion of Lepidoptera and Hemiptera but lower than average proportion of Diptera and Coleoptera. The composition of the fauna in Murphy (1990) and Veenakumari *et al.*

Table 3.5 Proportional Representation of Folivorous Insect Taxa in Three Mangrove Studies. Data comprises all mangrove species in each study: Murphy (1990) -21 species, Veenakumari et al. (1997) -17 species, this study = *A. marina* and *R. stylosa* only. The world average for herbivorous insects is taken from Strong *et al.* (1984).

	Murphy (1990)		**Veenakumari *et al.* (1997)**		**This Study**		**World Average**
	No. species	**% of species**	**No. species**	**% of species**	**No. species**	**% of species**	**% of species**
Coleoptera	14	14	32	25	3	5	33
Diptera	Several		3	2	9	15	9
Hemiptera	28	27	17	13	17	28	13
Hymenoptera	0	0	1	1	0	0	4
Lepidoptera	58	57	73	57	22	36	32
Orthoptera	2	2	2	2	5	8	6
Other Orders	0	0	0	0	5*	8*	3
Total	**102+**	**100**	**128**	**100**	**61**	**100**	**100**

* represent galls or leaf-mines whose causative agents have not yet been determined

(1997) are similar with both being dominated by Lepidoptera (both 57% of the fauna) and then either Hemiptera or Coleoptera. By contrast, in the current study, Lepidoptera and Hemiptera were co-dominant, Diptera are also common and Coleoptera are poorly represented.

3.3.3 Comparison to Folivore Diversity Studies in the Literature

Folivore diversity was compared between this and other published studies. No study was truly comparable in a quantitative sense, but 13 published studies did meet the criteria of (i) providing species lists with (ii) confirmed herbivorous host associations on tropical or subtropical trees or shrubs in (iii) surveys conducted over limited geographic areas with (iv) sufficient search effort to provide a comprehensive list of species present. Fortunately, several of these 13 studies include data for several to many plant species, thus increasing the number of available comparisons. A summary of folivore diversity from these studies is presented in Table 3.6. Significantly, non-quantitative visual surveys as performed in the current study, formed either the major, or at least a substantial supplementary, sampling technique in all studies listed.

The diversity of folivorous insects found on *A. marina* and *R. stylosa* at the two sites surveyed in this study compares favourably with the studies listed in Table 3.6. All six studies that found greater folivore diversity than in this survey (Boldt and Robbins 1987, 1994, Woods 1992, Van den Berg 1980a,b,c, 1982a,b,c and Wilson *et al.* 1990) surveyed larger geographic areas. The lists of Van den Berg (1980a,b,c and 1982a,b,c) and Swain and Prinsloo (1986) only included Lepidoptera, Coleoptera and Hemiptera so are underestimates of the true folivore diversity, although these three groups usually dominate herbivore diversity of most plants. The number of Lepidoptera, Coleoptera and Hemiptera folivores from *A. marina* and *R. stylosa* in this study were 18 and 27 species respectively. This compares favourably with Swain and Prinsloo (1986) but is fewer than in the studies of van den Berg. Fewer folivores were found in the study of Kay and Brown (1991), although their study was based on an experimental crop planting. Notably, fewer folivores were also found in the surveys of Hurley (1995) and Jackson (1995) which were based on plants in tropical wet/moist forests and rainforests near Townsville.

Table 3.6 Number of Folivore Species Reported in the Literature From Tropical or Sub-Tropical Shrubs and Trees.

Location	Habitat Type	Plant Species	No. Folivore Species	Reference
Australia				
Northern NSW	Coastal crop	*Melaleuca alternifolia*	55	Treverrow 1992
Northern Territory	Floodplain	*Mimosa pigra*[1]	57	Wilson *et al.* 1990
Burdekin Area	Irrigated crop	*Hibiscus cannabinus*	32	Kay and Brown 1991
Cardwell	Tropical Moist Forest	*Laportea cordifolia*	27	Hurley 1995
Cardwell	Tropical Moist Forest	*Dendrocnide moroides*	24	Hurley 1995
Paluma	Rainforest	*Alphitonia* (x3 spp.)	15	Jackson 1995
SE Australia	Variety of subtropical forests	*Acacia* (x5 spp.)	X=31 (range15-43)[2]	Van den Berg 1982,a,b,c
SW Western Australia	Variety of subtropical forests	*Acacia* (x2 spp.)	41-49[2]	Van den berg 1980a,b,c
Overseas				
Arizona/Mexico	Desert	*Parkinsonia aculeate*	46[3]	Woods 1992
Mexico/USA	Rangelands	*Baccharis* (x3 spp.)	X =36 (range24-43)	Boldt and Robbins 1994
Texas	Rangelands	*Baccharis neglecta*	54	Boldt and Robbins 1987
South Africa	Forests	12 species of forest trees	X =28 (range7-52)	Moran *et al.* 1994
South Africa	Forests	14 species of forest trees	X =15 (range 6-28)[2]	Swain and Prinsloo 1986
Hawaii	Variety of forests	23 ‘common and widely distributed’ tree taxa	X =34 (range 11-114)[4]	Southwood 1960

[1] An exotic species introduced from South and Central America.

[2] Based on Lepidoptera, Hemiptera and Coleoptera taxa only.

[3] The plant part fed upon was not stated in the publication but was deduced as far as possible from known habits of the taxa involved. To be conservative, uncertain species were deemed to be folivorous

[4] Includes all herbivorous insects, not just leaf-feeders, as these were not separated in this publication. Based on Group 3 of the four groups of Southwood (1960) which was considered most appropriate for comparison with the current dataset.

Folivore diversity on *A. marina* and *R. stylosa* in the current study was similar to the means from the multi-species summaries of Moran *et al.* (1994) and Southwood (1960). Moran *et al.* (1994) studied only one pocket of remnant forest vegetation, albeit intensively, over an 11-month period. They concluded that the forest they studied was depauperate in comparison to other forest types in the world, though the conclusion was based on limited comparison with published literature. Although very brief, Southwood (1960) is a very well known paper in this area of study. No specific methodology or level of effort on each tree species was described other than to say that the effort was comprehensive. Herbivore insect diversity was summarised for 50 tree species in Hawaii. The particular habits of the herbivores was not stated, and I have assumed that all herbivorous habits, including flower and wood-feeding are included. Thus the actual number of folivorous species from Southwood (1960) would be less than that stated in Table 3.6. The 50 tree species were divided into four groups, based on their abundance. Group 3 was selected for comparison with *A. marina* and *R. stylosa* as these represented the common and widely distributed tree species. Group 1 (local and rare trees) averaged 5.6 insect herbivore species, Group 2 (not uncommon trees) averaged 15.8 insect herbivore species and Group 4 (comprising of only two abundant tree species) averaged 123 insect herbivore species.

The studies of Kay and Brown (1991), Hurley (1995), Jackson (1995) are most relevant for comparison with this study in that they occurred close to Townsville and covered similarly limited geographic ranges as my survey. Folivore insect diversity on *A. marina* and *R. stylosa* in the current study is higher than for the plants surveyed in those studies.

3.3.4 Comparison of Folivore Species Richness With That of Adjoining Plant Species

The number of folivorous insects collected in laboratory-sorted field collections from *A. marina*, *R. stylosa* and a variety of other coastal tree species in the Townsville area is presented in Table 3.7. All cases include data from 16 samples and involved the same methodology. Folivore species richness was similar for all plant species listed. The two mangrove species recorded more folivores than *M. leucadendra* and *C. viminalis*, but fewer than *M. viridiflora* (n=37 species), *M. dealbata* (mean=40.5 species), *M. quinquenervia* (mean=38.6 species) and the combined *Acacia* species (n=45 species), although this latter group included samples from four tree species, which may have increased species richness. It should be noted that further taxonomic evaluation of some insects and unoccupied galls collected from *A. marina* would probably increase the number of species recorded from this host. The identity and taxonomy of herbivores collected from the various *Melaleuca* species listed is particularly well-known (Balciunas and Burrows 1995), so no extra species are anticipated there.

Table 3.7 Comparison of the Number of Folivorous Insects Collected in Laboratory Sorted Field Collections From Mangrove and Adjoining Coastal Tree Species in Northern Queensland (n=16 samples in all cases – Burrows unpub. data).

Species	No. Folivore Species	Sampling Location
Avicennia marina	30	Townsville area
Rhizophora stylosa	31	Townsville area
Melaleuca quinquenervia	41	Townsville area
Melaleuca quinquenervia	51	Forrest Beach, E of Ingham
Melaleuca quinquenervia	35	Murrigal, S of Tully
Melaleuca quinquenervia	31	Feluga, N of Tully
Melaleuca quinquenervia	35	Cairns
Melaleuca dealbata	37	Townsville area
Melaleuca dealbata	44	Tully Heads, E of Tully
Melaleuca leucadendra	24	Townsville area
Melaleuca viridiflora	37	Townsville area
Callistemon viminalis	30	Townsville area
Acacia spp. (4 coastal dune species)	45	Townsville area

3.4 Discussion

3.4.1 Diversity and Composition of the Insect Folivore Community

The total of 61 folivorous insect species recorded in this study is more than double the number previously recorded from mangroves in Australia. Worldwide, only two other studies in mangroves (Murphy 1990, Veenakumari *et al.* 1997) have reported greater numbers of folivore species, both of which involved much greater searching effort on a wider variety of mangrove tree species. The number of folivore species collected was greater at Saunders Beach than at Gordon Creek and over half of the species collected in this study were found at both sites, including all of the most common species. Despite slightly greater species richness at Saunders Beach, there are no major anomalies between the faunas of the two sites. Folivore species richness was approximately equal for *A. marina* and *R. stylosa*, though there were substantial differences in the composition of the fauna of the two species. The Lepidoptera were the most diverse folivore group for both mangrove species and these caused most leaf damage in both species (see Chapter 4 and 5). The Hemiptera (sap-feeding bugs) were the next most diverse group overall, though on *A. marina*, gall-forming flies were the second most diverse group. Folivorous beetles (Coleoptera) were surprisingly rare on both mangrove species. Leaf-mines were much more abundant on *A. marina* than on *R. stylosa,* though diversity was greater on the latter species. A wide variety of galls were present on *A. marina*, but this guild was entirely absent from *R. stylosa*.

Like eucalypts (Landsberg and Cork 1997), the mangroves in the current study supported a wide diversity of sap-feeding insects. Diaspididae scale insects and Flatidae planthoppers were particularly common in the current study. Psyllids are common and damaging herbivores on many Australian trees, but because of their small size are often overlooked. Just over two-thirds of the Australian psyllid fauna utilise eucalypts as hosts (Majer *et al.* 1997). Psyllids are also common on *Melaleuca* species adjacent to mangrove habitats throughout Queensland, with at least 12 species recorded, one of which was shown to be host-specific to *M. quinquenervia* and a few of its close relatives (Purcell *et al.* 1997). They were particularly damaging to their hosts, often killing the leaves upon which they fed (Balciunas and Burrows 1995, Purcell *et al.* 1997). Psyllids were rarely noted on mangroves during this study, though because of their small size and inconspicuous nature, they are easily overlooked in general surveys, unless they are lerp-forming species. Veenakumari *et al.* (1997) record the psyllid *Boreioglycaspis forcipata* from *Sonneratia* mangroves in the Andaman and Nicobar Islands. This species was also recorded from *S. alba* in South East Asia by Burkhardt (1991) but does not occur in Australia. A psyllid species has been noted as common on *A. germinans* in Florida and central America, attacking buds and reducing leaf area by as much as 35% (Ilka Feller, Smithsonian Institution pers. comm.).

In this study, *Avicennia* and *Rhizophora* differed in the absolute and proportional species richness of sap-feeding bugs (Hemiptera) though this is not indicated by the host record literature. A review of published host records from around the world reveals a total of 20 sap-feeding insect species recorded from *Avicennia* spp. and 21 species from *Rhizophora* spp. (Ben-Dov 1994, Mound and Hasley 1978, Mound and Palmer 1981, Newberry 1980, Russell 1963, Veenakumari *et al.* 1997, Williams 1985, Williams and Watson 1988a, 1988b, 1990, Murphy 1990). However, in the current study, and those of both Murphy (1990) and Veenakumari *et al.* (1997), the number of Hemiptera species was much less on *Avicennia* than on *Rhizophora* (Table 3.4) indicating that this may be a more general feature of mangrove folivore faunas.

The smaller number of Hemiptera attacking *Avicennia* compared to *Rhizophora* and other mangroves was attributed by Murphy (1990, p. 125) to salt excretion (*Avicennia* spp. excrete salt on to leaf surfaces, often forming salt crystals there), though it was not specifically tested. In the current study, hemipteran species comprised 19% of the *A. marina* fauna and 38% of the *R. stylosa* fauna. Murphy (1990) found a similar result, although for the *Avicennia* and *Rhizophora* mangroves in Veenakumari *et al.* (1997), the respective figures were 9% and 21%. Newberry (1980) found that salt secreted on *A. marina* leaves affected the distribution of the coccid, *Icerya seychellarum,* though it was still able to feed and establish abundant populations on this plant.

Although the lower number of hemipteran species on *Avicennia* compared to *Rhizophora* may be a general trend, the overall diversity of Hemiptera on mangroves, even on *Avicennia* spp., is still comparable to other plant species. For instance, 31% of the folivorous insects found on *M. quinquenervia* were Hemiptera (Balciunas and Burrows 1995). Other surveys cited in section 3.3.3 indicate that Hemiptera comprised 25% of the folivores in the study of Wilson *et al.* (1990), 19% (Kay and Brown 1991), ~40% (Hurley 1995), 50% (Boldt and Robbins 1987), 60% (Boldt and Robbins 1994), 25% (Treverrow 1992), 10% (Harley *et al.* 1995) and <6% (van den Berg 1980c,1982a). Although highly variable, these figures do not indicate any obvious trends for lower proportional diversity of sap-feeding bugs in mangroves compared to other tree and shrub species.

The diversity of gall-forming species, mostly Cecidomyiidae flies, on *A. marina* is notable. This guild is usually only a minor component of the diversity on most plant species, if present at all. A total of 10 different types of cecidomyiid-caused galls were recorded from *A. marina* in the current study. There are also several other galls for which no causative agent has been identified. Law (1995) recorded five cecidomyiid galls from *A. marina* in the Brisbane area, four of which were not recorded in the current study. Given that these two locations cover only a portion of the range of *A. marina* in Australia, the low level of overlap between them suggests that the diversity of galls on *A. marina* may be even higher. All five gall-forming species collected by Law (1995) were from the one genus – *Actilasioptera* – which was erected specifically for these species (Gagne and Law 1998). Initial inspection of the gall-formers from *A. marina* in the current study suggest that many are also from the same genus (R. Gagne, pers. comm.).

The diversity of galls on *A. marina* contrasts with their complete absence on *R. stylosa* and indeed every other Rhizophoraceae species I have examined during the course of this study. I can find only two references to galls having been recorded from any member of the Rhizophoraceae anywhere in the world. Jayaraman (1985) reported a gall from *Ceriops roxburghiana* in India and F. Mogel (pers. comm.) has located galls on *R. mangle* in Brazil. In contrast to their rarity on members of the Rhizophoraceae, galls have been recorded from various *Avicennia* species in Australia (Law 1995, Gagne and Law 1998), New Zealand (Lamb 1952, Chapman 1976), India (Mani 1973, Jayaraman 1985), Java (Docters van Leeuwen 1919, Felt 1921), Singapore (Murphy 1990), Thailand (Wium-Andersen and Christensen 1978, Rau and Murphy 1990), Florida (Gagne and Etienne 1996), Belize (Farnsworth and Ellison 1991) and Brazil (Goncalves-Alvim *et al.* 2001) (see Appendix A for more details). Both Chapman (1976) and Murphy (1990) described insect galls as being conspicuous features of *Avicennia*. This is therefore a distinct difference between the fauna of the two main mangrove groups – *Avicennia* and the Rhizophoraceae. Galls have also rarely been reported on other mangrove species. Murphy and Tan (1980) report cecidomyiid-caused leaf galls from *Heritiera* sp. and *Hibiscus* sp. (a non-obligate mangrove species) in Singapore, Veenakumari *et al.* (1997) record moth-caused galls from *Sonneratia* in the Andaman and Nicobar Islands and I have found galls (causative agent unknown) on *Lumnitzera racemosa* in Townsville.

The diversity of leaf-miners recorded in this study is also notable. Although more species were recorded from *R. stylosa*, they are all rare or uncommon, whereas one of the three types of leaf mines recorded from *A. marina* occurred on >30% of leaves. Three additional species of leaf-miners are common on *A. marina* in southern Queensland (Law 1995, pers. obs.). Murphy (1990) notes at least four species of leaf-miners on *Avicennia* in Singapore (all from the same lepidopteran genus) but none on any Rhizophoraceae. Veenamukari *et al.* (1997) record two species of leaf-mines' from *Avicennia* sp. and one from *R. apiculata* as well as additional species from *Excoecaria* spp. and *Heritiera* spp.

The low diversity of folivorous beetles (Coleoptera) (five species) in this study is of particular interest as the Coleoptera are the most speciose animal group on the planet and most are herbivorous (Strong *et al.* 1984). In Australia, folivorous Coleoptera have been found to be particularly diverse on eucalypts (Landsberg and Cork 1997), *Acacia* spp. (van den Berg 1980b, 1982c) and *M. alternifolia* (Treverrow 1992) but less so on *M. quinquenervia,* where they comprised only 14% of the insect folivore fauna (Balciunas and Burrows 1995). Mangrove habitats actually harbour significant numbers of Coleoptera as wood-borers and twig inquilines (Hockey and de Baar 1988, Feller and Mathis 1997, Feller and McKee 1999, Feller 2002) but not as folivores. Murphy (1990) also recorded a similarly low diversity of folivorous Coleoptera on *Avicennia*, *Rhizophora* and the other mangroves he studied. The low diversity of folivorous coleopterans is not restricted to *Avicennia* and *Rhizophora*, and it appears to be a general feature of mangrove habitats. Because the tree species that comprise mangrove habitats come from a variety of different ancestral lineages, it is likely that this feature is related to the ecology of the system, not to aspects of particular plant lineages. It may be that because many beetles have root-feeding larvae, tidal inundation has restricted their diversity in mangroves. However, several of the beetle species found in mangroves belong to groups known to have root-feeding larvae. For instance, larvae of *Monolepta* (found in the current study, Murphy (1990) and Veenakumari *et al.* (1997)) are commonly known as root-feeders. Murphy (1990) described how *Monolepta* aff. *bicavipennis* bores into *Avicennia* pneumatophores, forming galleries that are protected from tidal immersion.

Two species of *Apion* weevils were abundant on leaves of both *A. marina* and *R. stylosa* in this study but no feeding was ever observed and they died in the laboratory without feeding, despite being offered a variety of leaves. Thus, these two species have not been counted as herbivores of either *A. marina* or *R. stylosa*. Hockey and de Baar (1988) recorded *Apion* sp. from Port Alma near Rockhampton, but also failed to elicit any feeding damage. Why they are so common on these two species remains to be determined. Many *Apion* species have stem-boring or flower-feeding larvae with very short life cycles but as this study was focused on folivores, these plant parts were not searched for these weevils.

Some caution should be used when interpreting herbivore faunal lists as the proportional representation of some groups will change with increasing survey effort. For instance, prior to this survey, of the 30 literature records for herbivores feeding on mangrove leaves in Australia, 21 were from Lepidoptera. Lepidoptera are more readily collected in the incidental collecting efforts which comprise the existing literature. In contrast, Lepidoptera only represent a third of the folivore species in this study. With increasing effort, the number of mobile species, especially Lepidoptera, Orthoptera, Coleoptera and many Hemiptera, should increase more than stationary species such as gall-formers, leaf-miners and many scale insects. Galls, leaf-mines and some scale insects are visually obvious and their distinctive structures remain on a leaf long after their causative agent has disappeared, thus increasing their apparency. These types of insects are readily collected in the initial stages of surveys. In addition, most of these insect groups are stationary, so cannot escape collection and are also more likely to be host-specific and thus will only be found on their main hosts. In contrast, Lepidoptera, Coleoptera, Orthoptera and several Hemiptera taxa do not generally occupy distinctive structures, and are mobile and more likely to be polyphagous. Thus, encounters with species from these groups will continue to occur with increasing effort, increasing their proportional representation.

3.4.2 Specialisation and Host-Specificity of the Folivore Fauna

Despite previous speculation that animal-plant co-evolutionary relationships were rare in mangroves (Tomlinson 1986) and that mangroves lacked a specialised herbivorous insect fauna (Chapman 1976, Berjak *et al.* 1977, Hogarth 1999, Kathiresan and Bingham 2001), this study has confirmed the findings of Murphy (1990), that neither of these positions appear to be true. Many components of the folivore fauna are adapted to and even host-specific to their mangrove hosts, and are highly specialised to life in mangrove habitats, including being tolerant of tidal immersion (usually by enclosing themselves in galleries or cocoons) (Lever 1952, Murphy 1990, pers. obs.). Many of the most common folivores found on *A. marina* and *R. stylosa* in the current study are likely to be specific to the species they were found upon, or several close relatives. For *R. mangle* in Florida, Onuf *et al.* (1977) also considered the four main folivore species found upon it to be host-specific to that species.

The host-plant range of herbivorous insects may be either monophagous (feeding on just one plant species), oligophagous (feeding on a few related plant species) or polyphagous (feeding on a variety of plant species). Despite its apparent advantages, polyphagy is relatively rare, with estimates of polyphagy as low as 25% of phytophagous insect species (Bernays and Chapman 1994). The breadth of host range varies between taxonomic groups. For instance, over 60% of Orthoptera species but less than 10% of Diptera species, are polyphagous (Bernays and Chapman 1994). Within certain families, narrow host ranges may be common. For instance, nearly all members of the superfamily Psylloidea are monophagous or oligophagous (Bernays and Chapman 1994). High levels of host fidelity may also be found across functional groups such as gall-formers (Gagne 1989) and leaf-miners (Hespenheide 1991), or those which are specialised on specific plant parts such as flowers or apical buds.

Most of the Orthoptera and the external leaf-feeding Lepidoptera collected in this study are not likely to be specific to either *A. marina* or *R. stylosa* and many probably also have non-mangrove hosts. This is the case for many of the species listed in Table 3.1. *Procalyptis parooptera* and *S. janetta* have been recorded from several other mangrove species, although in the case of the former, they are all members of the Rhizophoraceae (Table 3.1). Over its entire range, *H. apelles*, the most conspicuous herbivore on *R. stylosa*, is known to utilise several mangrove and non-mangrove hosts (see Appendix A for a review). However, local populations appear to have specific adaptations, as at any one location, they are known to only utilise a smaller range of hosts (Braby 2000). In Townsville, I have only observed *H. apelles* damage on members of the Rhizophoraceae, not *A. marina* or any non-mangrove species, even though these are known to be hosts in other regions (see Appendix A for a list of hosts). Although the external leaf-feeding Lepidoptera have a low degree of specificity, the leaf-mining Lepidoptera have a high degree of specificity because of their more intimate mode of feeding. For similar reasons, it is most likely that all of the gall-forming species on *A. marina* are specific to that species, or at least to *Avicennia*. The majority of known Cecidomyiidae gall-formers are host-specific

(Gagne 1989). *Avicennia marina* may be the dominant host of the petiole-feeding weevil, *Alcidodes ?bubo*, as it is commonly found on this species but not other mangroves. It has been recorded on a few rare occasions from *M. quinquenervia* (Balciunas and Burrows 1995) and *Indigofera* grass in India (Gardner 1934). Several hemipteran species may also be host-specific but further taxonomic work and field survey is required for this group.

Because of the high proportion of gall-formers and leaf-miners on *A. marina*, it is likely that around half of the recorded folivore fauna are specific to it, or at least to the genus *Avicennia*. The proportion is much lower for *R. stylosa*, and many of its herbivores would also be found on other mangrove members of the Rhizophoraceae. Murphy (1990) also noted the greater degree of host specificity on *Avicennia* compared to *Rhizophora* and suggested that this was due to the taxonomic isolation of *Avicennia* (being the only genus in its family). However, the apparent greater degree of host specificity on *Avicennia* is substantially enhanced by the diversification of gall-forming *Actilasioptera* upon *Avicennia*.

It is not unusual for high degrees of host fidelity to be reported. Using chemical knock-down to compare eucalypt canopy insect communities between southwestern and southeastern Australia, Recher *et al.* (1996) found that 40% and 53% of herbivorous insects, respectively, were not shared by pairs of tree species in each forest (ie, had restricted host-ranges). In a sub-alpine eucalypt forest, Morrow (1977) found that 63% of 48 herbivorous insect species only occurred on one of the three co-occurring eucalypt species surveyed. In contrast, in northern Australian savanna woodlands, Fensham (1994) determined that only 21% of 34 herbivorous insect species, collected from eight tree species in six different genera, were host-specific. This led him to speculate that host specificity was less in tropical environments. Such a view was supported by the data of Stork (1987a) showing a lower than expected degree of host specificity in tropical rainforest trees.

There are several members of the Rhizophoraceae present in mangroves, so it might be expected that insects feeding on *Rhizophora* may also feed on other members of this family. Both Murphy (1990) and Veenakumari *et al.* (1997) demonstrated the very similar folivore fauna of the various Rhizophoraceae species in their studies. In contrast, Murphy (1990) considered the insect herbivore fauna of *Avicennia* and *Sonneratia* (another taxonomically isolated mangrove group) to be more distinctive than for other mangrove trees. In both studies, there was considerable overlap between various members of the Rhizophoraceae but of the 48 folivore species collected from *Rhizophora* and *Avicennia* species in Murphy (1990), only four were in common. Of the 61 species collected from *Avicennia* and *Rhizophora* by Veenakumari *et al.* (1997), only three were in common. Although they provided no supporting information, Farnsworth and Ellison (1991) claimed that none of the 66 folivore species they recognised from *A. germinans* and *R. mangle* in Belize were in common. In the current study, only four of the 61 species collected from *A. marina* and *R. stylosa* were in common. Apart from one species of cricket, the other three species that were collected from both hosts may, upon more detailed inspection, turn out to represent separate species, particularly for the *Monolepta* beetles. Both Murphy (1990) and Veenakumari *et al.* (1997) treated *Monolepta* spp. they collected from *Avicennia* and *Rhizophora* as separate species. Given the close proximity of sampled *Avicennia* and *Rhizophora* trees in all of the above-mentioned studies, the low level of host overlap indicates that these two tree species groups do indeed have distinctly different insect folivore faunas and the literature suggests that this distinction holds worldwide. The low level of faunal overlap between two of the most common mangrove tree species indicates that, contrary to current opinion, mangroves do support a specialised, rather than generalised, insect herbivore fauna.

3.4.3 Comparison With Other Mangrove Studies

Veenakumari *et al.* (1997) found a total of 128 insect folivores feeding on 12 mangrove species from seven families in the Andaman and Nicobar Islands. Of these, 22 folivore species were found on *Avicennia* sp. and 39 folivore species were found on two species of *Rhizophora*. The lower diversity on *Avicennia* compared to *Rhizophora* may be real but probably reflects the greater abundance and search effort on the *Rhizophora* species at their sites. In contrast, Murphy (1990) found a total of 102 folivorous insect species on 21 mangrove species from nine families in Singapore, with at least 31 species on *Avicennia* spp. but only 17 species on *Rhizophora* spp. Farnsworth and Ellison (1991) recognised 66 folivore species from *A. germinans* and *R. mangle* in Belize, but did not supply a list of species or any further information. Rau and Murphy (1990) listed 37 folivorous species from six mangrove species in Thailand. The 61 folivorous species reported in the current study (31 from *A. marina* and 34 from *R. stylosa* with four in common between the two) compares favourably with these studies.

Given significant differences in sampling methods and effort in published insect surveys, the geographic area of sampling and the experience of the searchers (a significant factor), it is not possible, with limited studies undertaken to date, to confidently identify any differences in insect diversity between mangrove systems. Ellison (2001) stated that there is an order of magnitude difference in mangrove insect diversity between SE Asia and the Neotropics. He cited the work of Murphy (1990) in support of this statement; however, Farnsworth and Ellison (1991) recognised 66 folivore species in Belize whereas Murphy (1990) found 102 folivore species in Singapore, thus failing to confirm of an order of magnitude difference. Due to more species of mangroves being present in SE Asia, it may be that mangrove insect richness is also higher there, but this remains to be demonstrated.

3.4.4 Comparison With Non-Mangrove Trees

There are numerous studies of insect fauna in a variety of other tropical forests and woodlands but most involve wide variation in both sampling effort and sampling methods, making comparison very difficult. This is not a unique problem. Definitive comparisons of herbivore diversity between different habitat types and surveys are very rare. Most studies that have attempted such comparisons have been conducted as part of the same project (eg, Fensham 1994, Southwood *et al.* 1982, Moran *et al.* 1994, Majer *et al.* 1994) or have utilised large extensive datasets (eg, Southwood 1960, Kennedy and Southwood 1984, Brandle and Brandl 2001). Despite these shortcomings, a search of the literature for insect surveys that involved a comprehensive search effort over a similarly limited geographic range, revealed that the diversity of folivores found on *A. marina* and *R. stylosa* was at least comparable to that of many other individual trees species within a variety of ecosystem types.

Interestingly, even surveys of several rainforest tree species just north of Townsville (Hurley 1995, Jackson 1995) found fewer folivore species than were found on the two mangrove species in the current study. This is in contrast to the tremendous diversity reported from individual trees in tropical rainforests elsewhere (Erwin 1995, 1997) although most such studies in rainforests have utilised mass-collection methods such as insecticidal fogging. For instance, using insecticidal fogging on 10 Bornean canopy rainforest trees, Stork (1987a) found an average of 121 phytophagous insect species (range=67-215) on each individual tree. Many of the species collected would not actually feed upon leaves of the trees sampled. Nevertheless, the numbers of folivores and other herbivores collected suggest that even allowing for tourists and insects feeding on attached plants (eg, epiphytes, vines, mosses etc) or adjacent plants, rainforest trees would still appear to hold especially diverse herbivore communities. For example, using visual techniques to collect leaf-chewing insects (Lepidoptera, Coleoptera, Orthoptera and Phasmatidae) in lowland rainforest in Papua New Guinea, Novotny and Bassett (2000) found 383 herbivore species on 15 Euphorbiaceae species and 347 herbivore species on 15 *Ficus* species as well as 444 sap-feeding Auchenorrhyncha (Hemiptera) species on the *Ficus* species.

The comparison of data from the laboratory-sorted samples of *A. marina* and *R. stylosa* with identical methods used for six tree species from nearby coastal habitats in northern Queensland provides a better comparison of folivore diversity between mangroves and tree species from adjacent habitats. The diversity of folivores found on *A. marina* and *R. stylosa* was comparable to these other tree species (*Melaleuca* spp., *Callistemon* and *Acacia* spp.). Further effort is required to fully elucidate such comparisons in insect folivore diversity between mangrove and non-mangrove habitats. However, these results indicate that the insect folivore diversity of mangrove tree species is comparable to many other tree species in a variety of other habitat types and refutes suggestions that the insect herbivore fauna of mangroves is particularly depauperate.

3.4.5 Potential Worldwide Similarities in Mangrove Folivore Faunas

There is some evidence to suggest that there are interesting similarities in the herbivorous insect fauna of mangroves in different parts of the world. For instance, galls have rarely been recorded from any member of the Rhizophoraceae anywhere in the world, yet they have been reported, in many cases as being common and diverse, from *Avicennia* species in Australia, India, Java, Singapore, Thailand, Florida, Belize, Brazil and Kenya. They appear to be a dominant feature on *Avicennia* in Australia (Law 1995; this study) and Singapore (Murphy 1990). They thus appear to be a common and distinctive part of the *Avicennia* fauna worldwide (see Appendix A for further discussion). As the majority of the causative agents for the galls have not been described, it remains to be seen whether there are taxonomic similarities between them. Cecidomyiidae flies appear to be the most common causative agents and of the seven species described from mangrove galls thus far, six are members of the recently-erected genus *Actilasioptera* which is currently only known from *Avicennia* spp. in Australia, PNG and Java (Gagne and Law 1998). The remaining described gall-former is from an unrelated Cecidomyiidae tribe on *A. germinans* in Florida (Gagne and Etienne 1996). Rau and Murphy (1990) suggested that the persistence of post-axial meristematic tissue makes *Avicennia* susceptible to galling in contrast to the extreme localisation of such tissues in the Rhizophoraceae.

Apical tip damage to *Rhizophora* species appears to be the dominant form of insect leaf damage in *Rhizophora* species across the world (studied and discussed in Chapter 6). This has been reported to be the case for Rhizophoraceae species in Belize (Feller 1995), Florida (Onuf *et al.* 1977), Thailand (Rau and Murphy 1990), Andaman and Nicobar Islands (Veenakumari *et al.* 1997) and in the current study (Chapter 6). In each case, the mechanism of feeding and tip damage appears to be the same but the taxonomic relatedness of the causative agents has yet to be verified. Just as the leaf-grazers *Hypochrysops apelles* and *Hypolycaena phorbas* (both Lycaenidae) are among the most damaging folivores on *R. stylosa* in several locations in Australia, Rau and Murphy (1990) found related *Hypolycaena* larvae which feed in the same manner, to be one of the most important pests on *R. apiculata* in Thailand. A number of other lycaenids are also known to be common on various mangrove species in Australia, India and a variety of SE Asian countries (Robinson *et al.* 2001). The unusually low diversity of Coleoptera in mangroves has been noted in several studies in Thailand (Rau and Murphy 1990), Singapore (Murphy 1990) and the Andaman and Nicobar Islands (Veenakumari *et al.* 1997), in addition to the current study. In each of these studies, of the few species that were present, several are in the genus *Monolepta*. These similarities are intriguing but further research will be required to reveal if these preliminary patterns have any substance.

3.4.6 Potential Diversity of Insect Herbivores in Australian Mangroves

It is of interest to consider what the true number of folivores and herbivores on mangrove species in Australia might be. New (1983) estimated that *Eucalyptus* and *Acacia* would host 15,000-20,000 herbivorous insect species. These plant genera contain 600 and 900 species respectively covering most parts of the country, although a recent taxonomic review of *Eucalyptus* has divided the genus (Hill and Johnson 1995). Over 450 herbivore species (including 282 folivores) have been recorded from *M. quinquenervia* over approximately half of its geographic range, and more than 100 additional species recorded from lesser effort on several closely related broad-leaved *Melaleuca* species (Balciunas and Burrows 1995). Given that *Melaleuca* has more than 250 species (Barlow 1988), in a wide variety of habitats over the whole country, it too may host many thousands of herbivorous insect species. That individual tree species may host several hundred herbivorous insect species is not unusual. Harley *et al.* (1995) record 441 herbivore species from *Mimosa pigra* over its geographic range in the Americas, including 193 folivores. Kennedy and Southwood (1984) list several tree species in Britain and Europe that have several hundred herbivore species known from them. The studies of Stork (1987a,b), Bassett (1991a,b), Erwin (1995, 1997), and Novotny and Bassett (2000) also indicate that many rainforest trees each host several hundred herbivorous insect species.

Characteristically, there is a large number of rare species encountered in insect surveys and species rarefaction curves seldom reach asymptotes (Strong 1974, Janzen 1988, Novotny and Bassett 2000), so increases in survey effort will lead to increases in the number of herbivore species collected from a particular host species. Increasing herbivore species richness with increasing host geographic range is also commonly reported (Strong *et al.* 1984, Brandle and Brandl 2001) and a host plant species may support regionally distinct insect faunas over its geographic range. For instance, there is a limited overlap between the fauna on *M. quinquenervia* in the Brisbane region of southern Queensland compared to that in the Townsville region of northern Queensland (Balciunas and Burrows 1995). There is also little overlap in mangrove canopy fauna between the current study and that of Hockey and de Baar (1991) and Law (1995) from the Brisbane region, though this distance is only a fraction of the total range of mangroves in Australia.

In addition to geographic area, species richness is increased by the variety of plant species present and their degree of relatedness (Brandle and Brandl 2001). Mangrove communities in Australia contain 39 species from 20 families (Duke 1992). The surveys reported here have revealed 61 herbivore species feeding just on leaves from two mangrove species in just one area. There is little overlap between the herbivore fauna on *Avicennia* and *Rhizophora* and apart from other members of the Rhizophoraceae, most other mangroves trees are not closely related. Because of taxonomic differences in the mangrove flora, the low herbivore overlap between different hosts, the large geographic range over which mangroves occur, and the faunal community differences across geographic regions, it is not unreasonable to believe that there may be several thousand insect herbivores feeding on mangroves in Australia. Thus the host records produced here and existing in the published literature, have only taken the first steps in exploring a much larger field of study. New locations and the other unsurveyed mangrove plants hold virtually unknown insect faunas and are fertile grounds for further exploration.

3.5 Conclusions

The survey of folivorous insects conducted in the current study found 61 species, more than doubling the number recorded from Australian mangroves. More species were found on *R. stylosa* than on *A. marina*. As has occurred in other mangrove insect studies, each tree species had a distinctly different fauna. Many of the folivore species collected are highly specialised, being either specific to their mangrove hosts or having adaptations to life in mangroves, such as being able to survive tidal inundation. The degree of folivore host-specificity is high for both tree species, particularly *A. marina*. This is largely because of the diversity of gall-forming species on *A. marina*. Galls are a conspicuous feature of *Avicennia* species all over the world. In contrast, they are rare on members of the Rhizophoraceae and other mangroves. Leaf-miners were found on both species though twice as many species were found on *R. stylosa*. However, the mines found on *R. stylosa* were uncommon or rare, whereas one of the mines on *A. marina* was very abundant. As is the case in other mangroves surveyed for insect folivores, Lepidoptera are the most diverse group. It has been suggested that diversity of sap-feeding bugs would be low on *A. marina* because of salt secretion mechanisms used in this plant. While the number of sap-feeding bug species on *A. marina* was less than half that of *R. stylosa*, it was not unusually low when compared to literature records from a variety of other tree species. Notably, the number of folivorous beetle species collected was low, a feature also noted in other published mangrove studies.

A literature review, and sampling of tree species adjoining the mangrove sites used in the current study, showed that *A. marina* and *R. stylosa* host similar richness of folivorous insects to these species, demonstrating that mangrove tree species do not have depauperate folivore faunas, except perhaps, in comparison to rainforests. Based on extrapolation from the literature, the results from the current study, and patterns of folivorous insect diversity on other tree species, it is suggested that up to several thousand herbivore species may feed upon mangroves within Australia and that considerable differences in the fauna exist at widely separated sites and on various mangrove tree species. The study of mangrove herbivore communities is in its infancy, and there awaits a considerable diversity yet to be documented in this fertile, relatively unexplored field of research.

CHAPTER 4 – HERBIVORY LEVEL

4.1 Introduction

Although herbivory is a complex ecological process, it has, more often than not, been reduced to simple measures assessing damage to leaf area, in particular the percentage of leaf area missing. Most studies that have examined herbivory in mangroves have used these indices and concluded that only a small fraction of the net above ground primary production in mangroves is lost to herbivory and that most of this production cycles through the detrital pathway via loss of senescent leaves (eg, Robertson and Duke 1987). At the other extreme, the many instances of insect outbreaks and mass defoliation events (eg, Piyakarnchana 1981, West and Thorogood 1983, 1985, Whitten and Damanik 1986, Gara *et al.* 1990, McKillup and McKillup 1997) reported in mangroves are treated as curiosities. These have been regularly reported but, apart from a few exceptions (Gara *et al.* 1990, Anderson and Lee 1995 and Duke 2002), they are rarely studied in any detail.

Because herbivory in mangroves is generally considered to be low compared to other similar habitats, it is also assumed that herbivores are not particularly important in the ecology of mangrove ecosystems. However, there are a variety of mechanisms, in addition to leaf area missing, by which insect herbivores act upon plants. Plants also demonstrate a wide range of mechanisms for reducing, tolerating, or recovering from, herbivore damage. Thus assessments of leaf area missing alone do not adequately describe the role of insect herbivores in the ecology of any system. In some systems, low herbivory levels have significant effects, whilst in others, even chronically high herbivory does not alter plant population dynamics (Crawley 1983). However, before investigating these other mechanisms and whether or not herbivory is significant in the ecology of mangroves, it is important to address the issue of whether methods commonly used in assessing herbivory provide an accurate measure of the true level of herbivore damage to leaves. Studies comparing discrete and long-term methods have found that the former method may underestimate leaf damage by a factor of 1.1 to 6.9 times (see Table 4.11). There has been no previous comparison of discrete and long-term methodologies for mangroves with the majority of published papers using the discrete method only (see Table 4.9).

The aim of this chapter is to compare discrete and long-term methods of assessing leaf area damage in two common mangrove species – *Avicennia marina* and *Rhizophora stylosa* – and to examine the relative contributions of various types of leaf damage. The ratio of damage estimates produced by these two methods will provide an indication of their utility and of the validity of published mangrove herbivory studies that have used only the discrete method.

4.2 Methods

4.2.1 Discrete Sampling

For the discrete study (conducted October-November 1994), 10 trees of each species (*A. marina* and *R. stylosa*) were sampled at each site. On each tree, five mature leaves, as judged by their size and hardness, were taken from each of five branches in the lower (<2.2 m) canopy and the upper (2.2-4m) canopy. The lower canopy level was chosen from the maximum height reachable when sampling leaves by hand, as would be required for the long-term studies. The upper canopy height was set by the height which could be reached by a short pruning pole. For most of the sampled trees, this was also the maximum height that they attained at these sites.

Leaf area was measured in the laboratory with a CIAS Image Analysis System. This utilises a video camera to take a digital image of the leaf area. Where part of the leaf was missing, the estimated original leaf outline was traced onto graph paper and the number of 1mm^2 squares counted and added to the value obtained by the image analysis system. Leaf damage was measured by placing transparent graph paper over the damaged or missing area, and counting the number of 1mm^2 squares and/or taken from the values obtained for missing leaf area as described above. Damage was categorised into four main types - Missing, Grazed, Gall or Leaf Mine, and Necrosis. The four damage categories were readily defined in most cases. Leaf area missing was where part of the leaf lamina was entirely missing. Leaf area grazed was defined as any feeding of a leaf surface that did not result in complete removal of that section of the leaf lamina (ie, the leaf was not consumed all the way through the lamina). Gall and leaf mine damage were combined due to the low occurrence it was believed they would generate. The impact of galls is not appropriately measured by leaf surface area (see Appendix A), but no other suitable rapid technique is available. Leaf area for galls was defined by the area of resultant leaf swelling. Necrotic damage was any discoloration of the normal leaf colour directly due to insect feeding. It was usually directly caused by sap-feeding insects, producing a yellow leaf colour, or indirectly by wood-boring insects whose feeding resulted in leaf-wilting and browning.

In accordance with the standard methods for this technique, damage was expressed as the percentage of original leaf area affected by each damage type. This enables direct comparison with the many other studies that have utilised this discrete assessment method.

4.2.2 Long-Term Sampling

For the long-term study, 15 *R. stylosa* and 13 *A. marina* trees were chosen at each site. Greater time required to mark and sample leaves on *A. marina* leaves resulted in fewer trees of that species being used. On each tree, 10 branches were selected and tagged. All branches were in the lower canopy (<2.2m high), as they had to be easily reached for regular monitoring. Beginning in February 1995 and then each month for the next four months, newly emerged leaves were numbered consecutively with a permanent, waterproof pen on their lower surfaces. This four-month period covered most of the peak growing season for new leaf production for both species. For both *A. marina* and *R. stylosa*, leaves emerge as opposite pairs. Thus for each leaf emergence, there were two leaves to be marked. This proved to be convenient for detecting missing leaves where only one of a leaf pair was missing. Each month, until their death, all marked leaves were examined and the amount of damage, according to the four damage categories (missing, grazing, gall/leaf mine and necrosis), estimated as a percentage of the total leaf area. Not only did this provide data on long-term herbivory levels, it also provided data not before collected in mangroves, on age-based herbivory rates and the distribution of leaf life spans. For *A. marina*, a total of 1520 leaves at Gordon Creek and 1682 leaves at Saunders Beach, were tagged and monitored. For *R. stylosa*, a total of 1534 leaves at Gordon Creek and 1848 leaves at Saunders Beach, were tagged and monitored.

4.2.3 Accuracy of Field Damage Estimates

In comparing results from the discrete and long-term approaches, not only are two different sampling methods being tested but so are two different methods for estimating percent leaf area damaged. The discrete study measured leaf area missing in the laboratory whereas the long-term method relied on estimation of leaf area missing in the field. This is to be expected as the different damage assessment techniques are part of the difference in methodology that is being tested. However, it is important to know whether the use of field estimation introduced any bias into the long-term dataset.

Because of the need in the long-term method to repeatedly assess very large numbers of leaves in the field with minimal disturbance to the leaves, a rapid assessment method was required. Most studies utilise leaf area missing only, which can be measured with portable leaf area meters. However, because this study also aimed to assess other damage types (eg, grazing, galls, mines) which cannot be readily measured with such devices, and the frequency of these damage types on *A. marina*, it was deemed necessary to visually estimate insect herbivore damage. This method has been used successfully in similar studies in rainforests (Hurley 1995, Jackson 1995). Practice is the best method for improving accuracy with this technique. Considerable time was spent practicing estimating leaf damage and then comparing this to measured leaf damage until estimates within 10% of the measured value could be reliably produced. Drawn templates of leaves with various levels and patterns of damage were carried in the field for reference. Accuracy of estimation was greatest when damage levels were either very low or very high, and when damage consisted of single, rather than multiple, sites of damage. Very low levels of damage were by far the most common encountered in the field, thus providing accurate estimations for the vast majority of leaves in a rapid but reliable manner. For leaves where estimating damage was difficult because they were heavily damaged, or had multiple damage types and sites, transparent graph paper with 1mm^2 squares was overlain on the leaf to provide more reliable damage estimates. This was not possible as a routine method for all leaves because of time limitations.

To test the validity of estimating leaf damage in the field, 25 leaves of each species were collected. Leaves were specifically collected so that they represented a range of damage levels. Undamaged leaves were not collected for this task. The amount of leaf area damaged was estimated individually for all leaves as per the long-term method. After this, leaf area damaged was measured in the laboratory for the same leaves using the CIAS image system and transparent graph paper as per the discrete method. The two estimates were then compared for all leaves.

4.2.4 Loss of Entire Leaves

As premature leaf loss causes the greatest difference between the discrete and long-term methods, determining the cause of leaf loss is very important. This is achieved by visual field observation. Death and loss of healthy leaves can occur quite rapidly, thus requiring a relatively short sampling interval to detect the fate of lost leaves. A sampling interval of one month was considered a balance between the large amount of effort required to complete each sample and the need for frequent sampling to detect lost leaves. On some occasions, lost leaves (or their remnants) were located on the ground below the trees which often enabled determination of their cause of death.

Vertebrate herbivory is very rare in these mangroves and no signs of this damage were observed during the study. Very few leaves fell because of other physical reasons. Wind is not normally a factor within the protected mangrove forests. Even a cyclone (Cyclone Justin – Category 1) which impacted upon the study sites in March 1997 failed to noticeably increase leaf fall above background levels with very few marked leaves being lost and no obvious signs of greater litter present immediately after the event, even in areas above the tidal mark (pers. obs.).

In the majority of cases, causes for the loss of leaves could be confidently attributed to either insects or senescence. Mortality of leaves with significant levels of new herbivory recorded during one month and which were missing on the next visit, was attributed to herbivory. In many cases, the cause of leaf mortality was directly observable. On *R. stylosa*, many leaves that withered because of wood-borers remained on the tree for several months as did leaves killed by leaf-binders on *A.*

marina. For both species, insect herbivore damage to apical meristems or developing buds resulted in dead leaves that remained attached to the tree and were clearly attributable to herbivory. Senescence was readily identified by a distinct yellowing of the leaf and often occurred gradually over more than one sampling period, enabling it to be confirmed in most cases. Loss of all leaves >6 months old, that had minimal herbivory, and where senescence was not observed, were attributed to natural, age-related causes. Leaves <6 months old whose loss could not be attributed to insect damage, were, for conservative reasons, not considered to be the result of herbivory even though in reality, herbivory may have been involved in the loss of some, or even many, of these leaves. For some leaves, the cause of death cannot be confidently ascribed. Sometimes healthy, undamaged leaves vanished without trace between sampling dates. On other occasions, causes of leaf loss could be ascribed with moderate, but not complete levels of confidence. Thus this study provides maximum and minimum estimates of damage due to herbivory from the long-term study, reflecting the use of various assumptions regarding the cause of leaf loss.

Leaf material that is consumed by insects enters different food chains and energy pathways from abscised but otherwise intact leaf remnants. Thus, the overall amount of leaf material lost from a tree due to the activities of insect herbivores is the sum of direct herbivory (the amount of leaf material directly consumed or damaged by herbivores) and indirect herbivory (the amount of leaf material prematurely abscised from a tree due to the activities of insect herbivores). From the perspective of leaf loss from a tree, this division may be unimportant: whether consumed or abscised, the leaf is still lost. However, from the perspective of which food chain the leaf material enters (either insect biomass and insect frass, or leaf litter), the division is relevant to ecosystem considerations.

In this study, where the analyses discuss total leaf area lost from the tree, leaves whose mortality is attributable to insect damage are considered to be 100% missing. Where appropriate, in other analyses, the amount of leaf area known to have been directly damaged by insects and that which resulted from leaf fall, are kept separate. This separation is rarely considered in herbivory studies with most authors considering leaves to be 100% missing or eaten in all analyses (eg, Journet 1981, Lowman 1984, Clark and Clark 1991, Hurley 1995) and of course for discrete studies, which comprise the majority of herbivore literature, such a division is not possible.

4.2.5 Change in Area of Leaf Damage With Leaf Growth

Leaf damage on young developing leaves may change size as those leaves grow and expand, potentially leading to overestimation of the amount of leaf area consumed when sampling mature leaves. However, if proportional leaf damage is measured, as in this study, then leaf damage estimates on fully expanded leaves will remain accurate as long as the area damaged on young leaves expands at the same rate as the leaves. In order to determine whether this occurs on expanding *A. marina* and *R. stylosa* leaves, a single hole was punched into each of 30 leaves of each species at the Gordon Creek site, using a 5 mm diameter hole punch. For *R. stylosa*, holes were punched into leaves that had emerged from the apical bud within the previous 2-3 days. For *A. marina*, holes were punched into developing leaves 2-3 cm in length. Hole punching avoided leaf midribs and margins. The outlines of all leaves were traced on to graph paper. Six weeks later, when the leaves had reached full expansion, they were collected and their leaf area and hole area traced on to graph paper to determine their increase. Upon collection, one *R. stylosa* leaf and 10 *A. marina* leaves were found to be either missing or too badly damaged for use in the analysis.

4.3 Results

4.3.1 Discrete Study

The percentage of leaf area damaged in the discrete study is presented in Table 4.1. In three of the four comparisons, herbivory on the lower canopy was significantly greater than herbivory on the upper canopy (t-tests based on arcsin transformed data). Even in the fourth comparison (*A. marina* at Saunders Beach), the herbivory estimate on the lower canopy was 19% greater than on the upper canopy. For the other three combinations, the lower canopy had herbivory levels ranging from 42-81% higher than the upper canopies.

Table 4.1 Percent Leaf Area Damaged (±1S.E.) by Folivores in the Upper and Lower Canopies of *A. marina* and *R. stylosa* at Two Sites in the Discrete Study (n=250, df=498 for each case). Data were arcsin transformed for statistical analysis.

Species	Site	Upper Canopy	Lower Canopy	t	p
R. stylosa	Saunders Beach	2.68 (0.37)	4.23 (0.63)	2.53	0.01
	Gordon Creek	2.11 (0.35)	3.81 (0.67)	2.97	0.003
A. marina	Saunders Beach	5.90 (0.67)	6.75 (0.69)	1.10	0.27
	Gordon Creek	5.95 (0.60)	8.45 (0.91)	2.17	0.03

The proportion of damage caused by missing, grazing and other (galls, mines and necrosis combined due to low frequency of occurrence) forms of herbivore damage, also differed between the upper and lower canopies for three of the four comparisons (chi-square goodness of fit tests) but the magnitude of the difference is small (Table 4.2). For *R. stylosa* at Saunders Beach, well over half the damage was leaf area missing, one-quarter to one-fifth was grazing. In the other cases, leaf area missing was close to 50% of the total damage and grazing one-third to one-quarter of the damage. The main difference between the patterns for the two species was the greater proportion of leaf area on *A. marina* damaged by galls and leaf mines.

The proportion of leaves that were damaged in the upper and lower canopies of the discrete study is presented in Table 4.3. The proportion of leaves damaged by insect herbivores was not significantly different between the upper and lower canopies for *A. marina* at either site but was significantly different for *R. stylosa* at both sites (chi-square goodness of fit tests).

For both species at both sites there was, on average, greater leaf area damaged on damaged leaves in the lower canopy than in the upper canopy, although this difference was only significant for *R. stylosa* and *A. marina* at Gordon Creek (t-test, respectively df=449 and 454, *t*=2.09 and 2.45, p=0.04 and 0.01). Thus the greater damage recorded from the lower canopy is a combination of greater frequency of damage (at least in *R. stylosa*) and damage being more extensive when it does occur there.

Table 4.2 Proportion of Herbivore Damage by Damage Category Type in the Discrete Study (n=250 for each treatment)

Species	Site	Damage Type	Proportion of Leaf Area Damage		χ^2	p
			Upper Canopy	Lower Canopy		
A. marina	Gordon Creek	Missing	57	55		
		Grazing	26	23	31.87	<0.25
		Other	17	22		
	Saunders Beach	Missing	54	42		
		Grazing	24	28	6.24	<0.025
		Other	22	30		
R. stylosa	Gordon Creek	Missing	51	56		
		Grazing	29	34	6.35	<0.025
		Other	20	10		
	Saunders Beach	Missing	64	67		
		Grazing	19	27	10.63	<0.005
		Other	17	6		

Table 4.3 Frequency of Damaged Leaves and Damage Categories in the Discrete Study (n=250 for each treatment)

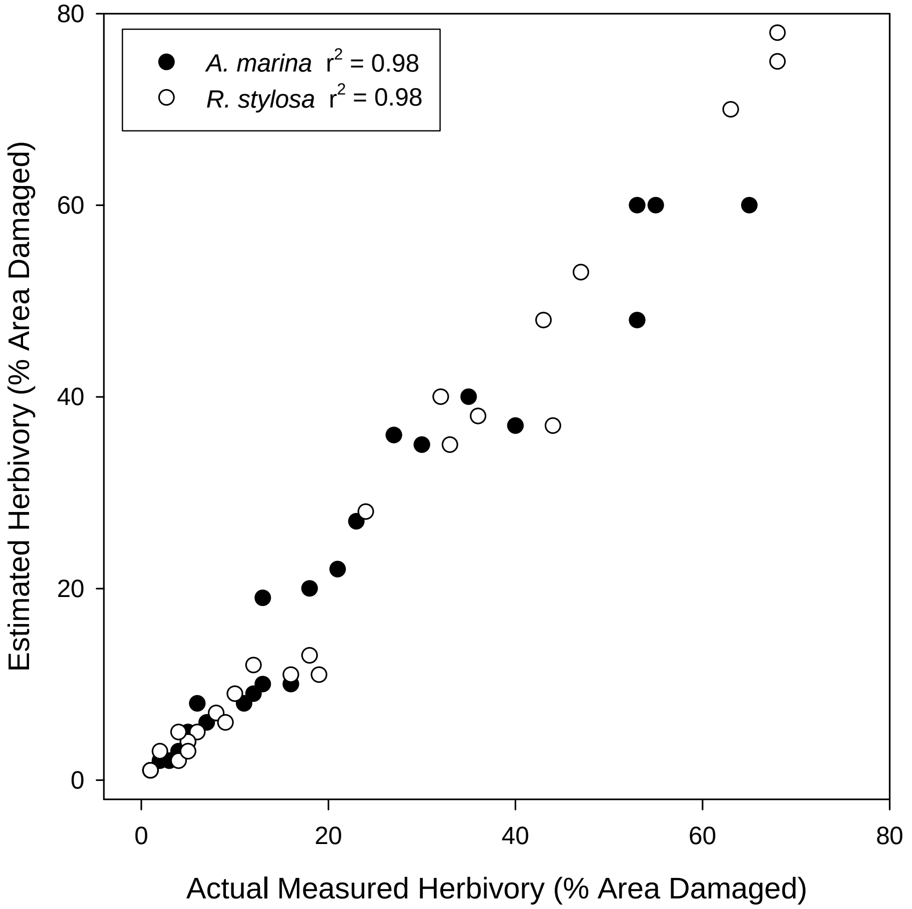
Species	Site	Damage Type	Proportion of Leaves Damaged		χ^2	p
			Upper Canopy	Lower Canopy		
A. marina	Gordon Creek	Missing	54	54		
		Grazing	62	64		
		Other	51	55		
		Undamaged	8	10	0.25	<0.50
	Saunders Beach	Missing	48	50		
		Grazing	62	58		
		Other	49	50		
		Undamaged	12	11	0.03	<0.75
R. stylosa	Gordon Creek	Missing	60	67		
		Grazing	54	71		
		Other	8	5		
		Undamaged	13	7	4.65	<0.025
	Saunders Beach	Missing	55	66		
		Grazing	42	54		
		Other	13	14		
		Undamaged	22	13	6.39	<0.01

For the remainder of this study, only the discrete results from the lower canopy will be utilised, since the long-term study was restricted to the lower canopy. Apart from Robertson and Duke (1987), who sampled from a raised boardwalk, no other mangrove herbivory study reviewed here has included samples from the upper canopy of mature trees, so the results presented here are comparable to those studies.

4.3.2 Accuracy of Estimation

For both *A. marina* and *R. stylosa*, the estimated and actual damaged leaf areas were highly correlated (r^2=0.98 and 0.99 respectively) and there was no significant difference between the means (paired t-tests, df=24, *t*=0.75 and 0.10 and p=0.46 and 0.92 respectively). For *A. marina*, most differences between estimated and actual values were less than 5% with the greatest difference being 9% (Figure 4.1). For *R. stylosa*, most differences were less than 4% with all bar one being ≤8% (Figure 4.1). Not surprisingly, greater differences between measured and estimated values occurred at greater levels of damage. Despite relatively few individual leaf damage comparisons producing precisely the same result, the overall means were almost identical, suggesting that the estimated values are unbiased. For *A. marina*, estimated values exceeded the actual measured value 10 times and measured values exceeded estimated values 10 times (5 were equal). For *R. stylosa*, the respective figures were 13 and 10 (2 were equal). Thus, overall, leaves with low levels of damage (which are the most common) could be accurately assessed and there was no bias in the relatively minor amount of estimation error. For the more heavily damaged leaves encountered in the field, where estimation error was higher, transparent graph paper placed over the leaves enabled more accurate results to be obtained for these leaves. Although accurate estimation of leaf damage is important, the greatest loss of leaf material resulted from loss of entire leaves. Leaves lost because of insect damage were considered to be 100% missing. Thus this large source of lost leaf area was measured very accurately.

Figure 4.1 Comparison Between Estimated and Actual Measures of Leaf Area Damaged



4.3.3 Comparison of Discrete and Long-Term Methods

The differences between the herbivory estimates obtained from the discrete and the long-term methods were significant and substantial (Table 4.4). The long-term method produced estimates that were 3-5 times higher for *A. marina*, and 2-3 times higher for *R. stylosa*. The largest part of this difference can be ascribed to the inclusion of entirely consumed leaves, or leaves that were prematurely abscised because of insect damage. However, for the long-term method, even the estimate for direct consumptive damage of leaf material before loss of the leaf from the tree (category 1 in Table 4.5), is higher than the estimates obtained from the discrete method (Table 4.4).

Table 4.4 Comparison of Estimates for Percent Leaf Area Damaged on *A. marina* and *R. stylosa* Leaves Obtained By Discrete and Long-Term Methods at Two Sites.

Species	Site	Discrete	Long-Term	Ratio
A. marina	Saunders Beach	6.8	36.1	5.3
A. marina	Gordon Creek	8.5	28.5	3.4
R. stylosa	Saunders Beach	4.2	13.2	3.1
R. stylosa	Gordon Creek	3.8	7.5	2.0

In the calculation of total herbivory in the long-term method (Table 4.4), leaves prematurely abscised from the tree due to insect damage were considered as 100% missing even though they were not directly consumed by insects. From the perspective of measuring leaf loss from a tree, this accurately represents the amount of leaf material lost. However, from an ecological point of view, it is important to know the amount of leaf material lost from the tree due to insect-related activities that enters the insect-feeding pathway (as insect frass or biomass) and the amount that enters the detrital pathway as prematurely-abscised litterfall. Table 4.5 breaks down this information into: 1) consumptive herbivory (estimated in the field as leaf material consumed by insects whilst leaves still on the tree; 2) loss of leaves definitely due to insects (leaf loss directly observed); 3) loss of leaves most probably due to insects (severely damaged leaves that do not persist for long after damage); and 4) leaves whose loss cannot be attributed to any cause (neither signs of herbivory or senescence were observed). Some of the leaves in the last category may have been lost because of herbivore damage but to be conservative, they were not included in the estimates presented in Table 4.4. All remaining leaves were observed to undergo senescence.

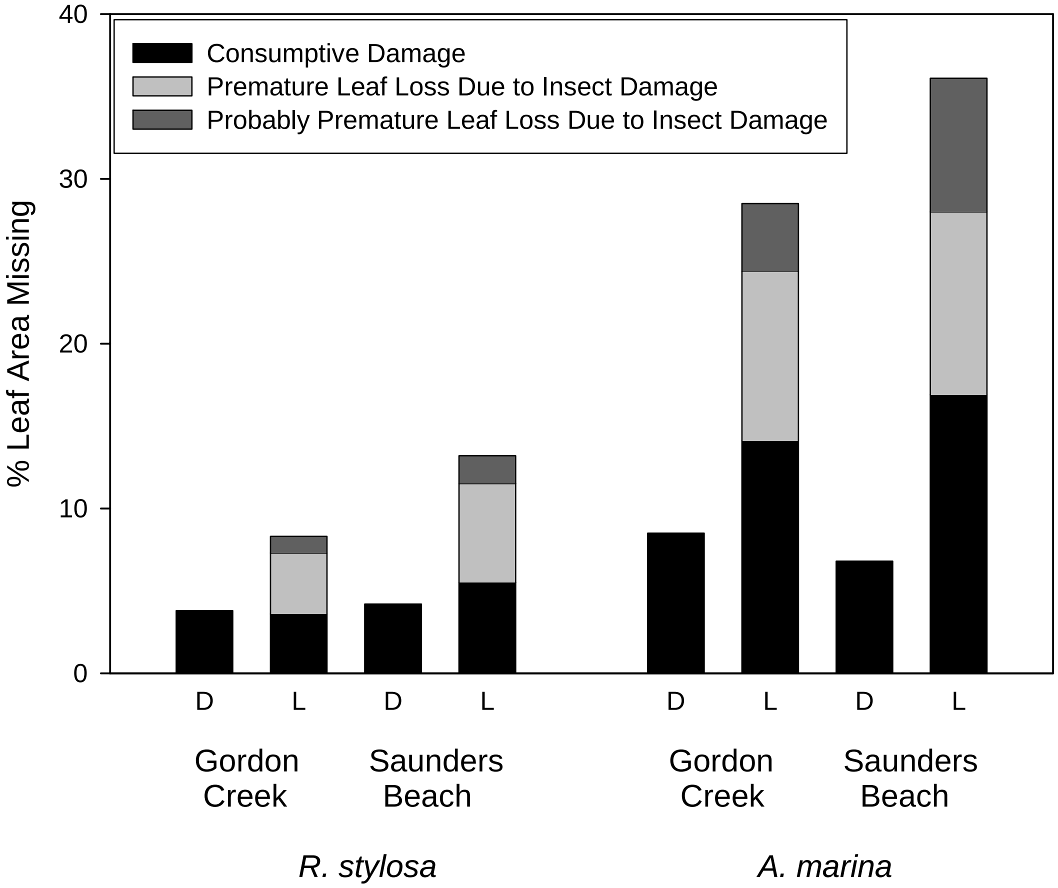
Table 4.5 Loss of Leaf Material (percent leaf area) Attributable to Direct Consumption by Insects or Leaf Loss Related to Insect Damage. Cumulative herbivory is presented in parentheses.

Species	Site	1) Consumptive Herbivory	2) Leaf Loss due to Insects	3) Probable Insect	4) Unknown
A. marina	Gordon Creek	14.1 (14.1)	10.3 (24.4)	4.1 (28.5)	7.9 (36.4)
A. marina	Saunders Beach	16.9 (16.9)	11.1 (28.0)	8.1 (36.1)	12.1 (48.2)
R. stylosa	Gordon Creek	3.6 (3.6)	3.7 (6.5)	1.0 (7.5)	3.0 (10.3)
R. stylosa	Saunders Beach	5.5 (5.5)	6.0 (11.5)	1.7 (13.2)	8.6 (21.7)

The data presented in Table 4.5 represent various degrees of confidence with regard to the degree of leaf loss due to herbivorous insects. The first three columns represent leaf loss due to insect damage that was directly observed or was the most likely explanation for leaf loss. The sum of these values is used in this study as the herbivory estimate from the long-term method (eg, in Table 4.4). Adding the leaves from category 4 (leaves whose fate could not be determined) provides a theoretical maximum herbivory loss, although for conservative reasons, these values are not used any further in this study.

For both species, approximately half of the lost leaf area occurred as a result of insect consumption of leaf material and half from premature leaf fall because of insect damage (Figure 4.2). For *A. marina*, the consumptive herbivore damage was approximately twice that measured by the discrete method whereas for *R. stylosa*, estimates for consumptive damage in the long-term method are similar, or only slightly higher, than those from the discrete method (Figure 4.2). Thus for *R. stylosa*, the faster and simpler discrete method may provide a good estimate of direct herbivore consumptive damage, but not overall leaf loss due to herbivorous insects. However, for *A. marina*, the discrete method underestimated both direct consumptive damage and overall leaf loss due to herbivory.

Figure 4.2 Differences Between Discrete (D) and Long-Term (L) Estimates of Leaf Area Missing and the Contribution of Consumptive Damage Versus Premature Leaf Loss to Long-Term Estimates.



4.3.4 Attribution of Causes of Mortality

Despite most observations being made only at monthly intervals, the majority of leaf loss from the samples could be confidently ascribed to either herbivory or natural causes. Table 4.5 tabulated the damage estimates obtained when including fallen leaves. Table 4.6 summarises the number of individual leaves in each category.

Table 4.6 Number of Leaves Lost Due to Various Mortality Factors

Species	Site	Mortality Factor				
		Insect	Probable Insect	Unknown	Natural Cause/Senescence	Total
A. marina	Gordon Creek	220	73	120	1107	1520
A. marina	Saunders Beach	319	177	203	983	1682
R. stylosa	Gordon Creek	59	17	46	1412	1534
R. stylosa	Saunders Beach	121	33	159	1535	1848

The proportion of leaves whose mortality factor could not be confidently ascribed was higher for *A. marina* than for *R. stylosa* but in no case was the proportion >12% (Table 4.6). The higher result for *A. marina* may be due to the smaller leaves and higher herbivory levels making it more likely that leaves could be entirely consumed between sampling periods, or the tendency of *A. marina* to more readily and rapidly abscise leaves. Although most leaves reach senescence (more so for *R. stylosa* than *A. marina*), a substantial number are lost to insect herbivore damage. This important issue is examined in more detail in the next chapter.

4.3.5 Proportion of Damage by Category Between the Discrete and Long-term Studies

As was the case for data from the discrete study, in the long-term study, direct insect damage was divided into four categories – missing, grazing, galls/mines and necrosis. Due to their low levels, the latter two categories have been combined into the ‘other’ category. Table 4.7 shows the proportion of direct herbivory for each category for the discrete and long-term assessments used in this study.

Table 4.7 Proportion of Leaf Damage by Damage Category

Species	Sites	Damage Category	Percent of Leaf Area Damaged		χ^2	p
			Discrete	Long-Term		
A. marina	Gordon Creek	Missing	55	63	3.43	<0.10
		Grazing	23	22		
		Other	22	15		
	Saunders Beach	Missing	42	46	3.09	<0.10
		Grazing	28	32		
		Other	30	22		
R. stylosa	Gordon Creek	Missing	56	58	0.47	<0.25
		Grazing	34	34		
		Other	10	8		
	Saunders Beach	Missing	67	37	42.60	<0.005
		Grazing	27	56		
		Other	6	7		

For *A. marina* at both sites, the 'other' damage category affected less leaf area in the long-term study than in the discrete study, probably due to the premature loss of galled leaves not being accounted for by the discrete method. Despite this, for all cases except *R. stylosa* at Saunders Beach, the proportion of damage in each category was not significantly different between the discrete and long-term studies (chi-square goodness of fit tests – Table 4.7). For *R. stylosa* at Saunders Beach, this was the only site-species combination in either the discrete or long-term study, where grazing affected more leaf area than all other damage categories. Most of the grazing damage on *R. stylosa* at Saunders Beach was caused by *H. apelles* larvae (see Appendix A). For *R. stylosa*, the 'other' category was relatively minor and consisted almost entirely of necrotic damage. The 'other' category was more important for *A. marina* where it was approximately equally dominated by galls, mines and necrosis.

4.3.6 Frequency and Types of Leaf Damage

The proportion of leaves with each damage type and the proportion undamaged, are presented for both the discrete and long-term studies in Table 4.8. In the long-term study 33-42% of *R. stylosa* leaves remained undamaged compared to 9-10% of *A.*

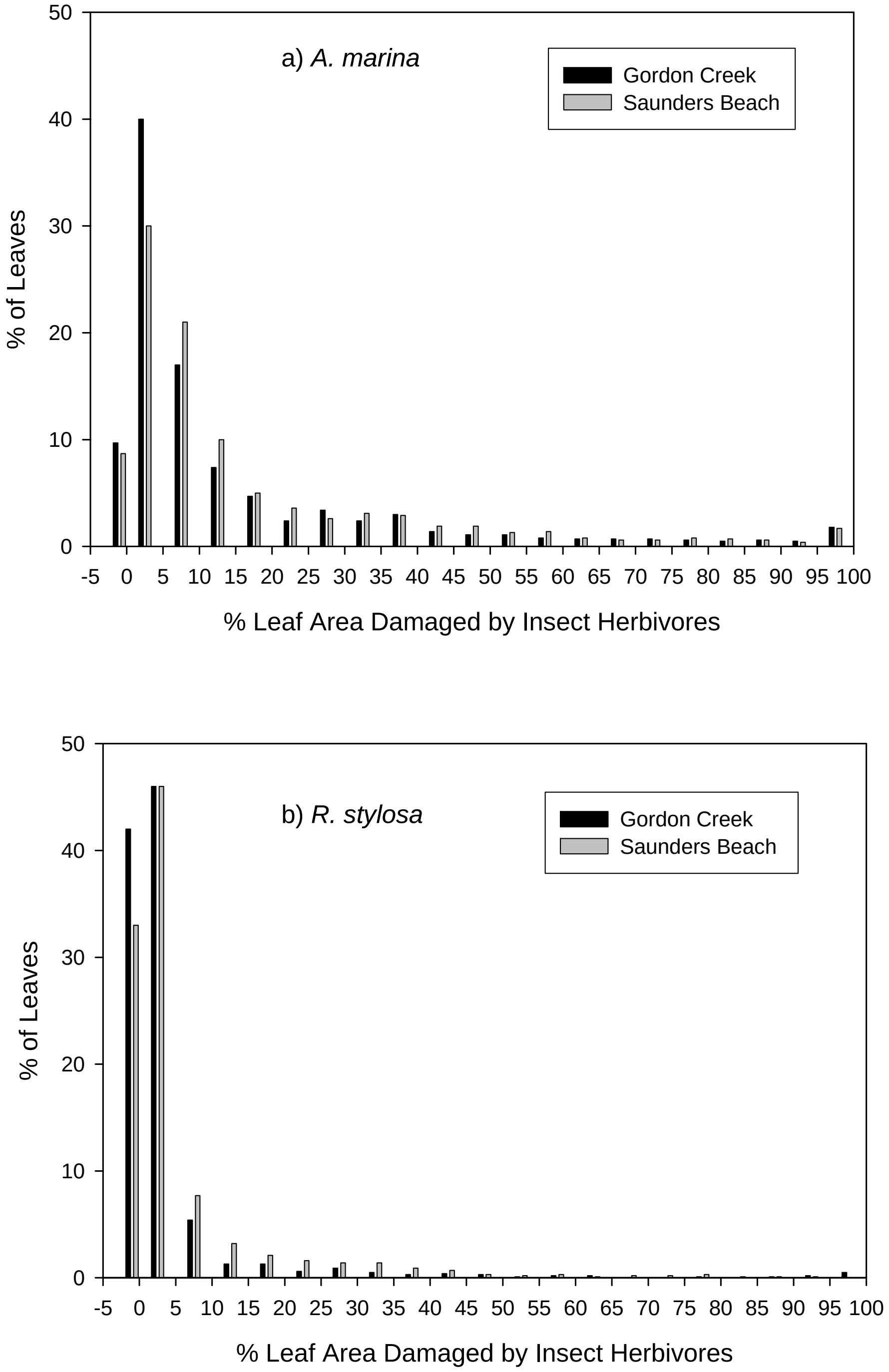
marina leaves. For *A. marina* at both sites, there was no significant difference in the proportion of leaves damaged between the discrete and long-term study. However, for *R. stylosa* at both sites, significantly fewer leaves were recorded as damaged in the long-term study than in the discrete study (chi-square goodness of fit tests Table 4.8).

Table 4.8 Frequency of Damaged Leaves and Damage Types in the Discrete and Long-Term Studies

Species	Site	Damage Category	% of Leaves Damaged		χ^2	p
			Discrete	Long-Term		
A. marina	Gordon Creek	Missing	54	55		
		Grazing	64	42		
		Other	55	60		
		No Damage	10	10	0.01	<0.975
	Saunders Beach	Missing	50	50		
		Grazing	58	34		
		Other	50	66		
		No Damage	11	9	0.28	<0.50
R. stylosa	Gordon Creek	Missing	67	31		
		Grazing	71	34		
		Other	5	4		
		No Damage	7	42	17.19	<0.001
	Saunders Beach	Missing	66	30		
		Grazing	54	44		
		Other	14	10		
		No Damage	13	33	48.86	<0.001

The frequency distributions of leaves with varying amounts of leaf area damaged by insect herbivores in the long-term study are shown in Figure 4.3. For both species, the distribution is strongly skewed towards smaller amounts of leaf area damage, especially for *R. stylosa*. For *A. marina*, leaves with 1-5% damage were the most common, followed by leaves with 6-10% damage. Leaves with 10-15% damage were approximately equally as abundant as undamaged leaves (Figure 4.3a). For *R. stylosa*, leaves with 1-5% damage were also the most common (46% of leaves at both sites) but undamaged leaves were the next most common (Figure 4.3b). Heavily

Figure 4.3 Frequency Distribution of Leaf Area Damage on Mangrove Leaves
a.) *A. marina* leaves b.) *R. stylosa* leaves



damaged leaves (≥30% leaf area damage) were rare on *R. stylosa* (3.6 to 6.2% of leaves at Gordon Creek and Saunders Beach respectively) but comprised 18.8 to 21.2% of *A. marina* leaves at the same two sites.

4.3.7 Accumulation of Herbivore Damage With Increasing Leaf Age

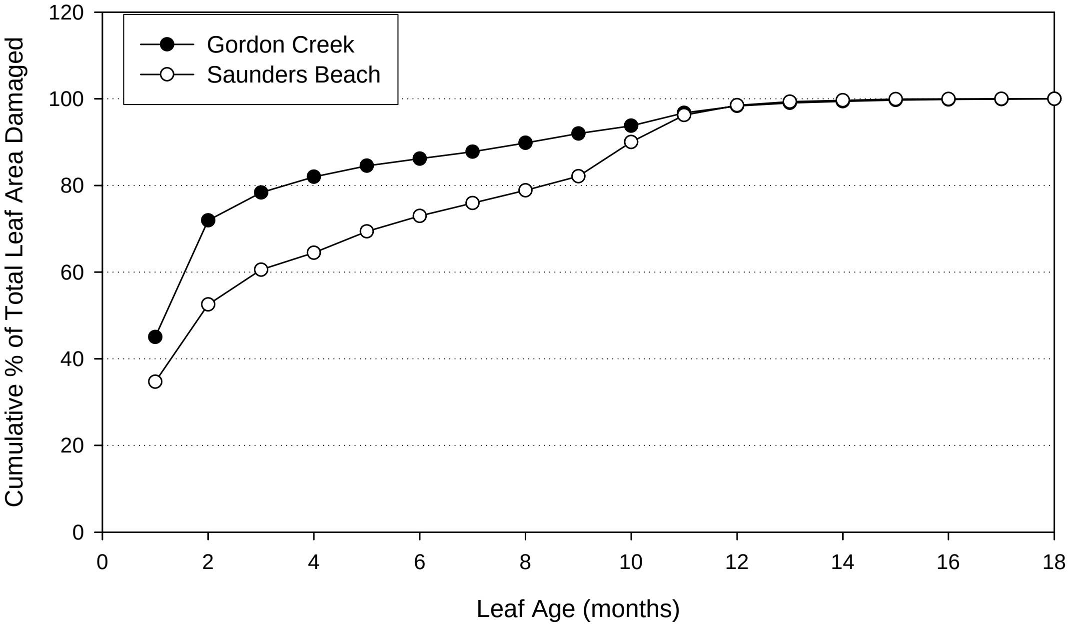
For both species in the long-term study, herbivory was greatest on young leaves and rare on older leaves. Figure 4.4 shows the cumulative proportion of leaf area damage as the cohorts of tagged leaves aged. Though the absolute herbivory levels differed between the two species, the concentration of herbivore damage on the young leaves showed a similar pattern for both species, with two-thirds to three-quarters of total herbivore damage occurring on leaves less than three months old. For both species, a greater proportion of herbivore damage occurred on young leaves at Gordon Creek than at Saunders Beach (Figure 4.4).

4.3.8 Change in Area of Leaf Damage With Leaf Growth

For *A. marina*, the ratio of increase in final to initial area was 1.78±0.35 (S.E.) for leaf area and 2.46±0.36 (S.E.) for hole area. For *R. stylosa*, the ratios were 1.80±0.06 (S.E.) for leaf area and 1.55±0.05 (S.E.) for hole area. Despite these differences, significant regression slopes (ANOVA, df=1,18 and 1,27, F=77.4 and 71.6 respectively, both $p>0.001$) with r^2 of 0.81 and 0.72 for *A. marina* and *R. stylosa* respectively, indicated that, for both species, area of the artificially punched holes increased proportionally with increases in leaf area (Figure 4.5).

Figure 4.4 Cumulative Herbivore Damage on *A. marina* and *R. stylosa* Leaves
(different x-axis scales due to greater leaf longevity of *R. stylosa* leaves - see Chapter 5)

A. marina



R. stylosa

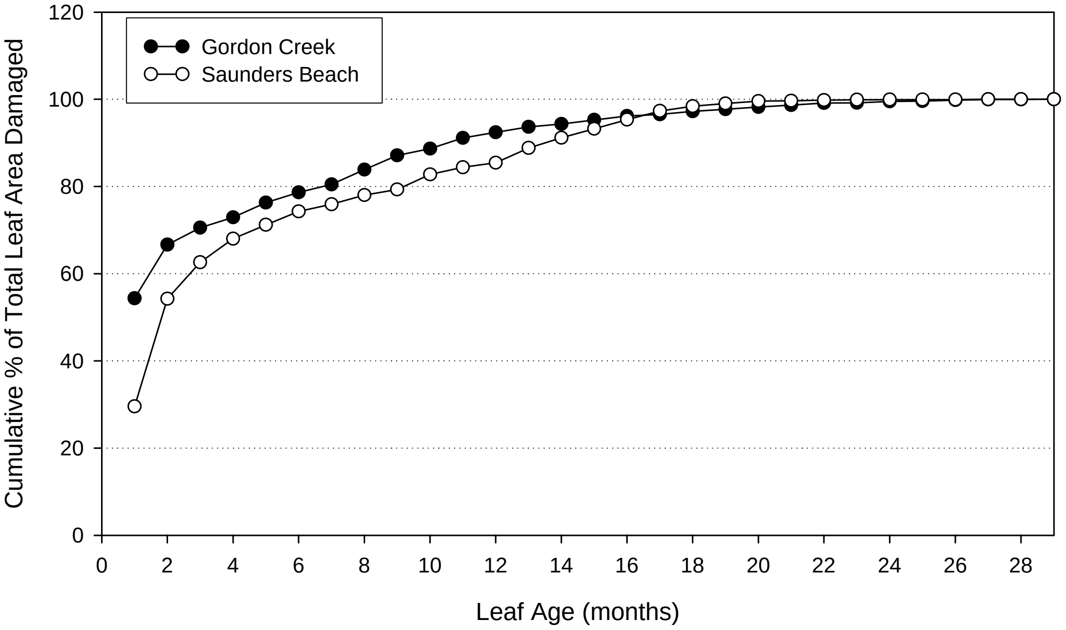
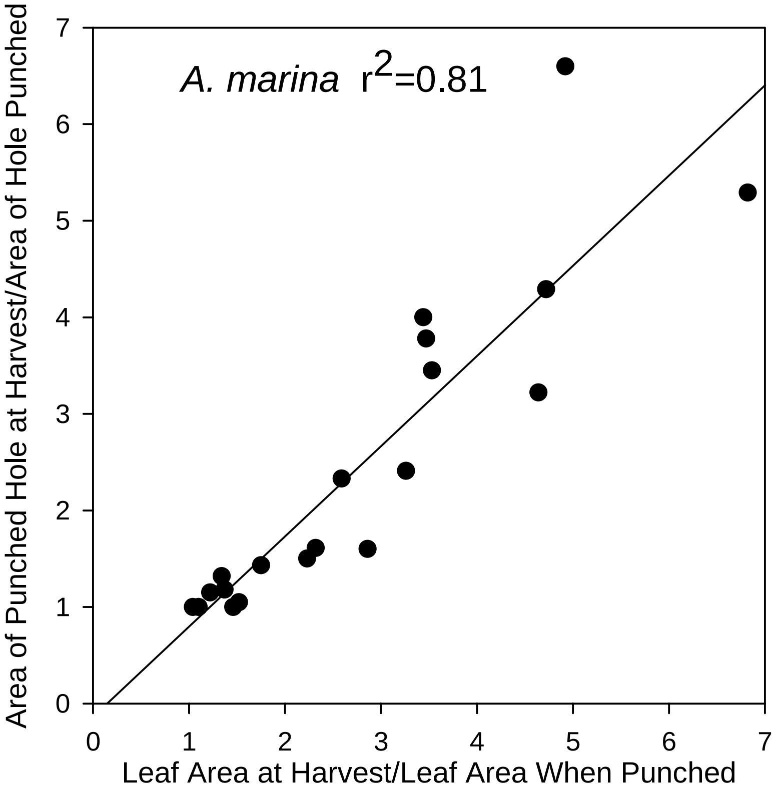
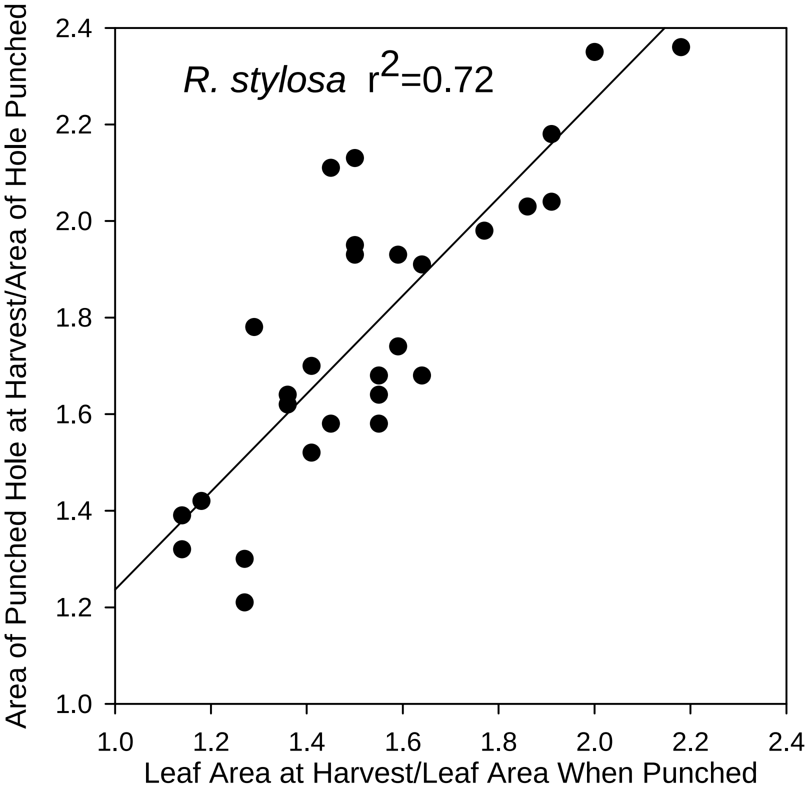


Figure 4.5 Regression Slopes for Change in Leaf Area and Hole Area for *A. marina* and *R. stylosa* Leaves





4.4 Discussion

4.4.1 Review of Mangrove Herbivory Results

Although this thesis aims to re-evaluate the status of insect folivory in mangroves, there has been no shortage of previous interest in the topic. A literature review revealed 26 studies that have assessed levels of insect folivory in mangrove ecosystems (Table 4.9). The studies are spread over North, Central and South America, SE Asia, Australia, New Zealand and India, with Africa being the only major region where mangroves occur in which no studies have been conducted. Studies that reported on aspects of insect folivory but did not collect any specific data on the level of attack (eg, anecdotal notes on insect herbivore damage) are not listed. A variety of methods have been used in the studies reviewed. Of all the mangrove folivory studies reviewed, only seven did not assess the proportion of leaf area damaged: Newberry (1980) and Ozaki *et al.* (2000) both studied the abundance of sap-feeding scale insects; Onuf *et al.* (1977), who mainly focused on leaf abscission, and reported herbivory on the basis of leaf biomass consumed rather than area damaged; Lugo *et al.* (1981), who only counted the number of feeding holes; Law (1995) and Goncalves-Alvim *et al.* (1999) who both assessed the abundance of galls along environmental gradients (primarily salinity); and Elster *et al.* (1999) who assessed frequency of attack on seedlings. Others, such as Feller and Mathis (1997), compared leaf loss due to wood-borers to leaf area damaged by insects feeding directly on the leaves. Duke (2002) made leaf damage assessments on fallen leaves collected in litter traps whilst Lee (1990) compared leaf damage assessments from both canopy leaves and fallen leaves collected in traps.

Except for Lee (1990, 1991) who only assessed *Kandelia candel*, all studies listed in Table 4.9 have included *Rhizophora* and/or *Avicennia* spp. Several studies also assessed additional species eg: de Lacerda *et al.* (1986) included *Laguncularia racemosa*, Rau and Murphy (1990) assessed four Rhizophoraceae species, Kathiresan (1992) assessed 10 species, Johnstone (1981) assessed 23 species, Robertson and Duke (1987) assessed 25 species and Kathiresan (1999) assessed four species. Table 4.10 presents a summary of leaf area damage results from the literature for *Rhizophora* and *Avicennia* species worldwide.

Table 4.9 Insect Folivory Studies in Mangrove Ecosystems (listed in chronological order)

Authors	**Location**	**Species**	**Methods**
Heald 1971	Florida	*R. mangle*	Discrete, sample of 50 leaves only
Onuf *et al.* 1977	Florida	*R. mangle*	Based on biomass consumed, not leaf area damaged
Newberry 1980	Indian Ocean atoll	*A. marina*	Level of infestation by sap-feeding coccid
Johnstone 1981	Papua New Guinea, Sinai, New Zealand	23 species	Discrete, examined within habitat variation
Lugo *et al.* 1981	Panama	*R. mangle*	Discrete, based on number of holes, not leaf area damaged
Lacerda *et al.* 1986	Brazil	3 species	Discrete
Robertson and Duke 1987	North Queensland	25 species	Discrete, compared three sites
Imbert and Rollet 1989	French West Indies	*R. mangle*	Discrete
Rau and Murphy 1990	Thailand	4 species	Discrete, compared three dates
Lee 1990	Hong Kong	*K. candel*	Discrete
Lee 1991	Hong Kong	*K. candel*	Discrete
Farnsworth and Ellison 1991	Belize	*A. germinans,* *R. mangle*	Discrete, compared three sites
Kathiresan 1992	India	10 species	Discrete
Ellison and Farnsworth 1993	Belize	*A. germinans,* *R. mangle*	Discrete on seedlings
Farnsworth and Ellison 1993	Belize	*A. germinans,* *R. mangle*	Long-term but ignored leaf loss and focused on herbivory patterns, not level
Anderson and Lee 1995	Hong Kong	*A. marina*	Discrete, but conducted during insect outbreak
Feller 1995	Belize	*R. mangle*	Various methods, including discrete
Law 1995	Australia	*A. marina*	Gall abundance along environmental gradients
Ellison and Farnsworth 1996	Belize	*R. mangle*	Long-term, but focus on patterns of change, not level of herbivory
Feller and Mathis 1997	Belize	*R. mangle*	Discrete and effects of wood-borers on leaf loss
Kathiresan 1999	Hong Kong	4 species	Discrete
Saur *et al.* 1999	French West Indies	*A. germinans,* *R. mangle*	Discrete
Goncalves-Alvim *et al.* 1999	Brazil	*A. germinans*	Gall abundance along a salinity gradient
Elster *et al.* 1999	Colombia	*A. germinans*	Frequency of attack on seedlings
Ozaki *et al.* (2000)	Bali	*R. mucronata*	Level of infestation by sap-feeding scale insect
Duke 2002	Central Queensland	*R. stylosa*	Assessed damage to fallen leaves collected in litter traps

Several studies have assessed herbivory over considerable time frames. Duke (2002) included 18 samples covering >2 years. Lee (1991) made 12 separate discrete collections over 21 months. Anderson and Lee (1995) made six separate discrete collections over <2 months during a defoliation event. A total of 17 herbivory studies in mangroves have utilised discrete sampling methods (Table 4.9). Only two studies have undertaken long-term leaf damage assessments on tagged leaves in mangroves, but these provide little comparison to the current study. Farnsworth and Ellison (1993) measured herbivory on tagged *R. mangle* and *A. germinans* leaves in Belize on 13 occasions over a 310 day period but did not report overall herbivory level, concentrating instead on rates of herbivory between sampling periods. It is thus not possible to succinctly characterise their results or compare to the current study, although Figure 2 in that paper indicates that herbivory on *R. mangle* never exceeded 12% and on *A. germinans*, it never exceeded 4% of leaf area missing. Despite being a long-term study in the sense that tagged leaves were monitored over time, the tagged leaves were of a wide variety of ages when first tagged and were specifically chosen to be free of damage at the initiation of the study. Thus many of the leaves would have been past the developing stage when herbivory is greatest. Also, fallen leaves were not considered in their damage estimates, with the damage values for each successive sampling period only being made on leaf area missing from leaves remaining on the tagged branches at the end of each time period. Thus, on many important criteria, it is not comparable to the current study. Similarly, Ellison and Farnsworth (1996) monitored herbivory for four cohorts of *R. mangle* leaves over their entire lifespan (average = 9 months). Again the overall herbivory level was not presented and fallen leaves were not taken into account. The authors indicate in their discussion that overall, approximately 10% of standing leaf area was consumed, although Figure 3 in that paper indicates that several cohorts had much higher levels of cumulative herbivory, including up to 50% leaf area missing in one case.

The values obtained from the discrete study in this thesis are approximately within the mid-ranges of values reported in Table 4.10, but are generally lower than those obtained by Johnstone (1981) and Robertson and Duke (1987) for these same species. If the discrete method is taken as a relative measure of herbivory (see 4.4.6 for a discussion of this issue), then herbivory at the two sites used in this study would be considered to be similar to, or less than that recorded elsewhere.

Table 4.10 Literature Values for Leaf Area Damaged by Insect Herbivores on *Avicennia* and *Rhizophora* Species Worldwide. Values in parentheses represent ranges for studies that had multiple sites or samples.

Species	Location	% Leaf Area Damaged	Method	Reference
***Avicennia* spp.**				
A. germinans	French West Indies	3.3 (0.9-4.9)	Discrete	Saur *et al.* 1999
A .germinans	Belize	14.8 (7.7-36.1)	Discrete	Farnsworth and Ellison 1991
A. germinans seedlings	Belize	11.1	Discrete	Ellison and Farnsworth 1993
A. marina	Hong Kong	~7-75%[1]	Discrete[1]	Anderson and Lee 1995
A. marina	North Queensland	10.4 (8.8-12.0)	Discrete	Robertson and Duke 1987
A. marina	Papua New Guinea	5.9 (0.9-18.2)	Discrete	Johnstone 1981
A. marina	New Zealand	0-2.6	Discrete	Johnstone 1981
A. marina	Sinai	5.3	Discrete	Johnstone 1981
A. marina	India	9.3	Discrete	Kathiresan 1992
A. marina	Hong Kong	10.1	Discrete	Kathiresan 1999
A. marina	Townsville, north Qld	6.8-8.5	Discrete	This study
A. officinalis	Papua New Guinea	6.9 (5.2-8.5)	Discrete	Johnstone 1981
A. officinalis	India	12.0	Discrete	Kathiresan 1992
A. rumphiana	Papua New Guinea	5.9	Discrete	Johnstone 1981
A. schaueriana	Brazil	1.1 (0.5-1.5)	Discrete	Lacerda *et al.* 1986
***Rhizophora* spp.**				
R. apiculata	India	2.6	Discrete	Kathiresan 1992
R. apiculata	Thailand	6.2-7.8	Discrete	Rau and Murphy 1990
R. apiculata	North Queensland	4.8 (3.9-5.8)	Discrete	Robertson and Duke 1987
R. apiculata	Papua New Guinea	8.6 (2.8-18.0)	Discrete	Johnstone 1981
R. x *lamarckii*	India	0.8	Discrete	Kathiresan 1992
R. x *lamarckii*	North Queensland	1.4	Discrete	Robertson and Duke 1987
R. x *lamarckii*	Papua New Guinea	5.4 (5.1-5.8)	Discrete	Johnstone 1981
R. mangle	French West Indies	1.2	Discrete	Imbert and Rollet 1989
R. mangle	French West Indies	0.2	Discrete	Saur *et al.* 1999
R. mangle	Belize	12.4 (4.3-25.3)	Discrete	Farnsworth and Ellison 1991
R. mangle seedlings	Belize	3.7-7.1	Discrete	Ellison and Farnsworth 1993
R. mangle saplings	Belize	~10%	Long-term	Ellison and Farnsworth 1996
R. mangle	Brazil	5.5	Discrete	Lacerda *et al.* 1986
R. mangle	Belize	1.0-5.2[2]	Discrete[2]	Feller 1995
R. mangle	Belize	2.5-8.0	Discrete	Feller and Mathis 1997
R. mangle	Florida	5.1	Discrete	Heald 1971
R. mucronata	India	2.7	Discrete	Kathiresan 1992
R. mucronata	Papua New Guinea	3.5 (1.9-5.1)	Discrete	Johnstone 1981
R. mucronata	North Queensland	2.6	Discrete	Robertson and Duke 1987
R. stylosa	North Queensland	6.3 (5.1-7.6)	Discrete	Robertson and Duke 1987
R. stylosa	Papua New Guinea	6.2 (0.8-10.7)	Discrete	Johnstone 1981
R. stylosa	Gladstone, central Qld	30-40%	Discrete	Duke 2002
R. stylosa	Townsville, north Qld	3.8-4.2	Discrete	This study

[1] – Six separate discrete samples were taken over the course of a defoliation event

[2] – Estimated from the control site only in Figure 10 of Feller (1995). Measurements were based on leaves that were known to be at least six months old.

4.4.2 Discrete Study

The greater herbivory level in the lower canopy compared to the upper canopy in the current study was partly due to a greater frequency of damage (for *R. stylosa*, but not *A. marina*) and greater amounts of damage when damage did occur. The proportion of leaf area damage caused by various damage types (missing, grazed or other) was also significantly different between the upper and lower canopies in three of the four comparisons made, although no consistent pattern was apparent. For example, the ‘other’ category was more prominent in the lower canopy of *A. marina* at both sites but less prominent in the lower canopy of *R. stylosa* at both sites.

Whilst the canopy effect was significant, it was not feasible to establish branches for routine long-term field measurement in the upper canopy. In addition there are many other unexplored sources of spatial variation in herbivory that could be equally important. The purpose of this study is to compare methods for assessment in order to improve herbivory estimates, not to evaluate sources of spatial variability. However, the notion that the upper canopy had significantly less herbivory than the lower canopy should be borne in mind.

The finding that herbivory was greater in the lower canopy is not unusual. Landsberg (1989) found this for *Eucalyptus blakelyi*, though the difference there was only 17% compared to 19-81% in this study. Of the five rainforest species studied by Lowman (1985a), three had significantly higher herbivory (more than twice as much) in the lower canopy, and the remaining species were not significantly different although one had considerably greater herbivory in the lower canopy. In contrast to those results, for the rainforest tree, *Argyrodendron actinophyllum*, Bassett (1991a) found no significant difference in herbivory between the upper and lower canopy, Lowman and Heatwole (1992) found a general trend for greater herbivory in upper eucalypt canopies and Abbott *et al.* (1993) found significantly greater herbivory in the upper canopy of jarrah (*Eucalyptus marginata*) in two of the four comparisons made. Jackson (1995) studied three species of rainforest *Alphitonia* trees and found respectively, that leaves in the lower strata had significantly greater, significantly less and no significant difference in herbivory compared to leaves in higher strata. Her study was a very detailed assessment of sources of variability in herbivory and found that twig height was not a major influence on herbivory levels, even where it was statistically significant. Canopy height categories varied between the studies quoted above but they were all much higher than the canopy height in this study. In general, higher herbivory in the lower canopy is thought to be the result of shaded leaves being more palatable (Aide 1993, Coley 1980, 1982, 1983) although it could also be that insects are more common nearer the ground level (Bassett 1991a, 2001).

The frequency with which variation in herbivory with canopy height is reported suggest that it is common to many forest types, although most of the studies showing this are based on the discrete method. As has been shown in this study, the long-term method is a better estimator of true folivore damage, thus the contrast in herbivory between canopy height may not have held true had the long-term study also been conducted in the upper canopy. For instance, if damage types that are poorly represented in discrete studies (eg, leaf loss caused by tip-feeders and wood-borers) are more common in upper canopies (greater branching in the upper canopy may well favour these insects), then long-term studies would reveal greater herbivory increases in the upper canopy than the lower canopy, resulting in less difference between the two canopy heights.

4.4.3 Comparison of Discrete and Long-Term Methods

The long-term method of assessing herbivore damage revealed total leaf loss due to insect herbivores on *A. marina* and *R. stylosa* to be 3-5 times and 2-3 times greater, respectively, than for the discrete method. Given that the majority of mangrove (and also non-mangrove) herbivory studies have only utilised the discrete method, this does pose the question as to what herbivory results would have been achieved in those other studies had they also utilised long-term methods. The results from the discrete study indicate that herbivory at Gordon Creek and Saunders Beach is only in the lower to middle range of that obtained for *A. marina* and *R. stylosa* at three north Queensland sites by Robertson and Duke (1987) and comparable to other studies on these species (Table 4.10). Thus, the high herbivory estimates obtained from the long-term study presented here are unlikely to be due to these sites experiencing unusually high herbivore pressure and such herbivory levels may actually be common in mangroves.

The magnitude of the differences between discrete and long-term methods in this study is also within the range recorded in the literature for the few other species where this comparison has been made (Table 4.11). The higher ratio for *A. marina*, compared to *R. stylosa* in the current study reflects not only the higher leaf damage suffered by *A. marina*, but the resultant increased premature loss of insect-damaged leaves in the former species (Table 4.5) as greater insect damage promotes leaf abscission (see Chapter 5). Loss of damaged leaves continued over all age classes of *A. marina* whereas, for *R. stylosa*, loss of damaged leaves was mostly confined to the first two months (see Chapter 5 for further examination of this point).

Table 4.11 Summary of Leaf Herbivory Results From Studies That Utilised Long-Term Assessment Techniques

Habitat	Species	Discrete	Long-Term	Ratio	Reference
Rainforest	*Toona australis*	4.3	4.9	1.1	Lowman 1984
Rainforest	*Dendrocnide excelsa*	12.3	24.0	1.9	Lowman 1984
Rainforest	*Ceratopalum apetalum*	6.4	26.1	6.4	Lowman 1984
Rainforest	*Nothofagus moorei*	13.5	31.1	2.3	Lowman 1984
Rainforest	*Doryphora sassafras*[1]	12.0	12.3	1.2	Lowman 1984, 1992
Rainforest	*Doryphora sassafras*[1]	6.1	22.7	3.7	Lowman 1984, 1992
Rainforest	*Doryphora sassafras*[1]	5.4	14.9	2.8	Lowman 1984, 1992
Rainforest	*Laportea cordifolia*	9.2	19.5	2.1	Hurley 1995
Plantation	*Laportea cordifolia*	22.1	37.5	1.7	Hurley 1995
Rainforest	*Dendrocnide moroides*	8.1	21.4	2.6	Hurley 1995
Plantation	*Dendrocnide moroides*	19.0	44.9	2.4	Hurley 1995
Rainforest	*Alphitonia excelsa*	n/a	26.4	n/a	Jackson 1995
Rainforest	*Alphitonia petriei*	n/a	53.2	n/a	Jackson 1995
Rainforest	*Alphitoniawhitei*	n/a	20.4	n/a	Jackson 1995
Eucalypt woodland	*Eucalytpus blakelyi*	10.7	15.7[2]	1.5	Landsberg 1989
Eucalypt woodland and cleared pastures	11 eucalypt species	7.6-33.9	35.7 (14.3-60.5)	1.4-5.2	Lowman and Heatwole 1992
Eucalypt woodland	14 woodland species	n/a	22.2 (7.8-43.2)[2]	n/a	Fensham 1994
Eucalypt forest	*Eucalyptus marginata*	n/a	12.9-39.3	n/a	Abbott *et al.* 1993
Eucalypt forest	*Eucalyptus camaldulensis*	n/a	48.8-57.0[3]	n/a	Stone and Bacon 1985
Rainforest	Saplings of 32 lowland species	n/a	24.0 (6.0-61.0)	n/a	Aide 1993
Mangrove	*Avicennia marina*	6.8-8.5	28.5-36.1	3.4-5.3	This study
Mangrove	*Rhizophora stylosa*	3.8-4.2	7.5-13.2	2.0-3.1	This study

[1] From cool temperate, warm temperate and subtropical rainforests respectively

[2] Data does not include loss of leaves, only direct folivore damage

[3] Data includes leaves abscised from the tree regardless of reason for abscission

n/a Did not conduct or include discrete studies for comparison

Lowman (1984), Aide (1993), Lowman and Heatwole (1992), Hurley (1995) and Jackson (1995) all used similar methods of long-term assessment to the current study, whereby new leaves were tagged as they emerged and regularly assessed for herbivore damage for all or most of their lives. Leaves that were deemed to be abscised because of insect damage were included as 100% missing in the calculation of total herbivory estimates. The study of Landsberg (1989) involved tagging already emerged, mature leaves as well as newly emerging leaves and she was unable to confidently attribute the loss of any leaves to various causes, thus they were not included. Fensham (1994) stated there was no difference between discrete and long-term methods for eight tree species in a eucalypt forest on Melville Island, Northern Territory. The discrete data were not presented in that paper and the long-term study involved only three additional assessments after the initial marking, each spaced several months apart. Thus fallen leaves could not have been appropriately accounted for and the long-term result was based on direct consumptive damage only.

For Panamanian lowland tropical moist forests, Aide (1993) and Coley (1982) included leaves prematurely abscised because of herbivore damage and found that damage estimates on leaves increased by 2.4 and 1.6 times respectively. Coley's (1982) study only lasted for three months so the ratio could be expected to increase over a longer time frame. Both studies also only reported herbivory as a rate per day so their results cannot be compared to literature values listed in Table 4.11 and are not listed there.

Although the herbivory reported in the current study is among the highest reported for mangroves, this is only because of the more intensive and inclusive methods utilised in this study. However, losses of very large amounts of leaf material are occasionally reported for mangroves. Duke (2002) recorded leaf area losses of *R. stylosa* from Gladstone in central Queensland, ranging from 17-54% during an outbreak of leaf-feeding caterpillars, that was monitored for two years. Anderson and Lee (1995) found herbivory on *A. marina* in Hong Kong to be as high as 75% but this was the result of intentionally sampling during an outbreak of a defoliating caterpillar with the pre-outbreak level being measured at approximately 7% (this figure estimated from Figure 2 of Anderson and Lee 1995). Although not representative of normal background levels, such outbreaks may be particularly important. The outbreak investigated in Anderson and Lee (1995) has been observed regularly for over 30 years, including being recorded annually from 1986 (Anderson and Lee 1995).

Even using discrete methods under ambient herbivory conditions, higher levels of herbivory than that recorded with the long-term method here have been found on both *Avicennia* and *Rhizophora* species at individual sites by Johnstone (1981) and Farnsworth and Ellison (1991) (see Table 4.10). As these studies utilised discrete methods, it is likely that incorporation of long-term methods, insect-caused leaf abscission (see Chapter 5) and other mechanisms of insect leaf damage (see Chapter 6) would have revealed even higher leaf loss estimates than those reported. The finding that long-term methods produce much higher herbivory estimates than the more commonly utilised discrete methods suggests that herbivory is a much more important component of the ecology in mangrove systems than is currently recognised.

4.4.4 Direct Herbivory Versus Leaf Loss

For both species at both sites in the current study, losses of leaf material via premature abscission of insect-damaged leaves was greater than, or at least equal to, the amount of leaf material directly damaged or consumed by insect folivores. For both species, indirect leaf loss was more important at Saunders Beach than at Gordon Creek. This is a significant result in itself as discrete studies ignore insect-caused leaf fall and most long-term studies consider loss of all leaf material to be 100% consumed without regard to the ecological pathways those leaves enter. Separation of directly damaged leaf material (consumed by insects) and loss of abscised leaves (fall as leaf litter) is rarely undertaken, even where authors have included premature leaf loss in their herbivory estimates.

Patterns of leaf fall are particularly important processes in mangrove ecology and productivity. That insects cause the premature loss of significant amounts of leaf material throughout the year, suggests that in addition to leaf consumption, they also have an ecologically important role in litter fall and cycling. This is already widely recognised in mangroves for sesarmine crabs (reviewed by Robertson *et al.* 1992, Lee

1998), which, from an ecosystem perspective, are considered to be more important as food processors than as food assimilators (Hogarth 1999). The significance of herbivore-induced leaf fall to the ecology of mangrove ecosystems is discussed further in Chapters 5 (in relation to the timing of leaf fall) and Chapter 7 (in relation to the quality of leaf fall).

Few studies are available that compare the amount of leaf material directly damaged by insect herbivores with that detached from the tree because of their damage. None of the available studies are for mangroves and none explicitly examined the proportions in these two categories. Landsberg (1989) monitored herbivory and leaf loss of *Eucalyptus blakelyi* leaves for one year. During that year, 6.2% of leaf area was recorded as being lost to direct folivore damage and an additional 15.5% loss of total leaf area was due to causes other than senescence (note that *E. blakelyi* leaves live for three years). Unfortunately, Landsberg (1989) could not confidently ascribe those losses to herbivory, but her data suggest that indirect herbivory was greater than direct herbivory. Stone and Bacon (1985) monitored herbivory and leaf abscission on *Eucalyptus camaldulensis* over six months. They found that direct herbivory accounted for 50-60% of total leaf area loss over that six months with leaf abscission accounted for the remaining 40-50%. Unfortunately, they did not separate abscission due to insect damage or senescence from the above figures, although senescence would be rare in that sample as *E. camaldulensis* leaves live 18 months or more (Stone and Bacon 1985). Journet (1981) made six repeated discrete samples over 12 months on *E. blakelyi* trees. Damage estimates on leaves retained on the tree were as high as 40%, but inclusion of prematurely abscised leaves pushed the figure as high as 70%. Fallen leaves were not individually attributed to herbivore or non-herbivore factors and the 70% figure is based on the assumption that loss of leaves at less than 40% of average life expectancy was due to insect herbivory.

4.4.5 Patterns of Herbivory by Type, Frequency and Age-Based Distribution of Leaf Damage

Many studies have only examined leaf area missing and have used leaf area meters to assess this rapidly. This method is convenient but does not include other types of leaf damage. In this study, only 37-67% of leaf area damaged consisted of completely missing leaf lamina, so this damage category represents only a portion of total leaf damage, even in discrete studies. Whilst being clear on not including galls or necrosis in their estimates, most studies have not indicated whether or not they have included leaf area grazed in their estimates. However, the distinction between grazed and missing leaf area is important as the damage is done by different groups of herbivores with different effects on the leaves and plants. Galls, leaf mines and necrosis were particularly important for *A. marina*, comprising 15-22% of leaf area damaged. In some locations, leaves killed by wood-borers (categorised as 100% necrosis in this study) can also be significant to leaf area loss. Thus, not only do discrete studies fail to incorporate heavily damaged leaves that are prematurely abscised, but many of these studies further underestimate leaf damage by not including leaf damage types other than complete consumption of leaf lamina.

Herbivory studies typically find that most leaves suffer very little herbivore damage (or none at all) and relatively few leaves suffer substantial damage. In a discrete herbivory study for the Rhizophoraceae mangrove *Kandelia candel*, in Hong Kong, Lee (1991) found that more than 90% of leaves suffered less than 30% damage. In the current long-term study, approximately 95% of *R. stylosa* leaves suffered less than 30% damage and 35 % were undamaged, but for *A. marina*, only 80% of leaves suffered less than 30% damage and less than 10% remained undamaged. Not only were *A. marina* leaves 50% more likely to suffer damage than *R. stylosa* leaves, but the average amount of damage suffered by leaves that were attacked was greater for *A. marina*. Thus, the higher herbivory on *A. marina* in the current study was the result of greater proportion of leaves being attacked, greater damage incurred during such attacks and greater premature loss of damaged leaves (Table 4.5 and 4.6 and which is further explored in Chapter 5).

Although the amount of leaf tissue lost to herbivory was significantly different between the two species, both species had similar patterns of age-based herbivory. Two-thirds to three-quarters of consumptive leaf area damage occurred on young leaves less than three months old, even though this phase occupied only about 25% of the average leaf lifespan for *A. marina* and about 15% of the average leaf lifespan of *R. stylosa*. In most plant species, young leaves are more vulnerable to herbivory than older leaves (Coley and Aide 1991). In a review of age-based herbivory that included data from 73 tropical plant species, Coley and Aide (1991) determined that between 40 and 75% of total lifetime herbivory (herbivory recorded over the entire lifespan of leaves) occurred on young developing leaves. For 32 species of tropical trees in Panama, Aide (1993) found that an average of 27% of total leaf lifetime herbivory occurred during the first month. Potential reasons for preferential herbivory on younger leaves in the current study, such as their higher nutrient contents and lower leaf toughness, are explored in Chapter 7.

4.4.6 Use of Discrete Studies as a Relative Measure of Herbivory

Many studies have used the discrete method for assessing herbivory. Although it significantly underestimates the true level and role of herbivory, it has substantial time and effort advantages that may make its retention useful, provided its limitations are appropriately acknowledged and that the resultant estimates correlate with the true level of herbivory (ie, provide a relative indicator of herbivory). The data from the current study and in Table 4.11 are equivocal about this. For *R. stylosa*, the Gordon Creek site had the lowest herbivory levels for both the discrete and long-term methods. For *A. marina*, Gordon Creek had a higher discrete but lower long-term estimate than Saunders Beach. When comparing between species, *A. marina* had higher herbivory than *R. stylosa* at both sites, regardless of method used. Thus, relative differences were maintained between the two species tested but not between the two sites. The studies of Lowman (1984) and Hurley (1995) show that the ratio of estimates between discrete and long-term methods varies considerably between species at the same site and within species at different sites. Despite this, Lowman (1985a) considered that discrete sampling would be useful for measuring relative differences in herbivory between samples, especially if repeated discrete samples were made. There would still seem to be a role for the use of discrete methods, but it is clear that they should be used with caution, and only after pilot studies that demonstrate their utility. In species where leaves are rarely prematurely aborted (eg, *Toona australis* – Lowman 1984 and several species in Fensham 1994), discrete sampling may be adequate. However, premature leaf abscission due to insect damage is a common occurrence for many tree species and would significantly affect the ratio between data obtained from discrete and long-term methods.

4.4.7 Comparison of Herbivory in Mangroves With Herbivory in Other Forest Types

Coupled with the popular notion that insect herbivory is relatively unimportant in mangroves is the belief that mangroves have lower levels of insect herbivory than other forest ecosystems (Heald 1971, Robertson and Duke 1987, Robertson *et al.* 1992, Lee 1991, Kathiresan and Bingham 2001). In a very influential paper on mangrove folivory, Robertson and Duke (1987) used the discrete method to assess herbivory on 25 mangrove species in north Queensland, with a resultant overall average of 7.0% leaf area missing (range 0.3-35%). Their results were then compared to Lowman's (1984) long-term study of five Australian rainforest species, which had herbivory values ranging from 14-27%, to provide evidence that mangroves have lower herbivory than other tropical forest ecosystems. However, Lowman's (1984) paper also provided discrete estimates, ranging from 2.9-16.5% for a mean of 8.6%, but these estimates were not mentioned by Robertson and Duke (1987).

Because there is so much variation in herbivory levels at many different scales, even moderately convincing evidence that unusually high or low levels of herbivory are consistently associated with any particular forest type or location is difficult to obtain. For instance, within rainforests, pioneer species have substantially different herbivory levels than persistent mature forest species (Coley 1982, 1983) and leaves exposed to sun have different herbivory levels to those in the shade (Maiorana 1981). Coley and Aide (1991) concluded from published herbivory studies that tropical rainforests probably suffered greater herbivore damage than temperate rainforests, but acknowledged the problems with comparing the various assessment methods used in the studies that were reviewed in their analysis. In the 1980's it was suggested that Australian eucalypt forests suffered greater herbivory than North American temperate forests (Fox and Morrow 1986). The ensuing debate generated several papers reviewing this topic (Ohmart *et al.* 1983, Ohmart 1984, Fox and Morrow 1988, Morrow and Fox 1989) and it is generally considered that true differences between the two systems have not been demonstrated. Evidence to suggest that any particular tropical forest type has more or less herbivory than any other forest type has proved elusive (eg, Lowman 1985b), even for systems where more data are available than in mangroves.

In a review of 38 published folivory studies worldwide, Landsberg and Ohmart (1989) showed that apart from occasional anomalies, most studies reported values from 3-17% of leaf area missing (mean of 8.8%). Average values from some key mangrove papers are: Robertson and Duke (1987), 7.0% (n=25 species); Johnstone (1981), 6.8% (n=23 species); Kathiresan (1992), 4.3% (n=10 species); and Rau and Murphy (1990), 8.2% (n= 4 species). Whilst these estimates are all slightly lower than the mean obtained by Landsberg and Ohmart (1989), it would be difficult to conclude, even with more thorough analysis, that they support the notion that mangroves have lower folivory than other forest types. In addition, the above comparison is based on discrete data and data that only accounts for leaf area missing, not other mechanisms of herbivory. For instance, mangroves appear to have high levels of wood-borer activity causing branch death and leaf loss (Feller and Mathis 1997, Feller and McKee 1999, Feller 2002) and loss of developing leaves and leaf buds is particularly significant in *Rhizophora* species (see Chapter 6).

There are few long-term studies available to enable comparison between tree species in different forest types. The two rainforest species studied by Hurley (1995) at Cardwell, 140km north of Townsville, had herbivory levels greater than *R. stylosa* but less than *A. marina* in the current study. Of the five rainforest tree species studied by Lowman (1984) in Queensland and northern New South Wales, all had lower herbivory than *A. marina*, and one had lower herbivory than *R. stylosa*, in the current study. Of the 32 moist forest species studied in Panama by Aide (1993) only six had greater herbivory than *A. marina* and only four had lower herbivory than *R. stylosa*. Of 14 tree species in a tropical eucalypt forest in the Northern Territory studied by Fensham (1994), *A. marina* would rank 4th and *R. stylosa* 10th. Of the 11 eucalypt species studied in the New England Tableland of northern New South Wales by Lowman and Heatwole (1992), only five had greater herbivory than *A. marina* though all had greater herbivory than *R. stylosa*. These results challenge the notion that mangrove tree species have less herbivory than other tropical species. It does appear, however, that *A. marina* is near the higher end of herbivory estimates and *R. stylosa* near the lower end. This highlights the point that herbivory varies substantially between individual species within a forest type. Herbivory studies are usually based on individual tree species, not entire forests. The herbivory level in any given forest will depend on the dominance of particular trees. Based on data from the current study, mangrove forests dominated by *A. marina* will have greater overall herbivory than those dominated by *R. stylosa* (or other similar Rhizophoraceae species which would probably have similar levels of herbivory).

4.4.8 Herbivory on *Avicennia* Versus Herbivory on *Rhizophora*

The lower herbivory on *Rhizophora* spp. compared to *Avicennia* spp. as indicated above, is generally suggested in literature, and is commonly attributed to the higher tannin and lower nitrogen levels found in *Rhizophora* species (Robertson and Duke 1987, Kathiresan 1992, Hogarth 1999, Kathiresan and Bingham 2001). Data presented in Table 4.10 (overall average herbivory values for *Avicennia* spp. are 8.1% and *Rhizophora* spp. 4.6%) indicate some support for the differences in herbivory.

Direct comparisons between various *Rhizophora* and *Avicennia* species have been made in seven published papers, all using discrete methods (Table 4.10). In Brazil, Lacerda *et al.* (1986) found *R. mangle* to have five times as much leaf area damage as *A. schaueriana*. In Belize, Farnsworth and Ellison (1991) found *R. mangle* to have greater herbivory than *A. germinans* at three of the four sites they studied. The fourth site had such a high level of damage on *A. germinans* (36.1%), that the overall average was higher on this species. In a later study, also in Belize, Farnsworth and Ellison (1993) found that across three tidal heights, *R. mangle* had greater herbivory than *A. germinans*. Johnstone (1981) tested 23 mangrove species from 12 genera in Papua New Guinea, including three *Avicennia* species and four *Rhizophora* species. At the genus level, *Rhizophora* (mean leaf area misisng=6.6%) ranked 7th and *Avicennia* (mean=6.0%) ranked 8th while at the species level, *R. stylosa* (mean=6.2%) ranked 14th and *A. marina* (mean=5.9%) tied with two other species for 15th.

Whilst these four studies do not support the notion that *Rhizophora* has less herbivory than *Avicennia*, the remaining three studies, plus this thesis, do. In the French West Indies, Saur *et al.* (1999) recorded greater damage on *A. germinans* than *R. mangle* although both had remarkably low leaf damage levels (1.2 and 0.2% respectively). Robertson and Duke (1987) assessed 25 species from 16 genera at three sites in north Queensland, including *A. marina* and four *Rhizophora* species. In that study, leaf area missing was 6.2% for *R. stylosa* and 10.8% for *A. marina*. In Kathiresan's (1992) study in India, the two *Avicennia* species studied had four times as much leaf damage as the three *Rhizophora* species studied. The current study demonstrates greater herbivory for *A. marina* than *R. stylosa* at both sites studied.

Thus, despite the common perception that herbivory is lower on *Rhizophora* species, the literature is evenly divided on the issue, including for the specific comparison of *R. stylosa* versus *A. marina* (Robertson and Duke 1987 supporting and Johnstone 1981 against). However, this assessment is based on discrete studies. As demonstrated in the current study, long-term methods provide more appropriate estimates. In the current study, premature abscission of insect-damaged leaves was more common in *A. marina*. The ratio of herbivory between discrete and long-term methods would be greater for species with these characteristics, thus potentially resulting in greater herbivory increases for *Avicennia* species than *Rhizophora* species, in long-term studies.

Theory predicts that longer-lived leaves will be better defended against insect attack than shorter-lived leaves and therefore have lower levels of herbivore damage (Chabot and Hicks 1982, Coley 1980, 1988) (see Chapters 5 and 7). In Australia and SE Asia, where herbivory estimates for species of Rhizophoraceae are generally lower than for *Avicennia* species, the *Rhizophora* species also have longer-lived leaves (Table 5.5 of Chapter 5). However, in the Neotropics (including Florida, Belize and Brazil) where herbivore damage estimates are generally more similar between the two groups, *R. mangle* is reported to have a mean leaf longevity that is similar to, or shorter than, that of *A. germinans* (Table 5.5 of Chapter 5). Relative longevity may also contribute to an explanation of why there is a tendency for reported herbivory to be greater on *R. mangle* there than on *R. stylosa* in Australasia. More work on both herbivory and leaf longevity, is required to fully elucidate the nature of the differences in herbivory between these two dominant mangrove plant groups.

4.4.9 The Influence of Leaf Hole Expansion in Herbivory Estimates

Most herbivory occurs whilst leaves are young and still expanding. Herbivore damage incurred during this time may not retain the same shape or area as the leaf continues to expand, so some authors have endeavoured to correct for leaf hole expansion in their herbivory studies. As most herbivory studies measure herbivory by the proportion of leaf area missing, rather than the actual biomass consumed, as long as the area of herbivore damage increases at the same rate as leaf area, then no correction factor is required.

In the first study to account for this process, Reichle *et al.* (1973) found that although leaf hole area increased from 1 to 7-fold over the life a leaf, it increased linearly with leaf area. For leaves of five rainforest species, Lowman (1987) also found that hole area increased linearly with leaf length (used as a surrogate for leaf area). For five rainforest species, Coley (1980, 1982) reported that holes punched in young leaves retained the same proportion of leaf area as the leaves expanded. In contrast, for *Eucalyptus blakelyi*, Landsberg (1989) found that as leaves expanded, hole area increased less than leaf area. For *E. marginata*, Abbott *et al.* (1993) found that as leaves expanded, hole area increased by 57% more than leaf area and recommended that a correction factor be applied, though the significance of this difference was not tested. In the current study punched hole area increased less than leaf area in *R. stylosa* and more than leaf area in *A. marina*, though neither difference was statistically significant.

In mangroves, evaluation of hole size increase has been undertaken in just two studies. For *R. stylosa* and *Ceriops tagal*, Robertson and Duke (1987) found that hole area increased by a factor of 2.08 and 2.37 respectively as leaves expanded, and duly corrected their herbivory estimates by this ratio. However, they did not test whether hole growth was proportional to leaf growth. As they measured herbivory by proportional leaf area missing rather than absolute biomass consumed, the application of a correction factor to the collected data is only applicable if hole growth is different from leaf growth. Farnsworth and Ellison (1993) found that leaf hole expansion ratios varied with tree age, tidal position, leaf age and leaf growth rate, and that these factors had different effects for different tree species. Overall, they found that leaf holes expanded by an average of 1.11 and 1.24 in *R. mangle* and *A. germinans* respectively. They also found that hole growth was proportional to leaf growth in *R. mangle* but not *A. germinans*, although for the former they did not state whether hole area or leaf area grew fastest. Overall, they concluded that the application of a correction factor to their herbivory data was not warranted.

Blanket application of a correction factor also assumes that all herbivory occurs when leaves are newly opened (or at least by the same stage as when the leaf holes were punched), which is clearly not the case. Although two-thirds to three-quarters of leaf herbivory occurs whilst the leaves are immature, this period covers more than just the leaf expansion phase. Rhizophoraceae leaves expand rapidly when they emerge, reaching full size in about five weeks (Robertson and Duke 1987, pers. obs.). The process of hardening and maturation takes longer, during which the leaves remain vulnerable to insect attack, even though they are full-sized or nearly so. In addition, there are other mechanisms of leaf damage that have never been tested for their expansion rates in any study. Leaf grazing, which is a very prevalent form of leaf damage, but very difficult to replicate in its effect (Baldwin 1990) may not respond in the same manner as leaf holes. Leaf area affected by galls and leaf mines increases as leaves expand, but this growth represents new damage so does not require correction.

Results from this and other studies where proportional leaf area loss is measured, suggest that application of correction factors for hole expansion would not usually be warranted. In the current study, application of a small correction factor to that proportion of newly emerged leaves that suffered loss of whole leaf lamina would make no difference to the overall outcomes, especially in comparison to the large discrepancies associated with discrete versus long-term methods. Increasing knowledge of the role of herbivory in mangrove ecosystems would be better served by focusing efforts on more appropriate methods of assessment, where large errors are likely to occur, than with relatively minor correction factors.

4.5 Conclusions

This study has found that for *R. stylosa* and *A. marina*, the two most common and widespread mangrove species in Australia, the long-term method of assessing leaf damage produces estimates 2-3 and 3-5 times higher, respectively, than the more commonly used discrete method. Thus, previous studies of herbivory in mangroves, which have relied on discrete methods, have significantly underestimated the true level of insect herbivore damage. In addition to methodological issues, common forms of leaf damage such as galls, leaf-mines, necrosis and wood-boring are often not considered adequately in herbivory studies.

This study has also shown that insect herbivore damage promotes premature leaf drop and that the amount of undamaged leaf material abscised from a tree because of insect damage is similar to, or greater than, that directly consumed or damaged by insects. Between 16 and 30% of *A. marina* leaves and 5 and 8% of *R. stylosa* leaves are prematurely abscised because of insect damage. The role of insects in promoting leaf fall has rarely been considered in mangrove studies despite being demonstrated by Lee (1990). This process has particularly significant ramifications for the ecology of mangrove ecosystems where leaf loss is considered one of the most important pathways in the food web (Robertson *et al.* 1992, Lee 1998).

Evidence to support the suggestion that mangroves have lower levels of herbivory than other tropical forested ecosystems is lacking and the notion is contradicted by the results of this study. The other popular notion, that *Avicennia* species have greater herbivory than *Rhizophora* species, although supported by the results of the current study, is also shown not to be generally applicable. Overall, these results suggest that the level of herbivory and leaf loss caused by insect herbivores in mangroves is much greater than currently believed and that their role in the ecology of mangrove forests needs to be re-evaluated in light of this.

CHAPTER 5 – EFFECT OF INSECT HERBIVORY ON LEAF LONGEVITY AND PREMATURE LEAF LOSS

5.1 Introduction

5.1.1 Ecological Significance of Leaf Longevity

Plants abscise their leaves when the cost of maintaining them is greater than the return they will receive from them or from investing in new leaves with a greater carbon gain potential. Extended leaf longevity is often the result of environments in which more time is required to provide a positive carbon return on the investment in leaf construction (Kikuzawa 1995). Species whose leaves have longer lifespans may require greater investment in anti-herbivore defences to ensure that the required longevity can be achieved (Coley 1988, Kikuzawa 1995). The increased construction and maintenance costs of these defences (usually physical or chemical compounds) further increases the lifespan required to pay back the increased investment (Chabot and Hicks 1982). Leaf construction costs are a function of the leaf mass per unit area and are generally positively correlated with mean leaf life-span (Reich *et al.* 1992, Kikuzawa 1995, Wright *et al.* 2002). The pay-back time will vary considerably between species and within species growing in different locations. For example, deciduous trees may require as little as nine days to have a positive return, whereas evergreens, which have a greater investment in each leaf, may require up to 30 days (Chabot and Hicks 1982). In *Fragaria virginiana*, the break-even point varies from 12 days to more than 30 days, and the leaf lifespans vary from 50 to 240 days, depending on the microenvironment in which the leaf is positioned (Jurik *et al.* 1979).

In addition to construction costs, dilution of photosynthetic tissue with non-photosynthetic defensive tissue may reduce net photosynthetic rate, further delaying the break-even point (Williams *et al.* 1989, Kikuzawa 1995). Coley (1988) reported positive correlations between leaf lifespan and concentration of defensive chemicals, fibre and lignin in the leaves of 41 tropical tree species in Panama. Koike (1988) also found a correlation between leaf longevity and the ratio of cuticle thickness (a protective material) to leaf thickness for deciduous broad-leaved trees in northern Japan.

Plasticity of leaf longevity within the same species and within individual plants is well documented. Light intensity (Kikuzawa 1988, Kai *et al.* 1991), shading (Kikuzawa 1988, Kai *et al.* 1991, Steinke 1988), flooding (Terazawa and Kikuzawa 1994), plant size (Kikuzawa and Ackerly 1999) and nutrient availability (Aerts 1989, Ackerly and Bazzaz 1995) have all been found to affect leaf longevity within the same species. Plasticity of leaf lifespan is not merely a response to the environment in which the plant lives; it may be a strong factor determining the environments in which a plant can live. Plants with greater plasticity in leaf lifespan and related traits may be able to grow well in a wide variety of habitats whereas those with less plasticity will occupy a narrower range of habitats (Reich *et al.* 1991). Plants can allocate resources either to provide high photosynthetic rates and increased carbon assimilation over short time frames or to providing defensive structures that reduce carbon assimilation over longer time frames, but not to both (Reich *et al.* 1991). In a review of the topic, Kikuzawa (1991) found that leaf longevity is short when leaf photosynthetic rate is high, when the photosynthetic rate decreases rapidly with time or when the construction cost of a leaf is small. Thus leaf longevity may be seen as a trade-off between rapid photosynthesis, leaf construction costs and investment in defences. The wide variety of leaf lifespans and how they vary under different environmental conditions demonstrates that leaf longevity is an important ecological and adaptive strategy of plants.

5.1.2 Leaf Longevity and Insect Herbivory

Because of the many factors that affect leaf longevity, it has been assumed that leaf longevity and habit (eg, evergreen or deciduous) cannot be explained by a single factor (Karlsson 1992, Chabot and Hicks 1982). However, Kikuzawa (1991, 1995) showed that leaf longevity and habit are part of an adaptive strategy that is optimised to maximise plant carbon gain. Loss of leaves due to external factors such as mechanical removal by wind or large animals, or consumption and premature detachment by insects, can disrupt the optimisation of resource use that the plants are trying to achieve.

Because the leaf carbon yield varies with time, the timing of herbivory also makes a significant difference to its impact. Herbivory of the leaf primordia eliminates the opportunity to make a profit but not the investment costs in leaf production. Herbivory on a developing leaf would eliminate most of the profit opportunity and some investment in construction costs. Herbivory of mature leaves would only eliminate the potential yield of the remaining life span. Thus insect herbivory can impact upon a plant's ability to optimize carbon yield by the amount of herbivory *per se* and by its timing and location.

The tendency to shed leaves prematurely depends greatly on the life-history traits and immediate environmental characteristics of the plant and its leaves, as well as the amount and type of tissue removed and its location on the leaf. For immobile herbivores such as gall-formers and leaf-miners, plants may shed leaves in order to remove the herbivores and reduce their populations (Owen 1978). Environmental effects can work in synergy with herbivory and leaf abscission. For instance, both Abbott *et al.* (1993) and Stone and Bacon (1993) found that insect-damaged eucalypt leaves were more prone to abscission when trees were under moisture stress.

5.1.3 Leaf Longevity in Mangroves

Because of the importance of leaf litter in mangrove food webs, the longevity of mangrove leaves has been relatively well studied. These data have been interpreted extensively with regard to the biomass and nutrient content of the material being returned to the forest floor but there have been few attempts to examine variations in leaf longevity. There is also disagreement in the literature on whether mangroves should be considered to have short-lived or long-lived leaves. Choong *et al.* (1992) and Turner (1995) considered that they had short-lived leaves, basing this on comparison with data from Coley and Aide (1991) for shade-tolerant rainforest trees from Panama. Others, such as Feller (1995) and Ellison and Farnsworth (1996) considered that mangroves have long-lived leaves. The relative longevity of mangrove leaves depends on which species are being considered and which other forest types they are being compared to. The variability in leaf longevity between mangroves, even related species, is quite considerable, clouding comparison with other forest types.

Although rarely quantified, in most forest types it is well accepted that insects contribute significantly to premature leaf fall (see section 5.4). In mangrove forests, this has been either ignored as a significant process or considered to be a relatively rare event (Robertson and Duke 1987, Lee 1990, Farnsworth and Ellison 1991, Saur *et al.* 1999).

The previous chapter demonstrated that accounting for insect-induced leaf abscission greatly increased herbivory estimates. This chapter examines leaf longevity of *A. marina* and *R. stylosa*, especially the influence that insect herbivory has on average leaf longevity and the role that it may play in regulating the age and temporal patterns of leaf litter input to the mangrove forest floor.

5.2 Methods

Data for this chapter are taken from the long-term study described in Chapters 2 and 4. These data entail tagging numerous leaves of *R. stylosa* and *A. marina* at Gordon Creek and Saunders Beach. Leaves were checked monthly until they fell from the tree. Thus, unlike many studies where average leaf longevity is determined empirically from patterns of leaf production and fall, this study has direct measurements of leaf longevity for thousands of individual leaves.

Data on leaf longevity were analysed in two ways. The first included all leaves and provided results on patterns of leaf longevity and leaf loss. The second method repeated the same analyses but excluded all leaves entirely consumed by insects or that were deemed to have been prematurely shed from the tree because of insect herbivore damage (as described in Chapter 4). The second analysis is intended to provide information on leaf longevity and leaf fall patterns for leaves that reached senescence. Unlike herbivory data, leaf longevity data conformed to a normal distribution so were not transformed for these analyses.

5.3 Results

5.3.1 Leaf Longevity

Mean leaf longevity for *A. marina* and *R. stylosa* leaves that whose deaths were attributed to insect damage and those that were not, are shown in Table 5.1. As the data are normally distributed, using median longevity produced only minor changes in longevity estimates, so the use of mean longevity is retained throughout this chapter.

Table 5.1 Mean Longevity (months ±1SE) of *Avicennia marina* and *Rhizophora stylosa* Leaves and the Effects of Insect-Induced Leaf Mortality

Species	Site	All Leaves	Insect-Killed Leaves	Leaves Not Killed By Insects	Decline in Mean Longevity (%)
A. marina	Gordon Creek	11.1±0.1	4.2±0.2	12.7±0.1	12.6
	Saunders Beach	10.0±0.1	6.4±0.2	11.5±0.1	13.0
R. stylosa	Gordon Creek	20.9±0.2	4.4±0.6	21.8±0.1	4.1
	Saunders Beach	15.4±0.1	5.7±0.3	16.2±0.1	4.9

Mean leaf longevity was greater for *R. stylosa* than for *A. marina* with the difference between the two species more pronounced at Gordon Creek than at Saunders Beach. For both species, average leaf longevity was less at Saunders Beach, especially for *R. stylosa*. Also for both species, the average age of insect-killed leaves was greater at Saunders Beach. Insect-induced leaf abscission decreased mean leaf longevity for both species at both sites, though the impact was greater in *A. marina* than *R. stylosa*. For both species, insect-caused decrease in average leaf longevity was greater at Saunders Beach than at Gordon Creek.

5.3.2 Between-Tree Variation in Leaf Longevity and Frequency of Insect-Killed Leaves

There was significant variation in leaf longevity between individual trees of both species at both sites and this remained the case whether the analysis included all leaves or just those that were not killed by insects (ie, that reached senescence, Table 5.2).

Table 5.2 Results of One-Way ANOVA's for Between-Tree Variation in Leaf Longevity

Species	Site	Source of Variation	df	F	P
All Leaves Included					
A. marina	Gordon Creek	Between Groups	12	7.947	<0.001
		Within Groups	1507		
	Saunders Beach	Between Groups	12	15.47	<0.001
		Within Groups	1669		
R. stylosa	Gordon Creek	Between Groups	14	15.63	<0.001
		Within Groups	1515		
	Saunders Beach	Between Groups	14	19.58	<0.001
		Within Groups	1833		
Only Leaves Not Killed By Insects Included					
A. marina	Gordon Creek	Between Groups	12	15.57	<0.001
		Within Groups	1214		
	Saunders Beach	Between Groups	12	8.63	<0.001
		Within Groups	1173		
R. stylosa	Gordon Creek	Between Groups	14	24.55	<0.001
		Within Groups	1439		
	Saunders Beach	Between Groups	14	21.60	<0.001
		Within Groups	1679		

The effects of including insect-killed leaves on mean leaf longevity varied considerably between trees, especially for *A. marina*. At Saunders Beach, excluding insect-killed leaves increased mean longevity estimates by up to 48.7% for Tree 4, but as little as 3.8% for Tree 8 (Figure 5.1). At Gordon Creek, increases in mean leaf longevity from excluding insect-killed leaves showed less between-tree variation, ranging from 6.6-24.5% (Figure 5.2).

Figure 5.1 Frequency of Insect-Induced Leaf Loss and its Effect on Leaf Longevity for All *A. marina* Trees at Saunders Beach

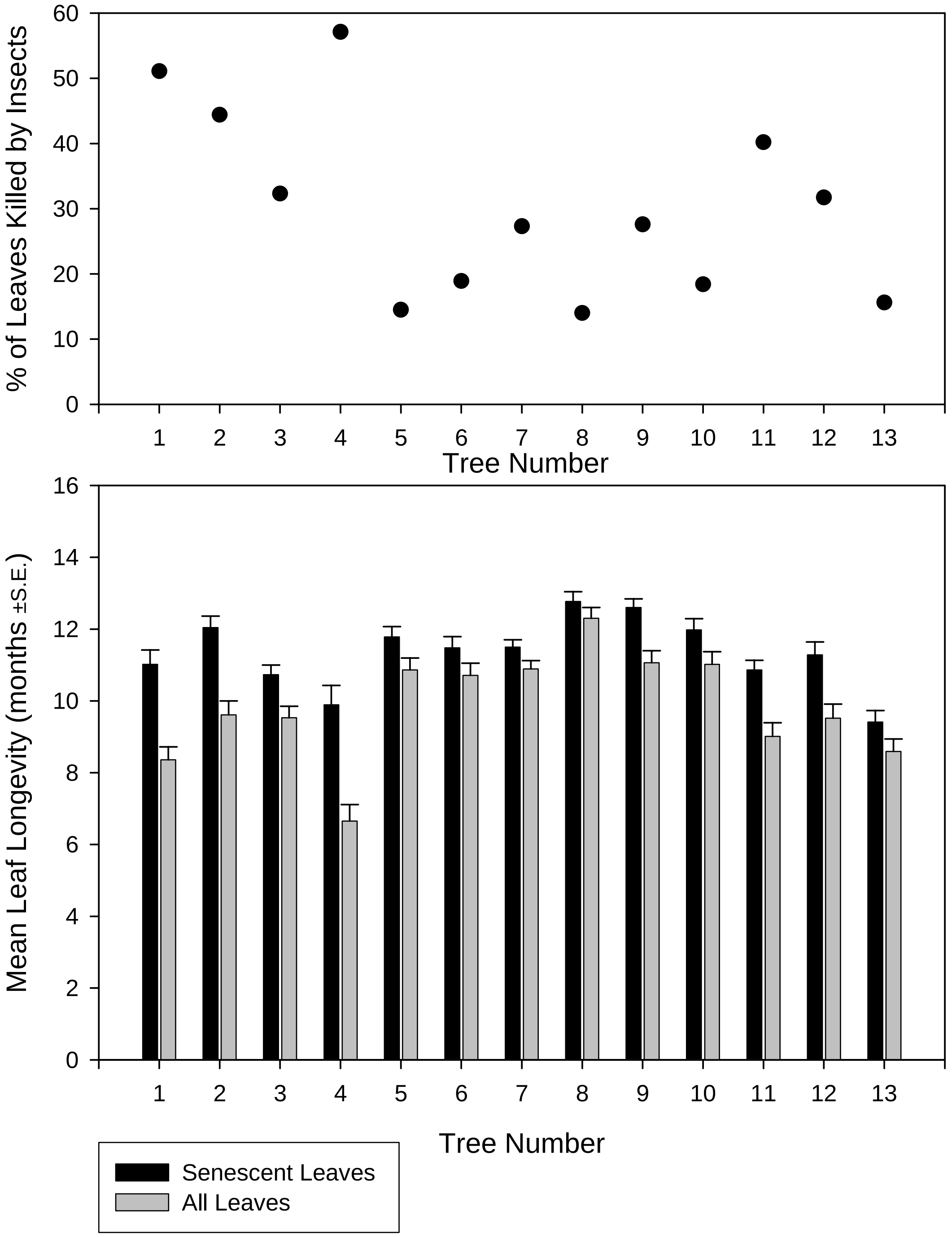
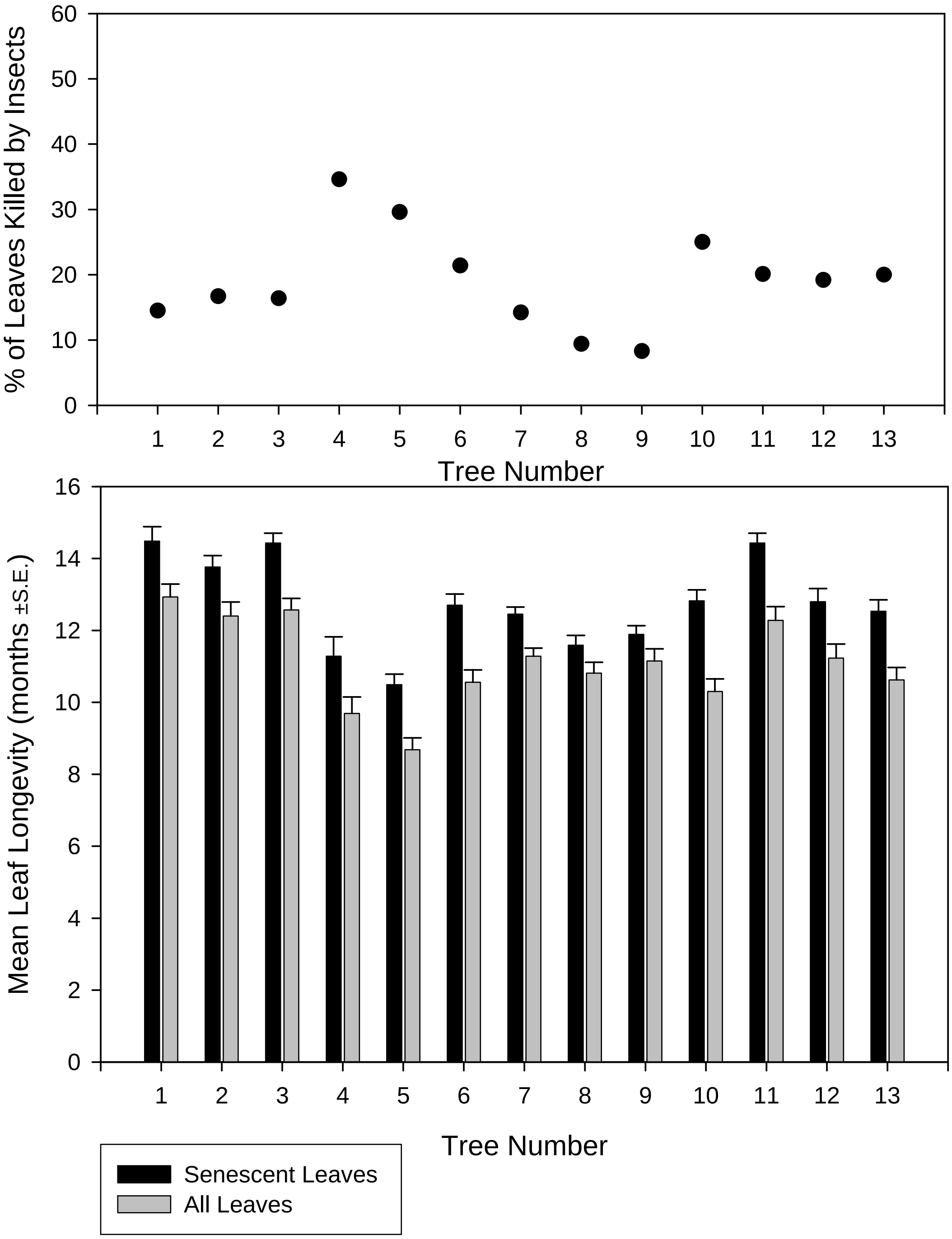


Figure 5.2 Frequency of Insect-Induced Leaf Loss and its Effect on Leaf Longevity for All *A. marina* Trees at Gordon Creek



Individual *R. stylosa* trees also showed considerable between-tree variation in leaf longevity at both sites (Figures 5.3 and 5.4). However, unlike *A. marina*, for many *R. stylosa* trees, the number of leaves killed by insects was too small to have much impact on mean longevity, and overall patterns of insect-induced leaf loss on *R. stylosa* were dominated by a few trees. Nearly 40% of all insect-killed *R. stylosa* leaves at Gordon Creek, occurred on just two trees (10 & 13 – Figure 5.4) and 53% of all insect-killed *R. stylosa* leaves at Saunders Beach, occurred on just three trees (5,8 & 9 – Figure 5.3). This pattern is largely the result of wood-boring beetle larvae whose feeding activities kill entire branches and thus numerous leaves, but whose occurrence is patchy. One *R. stylosa* tree at Saunders Beach and three at Gordon Creek recorded no leaves lost to insects (Figures 5.3 and 5.4). Although there were more *R. stylosa* leaves killed by insects at Saunders Beach than at Gordon Creek, their greater age at the time of death at Saunders Beach resulted in greater increase in mean longevity when insect-killed leaves were excluded from Gordon Creek (Table 5.1).

5.3.3 Patterns of Leaf Fall

Figures 5.5 and 5.6 show the pattern of leaf loss by age for both species at both sites. For *A. marina*, peak leaf fall occurred at around 12 months of age at both sites (Figure 5.5). A substantial proportion of leaves were lost in the first two months whilst the leaves were expanding and developing. Nearly all of these leaf losses were attributable to insect damage. Once full leaf size was achieved, by two months of age, the rate of leaf loss slowed and was relatively constant until senescence set in from nine months of age onwards (Figure 5.5). Leaf loss from 3-9 months of age was due to a combination of insect and non-insect processes. Leaf loss during this period was greater at Saunders Beach, resulting in a reduced peak in senescence at this site and a more even monthly pattern of leaf fall.

For *R. stylosa* (Figure 5.6), there was also a small peak of leaf loss in the first two months during which developing leaves were lost because of insect herbivore damage. Unlike *A. marina*, loss of leaves after this time was very low until mass senescence began after 11 months of age. At Gordon Creek, a total of only 15 tagged leaves (out of 1476) were lost from all 15 trees between the ages of 4-8 months. The higher numbers of leaves lost at Saunders Beach of the same age (n=146 from 1793 tagged

Figure 5.3 Frequency of Insect-Induced Leaf Loss and its Effect on Leaf Longevity for All *R. stylosa* Trees at Saunders Beach

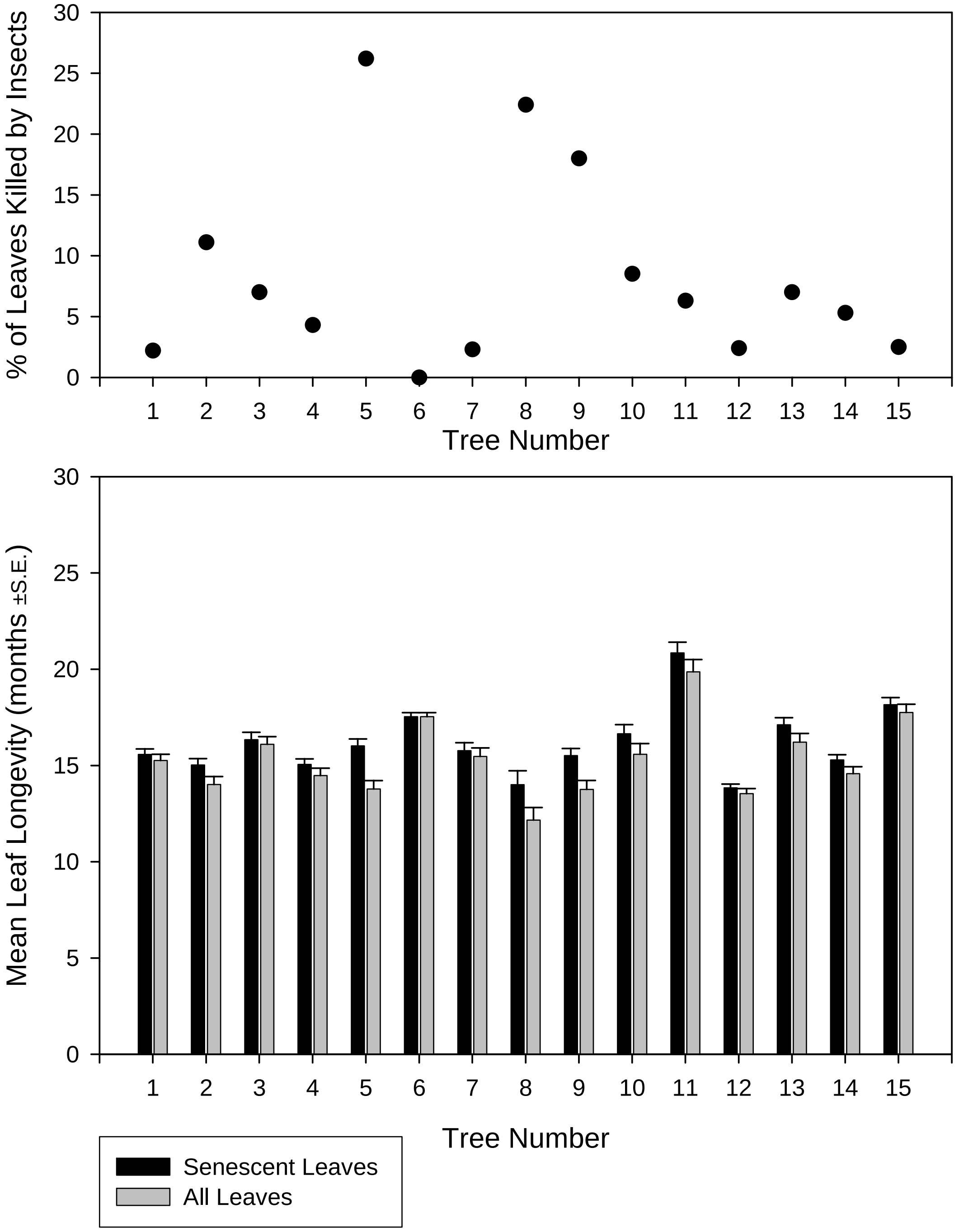


Figure 5.4 Frequency of Insect-Induced Leaf Loss and its Effect on Leaf Longevity for All *R. stylosa* Trees at Gordon Creek

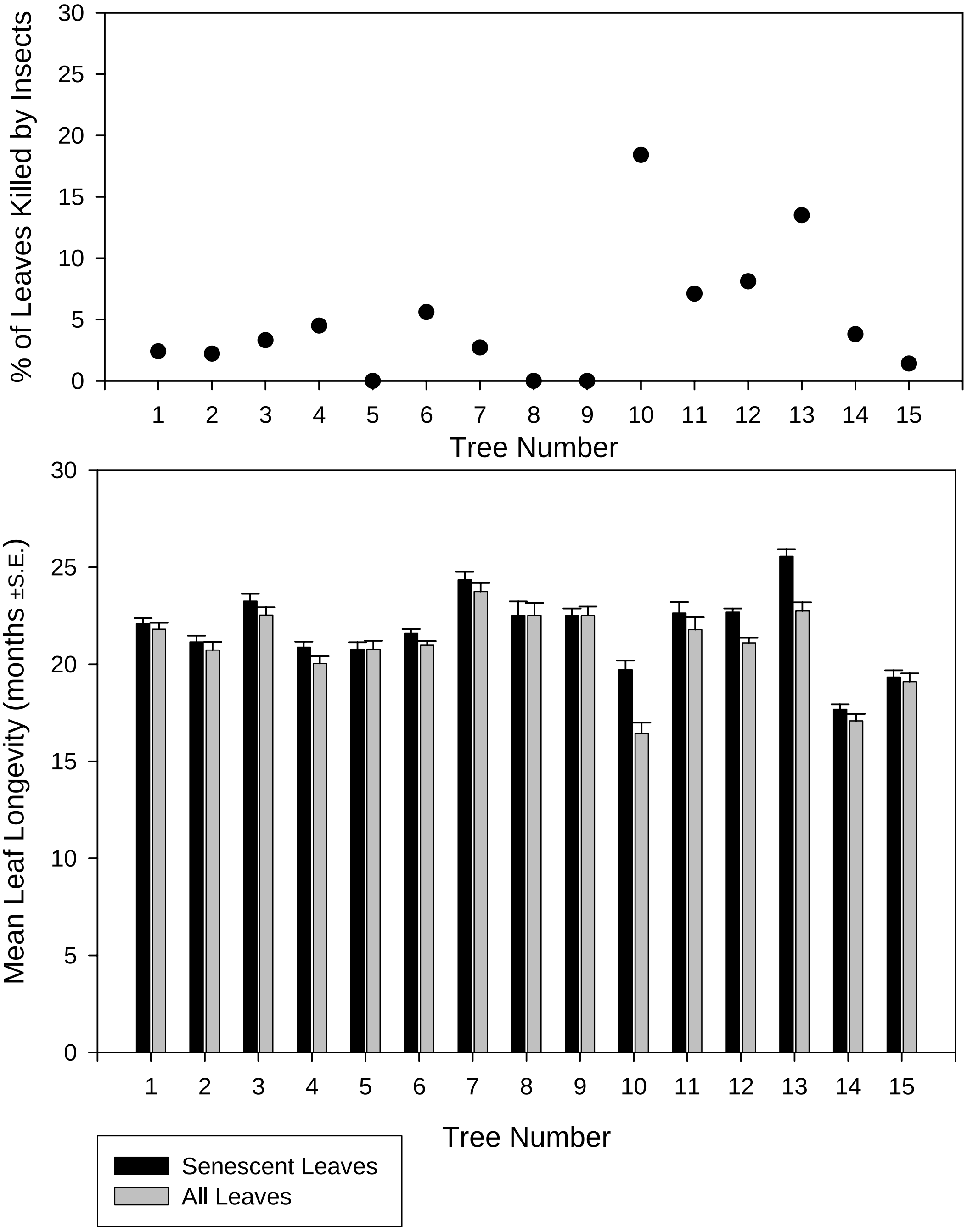


Figure 5.5 Longevity Distribution of *A. marina* Leaves

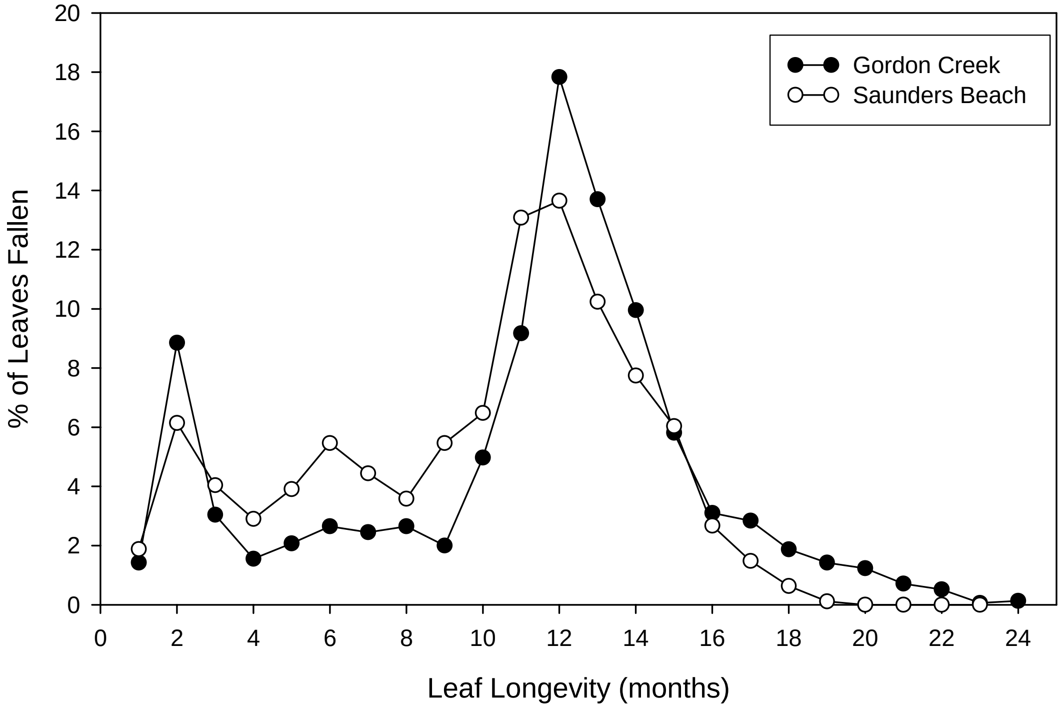
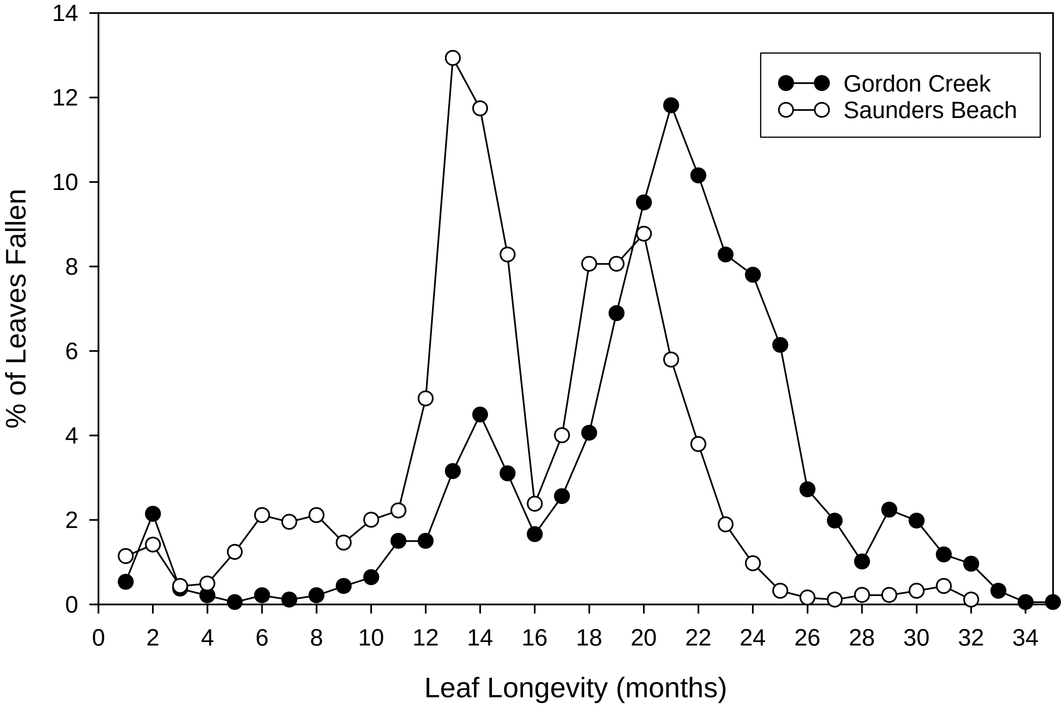


Figure 5.6 Longevity Distribution of *R. stylosa* Leaves



leaves) was largely due to wood-boring beetle larvae present on just a few trees, that killed stems with tagged leaves. There was considerable variation in leaf longevity at both sites with senescence ranging from 11-35 months. Bi-modal peaks of leaf fall were evident at both sites, although they were more prominent at Saunders Beach (Figure 5.6). At both sites, the peaks were spaced seven months apart but both peaks occurred on leaves one month younger at Saunders Beach than at Gordon Creek. The first peak (at 13 months) was the largest at Saunders Beach but at Gordon Creek, the second peak (at 21 months) was the largest (Figure 5.6).

For both species at both sites, the maximum leaf longevity recorded was approximately twice the mean or modal longevity, though long-lived leaves were more common at Gordon Creek than at Saunders Beach. Maximum leaf longevity for *A. marina* was 24 months at Gordon Creek and 19 months at Saunders Beach. Of the 68 *A. marina* leaves from both sites that lived 19 months or more, 66 were from Gordon Creek. Maximum leaf longevity for *R. stylosa* was 35 months at Gordon Creek and 32 months at Saunders Beach. Of the 368 leaves from both sites that lived 25 months or more, 90% (333) were from Gordon Creek. The occurrence of extended leaf longevity was not evenly spread across all trees. For instance, of the 41 *A. marina* leaves that lived 20 months or more at Gordon Creek, 25 were from just two trees. Of the 35 *R. stylosa* leaves at Saunders Beach that lived 25 months or more, 32 were from the one tree, even though this tree was close to, and under what appeared to be the same environmental conditions, as several other trees which had no leaves that lived more than 25 months.

5.3.4 Premature Abscission

For both *R. stylosa* and *A. marina*, leaves with high levels of herbivore damage died younger (Figures 5.7 and 5.8), confirming the observation that herbivore damage does promote premature leaf abscission. The difference in leaf area damaged with leaves of different longevity was significant for both species at both sites (Table 5.3). Tukey's multiple comparison tests (all $\alpha=0.05$) showed that for *R. stylosa* at both sites, leaves that lived only three months or less had significantly greater leaf area damaged than leaves that lived for more than four months, and leaves that lived 13

Figure 5.7 Effect of Insect Herbivore Damage on Longevity of *A. marina* Leaves

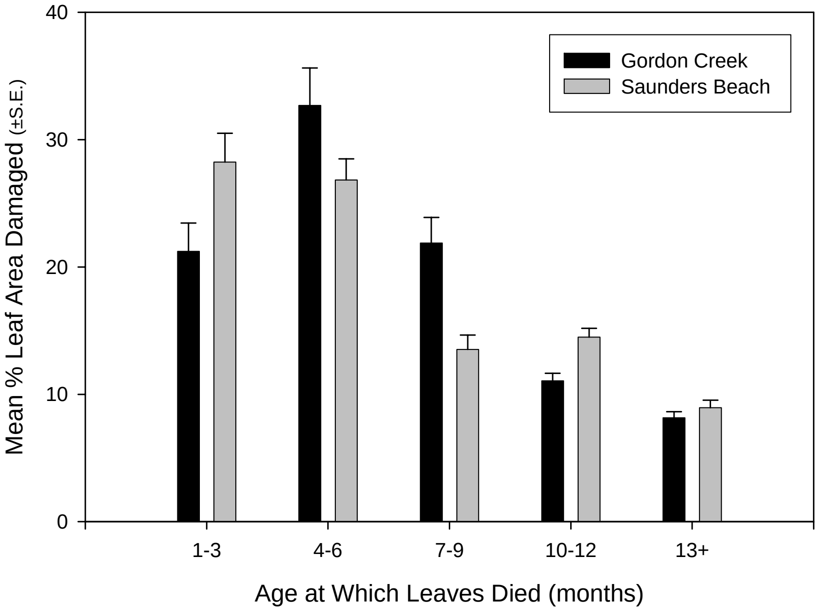


Figure 5.8 Effect of Insect Herbivore Damage on Longevity of *R. stylosa* Leaves

months or more had significantly less leaf area damaged than all other leaves (Figure 5.8). Leaves that lived from 4-12 months at Saunders Beach, and 4-9 months at Gordon Creek, had similar levels of herbivore damage. For *A. marina*, leaves that lived longer were again those which had significantly less herbivore damage (Figure 5.7), although in this case, at both sites, the effect of herbivore damage on premature leaf abscission occurred until 6-9 months of age rather than three months as for *R. stylosa*. At both sites, *A. marina* leaves that lived for approximately one year had significantly less herbivore damage than all other leaves (Figure 5.7).

Table 5.3 Results of One-Way ANOVA's Testing the Effect of Herbivore Damage on Leaf Longevity (data graphed in Figures 5.7 and 5.8)

Species	**Site**	**Source of Variation**	**df**	**F**	**P**
A. marina	Gordon Creek	Between Groups	4	47.09	<0.001
		Within Groups	1515		
	Saunders Beach	Between Groups	4	45.08	<0.001
		Within Groups	1677		
R. stylosa	Gordon Creek	Between Groups	2	161.31	<0.001
		Within Groups	1527		
	Saunders Beach	Between Groups	4	7.81	<0.001
		Within Groups	1843		

The probability of any individual leaf being lost due to insect damage was much greater for *A. marina* than *R. stylosa,* and for both species, was greater at Saunders Beach than at Gordon Creek (Table 5.4). Both *A. marina* and *R. stylosa* have opposite leaves (ie, each leaf emerges directly opposite another leaf at the same time). For both species at both sites, when one member of a leaf pair was lost due to insect damage, the risk that the other member of the pair would also suffer the same fate was greatly increased (Table 5.4). This tendency was much stronger for *R. stylosa* than for *A. marina* (Table 5.4).

Table 5.4 Proportion of Leaves Killed by Insects That Were Part of a Leaf Pair

	A. marina		*R. stylosa*	
	Saunders Beach	**Gordon Creek**	**Saunders Beach**	**Gordon Creek**
Prob. of leaf being killed by insects	29.5%	19.3%	8.3%	4.6%
Prob. for a leaf killed by insects that its partner leaf is also killed by insects	53.6%	51.9%	74.0%	68.4%

5.3.5 Causes of Premature Leaf Death

The proximate causes of leaf loss can be gauged from the level of damage recorded before they were lost, and other observations made during sampling (Table 5.5). In a few cases, more than one damage type was apparent and may have contributed to leaf loss, but in each situation, only the likely main cause is included.

Table 5.5 Numbers of Insect-Killed Leaves and the Type of Herbivore Damage They Suffered

Cause of Leaf Loss	*Avicennia marina*		*Rhizophora stylosa*	
	Saunders Beach	**Gordon Creek**	**Saunders Beach**	**Gordon Creek**
Excessive leaf consumption	128	81	3	17
Excessive leaf grazing	108	52	8	10
Detached leaves	24	4	12	6
Failure to emerge properly	26	53	11	25
Wood-boring larvae	30	19	87	5
Galls/Leaf mines	40	5	0	0
Loss of developing leaves with very little direct damage	110	79	28	13
Other	30	3	5	0
Total Number of Leaves	496	293	154	76

For *A. marina*, excessive damage caused by leaf-consuming and leaf-grazing insects was the main cause of premature leaf loss, especially at Saunders Beach. Numerous young leaves were also lost with relatively minor damage just after emergence or whilst developing. Detached leaves were dead leaves that had detached from the branch but were still attached to other leaves, as a result of leaf-binding lepidopteran larvae, and were a specific, and visually obvious, form of leaf-grazing. Galls were only commonly implicated in leaf loss on *A. marina* at Saunders Beach. Whereas other damage types affected leaves of a variety of ages, galls tended to cause leaf loss of very young leaves only. Old leaves with large galls were rarely located due to their tendency to be prematurely abscised. Wood-boring beetle larvae caused more leaf loss on *R. stylosa* than did leaf-feeding insects, and were especially prevalent at Saunders Beach. *R. stylosa* leaves that failed to emerge properly, or died shortly after emergence with very little direct damage evident, were the result of tip-boring caterpillars (see Chapter 6).

5.4 Discussion

5.4.1 Leaf Longevity in Mangroves

Reported mean leaf longevity in different plant species range from 15 days (Tsuchiya 1989) to more than 45 years (Schulze *et al.* 1986). In mangroves, reported mean leaf longevity ranges from 6 to 42 months with an average around 17 months (Table 5.6 and Table 5.7). Globally, *Avicennia* species show a lower mean longevity and a smaller range of values than *Rhizophora* species (Table 5.6). The lowest *Rhizophora* longevity estimates are for *R. mangle* from Florida and Belize. In Chapter 4, it was noted that although there were exceptions, and all studies utilised discrete methods, in general, in the Americas, *R. mangle* had lower herbivory than *A. germinans* whereas in Australia and SE Asia, *A. marina* had greater herbivory than the various *Rhizophora* species. Theory predicts that shorter-lived leaves will be less defended against insect attack than longer-lived leaves (Chabot and Hicks 1982, Coley 1980, 1988 and discussed in more detail in Chapter 7) which may provide one explanation for these observations.

For *A. marina,* mean leaf longevity was similar between the two sites in the current study but less than those reported from other studies on this species, including Duke (1990b), whose data was based on Black Soil Creek, south of Townsville. For *R. stylosa* in the current study, mean leaf longevity differed by six months between the two sites (Table 5.1) but these values were within the range of literature values for this species (Table 5.6).

Table 5.6 Summary of Literature Values for Mean Leaf Longevity (months) of Various Mangrove Species. Error terms were not presented in most papers.

Species	Location	Life-span (months)	Reference
Avicenniaceae			
Avicennia germinans	Florida	12	Teas 1976 in Steinke 1984
Avicennia marina	South Africa	13	Steinke 1988
Avicennia marina	Kenya	11±0.5 [a]	Ochieng and Erftemeijer 2002
Avicennia marina	Thailand	13(11[b])	Wium-Andersen and Christensen 1978
Avicennia marina	Townsville	13	Duke 1990b
Avicennia marina	Townsville	10±0.1-11±0.1 [a]	This study
Avicennia marina	Jervis Bay, NSW	15	Clarke 1994
Combretaceae			
Lumnitzera littorea	Thailand	9	Wium-Andersen and Christensen 1978
Malvaceae			
Hibiscus tiliaceus [c]	Indonesia	3.5	Moriya *et al.* 1988
Myrsinaceae			
Aegiceras corniculatum	Australia	>24	Clarke 1994
Rhizophoraceae			
Bruguiera cylindrica	Thailand	13	Wium-Andersen and Christensen 1978
Bruguiera gymnorrhiza	China	~10	Wang and Lin 1999
Bruguiera gymnorrhiza	Indonesia	12.8	Moriya *et al.* 1988
Bruguiera gymnorrhiza	Hinchinbrook Is.	27±8[d]	Duke *et al.* 1984
Bruguiera gymnorrhiza	Proserpine	25	Saenger pers.comm. In Duke *et al.* 1984
Bruguiera gymnorrhiza	South Africa	~20-32	Steinke 1988
Ceriops tagal	Thailand	24(18[b])	Wium-Andersen and Christensen 1978
Ceriops tagal	Hinchinbrook Is.	42±12 [d]	Duke *et al.* 1984
Ceriops tagal	Gladstone	27	Saenger pers.comm. In Duke *et al.* 1984
Ceriops tagal	Proserpine	21	Saenger pers.comm. In Duke *et al.* 1984
Kandelia candel	Hong Kong	9-14[e]	Lee 1991
Rhizophora apiculata	Indonesia	12.4	Moriya *et al.* 1988
Rhizophora apiculata	Thailand	17-18(15[b])	Wium-Andersen and Christensen 1978
Rhizophora apiculata	Hinchinbrook Is.	22±3 [d]	Duke *et al.* 1984
Rhizophora x *lamarckii*	Hinchinbrook Is.	27±12 [d]	Duke *et al.* 1984
Rhizophora mangle	Florida	6-12	Gill and Tomlinson 1971
Rhizophora mangle	Belize	9	Ellison and Farnsworth 1996
Rhizophora mangle	Belize	18	R. Twilley unpub. data in Feller 1995, 1996
Rhizophora mucronata	South Africa	~22	Steinke 1988
Rhizophora mucronata	Thailand	11	Wium-Andersen 1981
Rhizophora stylosa	Hinchinbrook Is.	19±4 [d]	Duke *et al.* 1984
Rhizophora stylosa	Gladstone	11	Saenger pers.comm. in Duke *et al.* 1984
Rhizophora stylosa	Proserpine	18	Saenger pers.comm. in Duke *et al.* 1984
Rhizophora stylosa	Townsville	15±0.1-21±0.1[a]	This study
Rubiaceae			
Scyphiphora hydrophyllaceae	Thailand	10	Wium-Andersen 1981
Sonneratiaceae			
Sonneratia alba	Indonesia	6.5	Moriya *et al.* 1988

[a] ± Standard Error, except Ochieng and Erftemeijer (2002) which is ± Standard Deviation

[b] values in brackets recalculated by Duke *et al.* (1984) or myself because of arithmetic errors in the original paper

[c] not an obligate mangrove species, but this data was taken from trees within a mangrove forest

[d] error terms are calculated as 95% confidence limits

[e] based on median, not mean, longevity

The values in Table 5.6 are all based on mean estimates, except Lee (1991) which is based on median longevity. In none of the listed papers was the age-based pattern of leaf fall presented, and in only two papers (Duke *et al.* 1984 and Ochieng and Erftemeijer 2002), was evidence of the variability of the estimates provided. In fact, several papers provide no or very little evidence as to how their longevity estimates were obtained. Thus, despite many studies that have examined leaf longevity in mangroves, this is the first to report on the nature and dynamics of age-based leaf fall. The dynamics of leaf fall are such that mean estimates of longevity, the basis for most of the studies reported in Table 5.5, do not capture the wide variation of longevity among individual leaves. For instance, the current study demonstrates frequent loss of developing leaves at very young ages (more so for *A. marina* than *R. stylosa*) and a wide range of leaf longevity, with maximum longevity more than twice the mean longevity in both species. For *R. mangle* leaves in Florida, Gill and Tomlinson (1971) also stated that some leaves lived more than twice as long as the mean longevity of nine months, but provided no supporting data.

In the current study, there was a greater spread of individual leaf longevities for *R. stylosa*, and for both species, the spread of individual leaf longevities was greater at Gordon Creek. For *A. marina* at Saunders Beach and Gordon Creek, only 25% and 32% of leaves respectively, fell within one month (~10% of mean longevity) either side of the mean. For R. *stylosa* at Saunders Beach and Gordon Creek, only 28% and 47% of leaves respectively, fell within two months (~10% of mean longevity) either side of the mean.

For *R. stylosa*, bimodal peaks of leaf fall were apparent at both sites; however, this did not cause a significant distortion of the mean values as compared to using median values (15.5 vs. 15 months at Saunders Beach and 20.9 vs. 22 months at Gordon Creek for mean and median longevities respectively), because, at both sites, one peak was dominant. However, at Saunders Beach, the first peak at 13 months was dominant and at Gordon Creek, the second peak at 21 months, was dominant. Thus the differences in leaf longevity and age-based patterns of leaf fall between the two sites are much greater for *R. stylosa* than for *A. marina*.

There is some disagreement in the literature as to whether mangroves have short or long-lived leaves compared to other tropical tree species. Whether the mangrove environment is one in which longer-lived leaves would be expected is also debatable. Species with longer-lived leaves tend to occur in stressful environments such as arid or desert regions, shaded forest understorey, or nutritionally stressed environments (Kikuzawa 1995). Mangrove environments are considered harsh by most standards, and are usually nutrient-limited (Boto 1992, Feller 1995), yet the most common species are well-adapted to these conditions and productivity levels are similar to many other forest types (Lugo and Snedaker 1974). The level of stress experienced by individual trees is likely to vary considerably across short spatial gradients (eg, tidal gradients).

Two studies have commented on leaf longevity comparisons between mangroves and other tropical forests: Choong *et al.* (1992) considered that mangroves had short-lived leaves, and Ellison and Farnsworth (1996) considered that mangroves had longer-lived leaves, compared to most tropical trees. This disparity is further complicated by the fact that Choong *et al.* (1992) used an estimate of typical mangrove leaf longevity nearly twice that (17 months vs. 9 months) of Ellison and Farnsworth (1996). The conclusion of Ellison and Farnsworth (1996) cannot be supported as most of the data upon which it is based (listed in Reich *et al.* 1991, 1992) found leaf longevity of tropical species to be greater than nine months. For example, Reich *et al.* (1991) found mean leaf longevity of 23 Amazonian rainforest species to vary from 1.5 to more than 50 months, with the majority being greater than 10 months, and half greater than 20 months. The mean leaf longevity for mangroves calculated from the studies listed in Table 5.6 is the same as that used by Choong *et al.* (1992) (ie, 17 months). Choong *et al.* (1992) felt that mangroves had lower toughness and sclerophylly than would be predicted from the resource availability hypothesis. However, this conclusion of lower than expected leaf longevity was based on comparison with shade-tolerant tropical rainforest species using data from Coley and Aide (1991), presented in Table 5.7.

The range of leaf lifespans covered by tropical rainforests encompasses that known for mangroves so there is little to be gained from comparing habitat types in this regard without further reference to more specific functional or sub-habitat comparisons. For example, Coley and Aide (1991) found that in tropical rainforests, shade-tolerant species had leaf lifespans several times longer than sun-demanding gap specialists. Mangrove forests have little vertical stratification in the canopy, and generally no understorey vegetation (Janzen 1985, Lugo 1986, Snedaker and Lahmann 1988). Thus, all species are heavily exposed to the sun (even if individuals of those species can sometimes be found growing in well-shaded environments), so are not functionally similar to the shade-tolerant species of Coley and Aide (1991). No gap-specialist species are recognised for mangrove communities either, with most gaps colonised by members of the surrounding species (Smith 1987, Clarke and Kerrigan 2000). Thus, there are also no mangrove species that could be considered functionally similar to the gap specialists found in rainforests as studied by Coley and Aide (1991). Though it might appear from the data in Table 5.7 that mangroves have an intermediate leaf longevity compared to trees in other tropical forests types, such comparisons require further data and consideration of modifying factors.

Table 5.7 Comparison of Mean Longevity Data from Published Literature for Various Forest Types. (Data are taken from Coley and Aide 1991 except the mangrove data which was compiled from Table 5.6)

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Even within mangroves, there is considerable variability in leaf lifespans (Table 5.6). The estimate of Twilley (unpub. data in Feller 1995, 1996) for *R. mangle* in Belize is twice that of Ellison and Farnsworth (1996) from the same area. Mean longevity for *R. stylosa* in north Queensland ranges from 11 months at Gladstone (P. Saenger pers. comm. in Duke *et al.* 1984) to nearly 21 months (Gordon Creek, this study). Reported mean longevity for *Ceriops tagal* at Hinchinbrook Island is twice that for the same species at Proserpine (Table 5.6). Even at the same site, values can vary considerably. For *Kandelia candel* in Hong Kong, Lee (1991), found that mean leaf longevity was 9 months for leaves produced in summer and 14 months for leaves produced in winter. In Florida, Gill and Tomlinson (1971) also reported different leaf longevity for *R. mangle* leaves produced at different times of the year. Steinke (1988) reported that longevity of *Bruguieria gymnorrhiza* leaves at Mgeni estuary in South Africa was affected by exposure, with leaves in sun, semi-shade and shade, having mean longevities of 89, 103 and 141 weeks respectively. Given the strong environmental gradients across short distances in mangrove habitats, and the range of sun-exposure gradients under which individual species grow, it is not surprising that a wide range of leaf longevities have been reported for mangroves. In the current study, there were significant differences in leaf longevity between individual trees for both species at both sites. This is despite the relative homogeneity of the stands at each site, especially for *R. stylosa*, the trees of which were believed to essentially be within the same micro-habitat at each site. From the current study and the data summarised in Table 5.6, it appears that variability of leaf longevity is greater for Rhizophoraceae species than for *Avicennia* species, but there is insufficient data at present to confirm this.

5.4.2 Reductions in Leaf Longevity Caused by Insect Damage

Although many studies have found that insect-damaged leaves are prematurely shed (Baldwin 1990, Risley 1993, see also 5.4.5), this has rarely been quantified, and the effect on overall mean longevity of any cohort or leaf population is not often determined. An exception is Wallace and O'Hop (1985), who found that feeding by larval and adult beetles on water lillies reduced average leaf longevity from more than six weeks to 17 days even though the average area of standing leaf crop grazed was only 13%. Similarly, Kouki (1991) recorded reductions in leaf longevity of up to 60% in water lillies infested by beetles. In a life-table analysis of leaves, Center (1985) demonstrated that insect herbivores reduced longevity of water hyacinth leaves by 34%. Lee (1991) demonstrated through artificial leaf damage that more than 40% loss of leaf area was required to cause premature leaf loss in *Kandelia candel* mangroves in Hong Kong. Because the frequency of such leaves was exceedingly low (<0.5% of leaves), it was concluded that insect herbivory is unimportant as a regulator of leaf litter dynamics. However, such artificial studies are notorious for significantly overestimating the amount of damage required to cause premature leaf detachment due to their failure to accurately simulate herbivore damage (Baldwin 1990).

Although premature leaf abscission in mangroves has often been observed (see section 5.4.5), this is the first study to quantify reductions in mean leaf longevity of mangrove species due to insects. This effect was much greater for *A. marina* than for *R. stylosa*, reflecting the greater herbivore damage suffered by *A. marina* and the higher proportion of leaves that were more heavily damaged (see Chapter 4). These estimates of longevity reduction may be conservative because the methodology did not allow investigation of whether the timing of senescence was influenced by herbivory. Given that regulation of leaf longevity is one of the main mechanisms by which plants maximise and regulate their growth and productivity (Kikuzawa 1995), significant departures from the optimum leaf longevity caused by insect-induced leaf abscission may be costly to tree productivity and vigour.

The average age of insect-killed leaves was similar for the two species studied. This is somewhat surprising as there are several herbivores that attack and badly damage mature *A. marina* leaves whereas mature *R. stylosa* leaves are relatively immune from such damage, except for leaves killed by the activities of wood-boring beetle larvae. For both *A. marina* and *R. stylosa*, the average age of insect-killed leaves was greater at Saunders Beach than at Gordon Creek. Thus site differences were more important than species differences for this parameter. For *R. stylosa*, the greater average age of insect-killed leaves at Saunders Beach compared to Gordon Creek can be attributed to the large number of older, mature leaves killed by wood-boring beetle larvae. For *A. marina*, the greater average age of insect-killed leaves at Saunders Beach can be attributed to a greater proportion of mature leaves ‘detached’ by leaf-grazing caterpillars and the lower proportion of very young leaves lost whilst still expanding.

5.4.3 Variation Between Trees in Leaf Longevity and Premature Abscission

For both species at both sites, there was significant between-tree variation in mean leaf longevity and the percentage of leaves killed or prematurely abscised because of insect damage. For *A. marina*, despite similar overall impact of insect-killed leaves on mean leaf longevity at both sites, between-tree variation of these effects was greater at Saunders Beach than at Gordon Creek. Excluding insect-killed leaves reduced the range in mean longevity between trees by 50% at Saunders Beach but only 6% at Gordon Creek. This reflects the greater number of leaves shed because of insect damage on some trees at Saunders Beach which therefore had strong effects on mean leaf longevity. When all leaves are included in mean longevity estimates, the variation between trees was greater at Saunders Beach (range 6.65-12.3 months) but when insect-killed leaves were excluded, the variation between trees was greater at Gordon Creek (range 10.49-14.48 months). Between-tree variation was greater for *R. stylosa* than for *A. marina*, exemplified by the fact that at Gordon Creek and Saunders Beach, 40% and 53% of insect-killed leaves were from just two and three trees respectively. Although between-tree variation is not to be ignored, the number of replicate trees selected at each site and the range of locations in which they occurred are sufficient to provide an accurate overall picture of site characteristics.

5.4.4 Pattern of Leaf Fall

For both species at both sites, the greatest proportional loss of leaves to insect damage occurred on developing leaves aged 1-2 months. Not only are younger leaves more likely to suffer greater herbivore damage (Chapter 4), but according to the models of Kikuzawa (1991, 1995), for any given level of damage, they are more likely to be shed because investing further energy into developing an already damaged leaf is sub-optimal when those resources could be re-allocated elsewhere (eg, into new undamaged leaves). The rate of loss of leaves due to insect damage declines after the leaves become fully developed, although this decline is less apparent for *A. marina*. In *R. stylosa*, once leaves become mature, few insects feed upon them and they are very rarely shed because of insect damage. However, many mature *R. stylosa* leaves were lost at Saunders Beach because of wood-boring beetle larvae that tunnel through branches. This factor created the major difference in herbivory level noted for *R. stylosa* between the two sites. In contrast, although the rate of insect-induced leaf loss was greatest during the first two months, for *A. marina* at both sites, 2-5% of leaves continued to be lost per month until senescence began, with most of these losses being attributable to insect damage.

Section 5.4.2 has shown that insects substantially reduce mean leaf longevity, but Figures 5.5 and 5.6 show that they also substantially alter the pattern of leaf fall. In the absence of insect herbivores, it can be assumed that prematurely abscised leaves would have reached senescence and fallen with the majority of the other leaves, reducing the temporal spread of leaf fall and increasing the peaks of senescent leaf fall. Examples of the differences between actual observed leaf fall and the pattern that would be expected if all leaves reached senescence, are shown for *A. marina* and *R. stylosa* at Saunders Beach in Figures 5.9 and 5.10. In both cases, leaf fall has been concentrated into a few months rather than spread over many months. Under such conditions, the patterns of leaf fall would mirror patterns of new leaf production much more closely than they currently do. Although both *A. marina* and *R. stylosa* continue to produce leaves year round, they have strong seasonal peaks in leaf production (Duke *et al.* 1984, Duke 1990b). It is likely that in the absence of herbivorous insects, the seasonality of leaf fall would become even more pronounced than it currently is, especially for *A. marina*.

Altering the pattern of leaf fall could have significant ramifications for the ecology of the ecosystem. Several authors (eg, Owen 1978, Springett 1978, Lamb 1985, Risley 1986, Risley and Crossley 1988) have suggested that the greater spread of insect-induced leaf fall would even out nutrient availability to plants, thus benefiting them. Mangrove productivity is tightly coupled to the ability of crabs to collect all leaf litter before tides wash it away (Robertson *et al.* 1992). The rapid removal and consumption of fallen leaves from the forest floor (Robertson 1986, Micheli 1993, Ashton 2002) suggests that fallen leaves may be a scarce and even limiting resource. Thus, one could speculate that the more even pattern of leaf fall throughout the year, and reduced seasonal peaks created by the activities of herbivorous insects (which are particularly evident for *A. marina*) could reduce exports of leaf litter, improve within-system nutrient cycling and may also provide year-round food sources to leaf-eating crabs. Thus there is potentially a significant role for insects in mangrove ecology through regulating the pattern of leaf litter delivery to the mangrove forest floor. In addition, as leaves and leaf fragments detached or abscised because of insect damage may not have gone through normal senescent processes such as retranslocation of nutrients, they can be expected to be of higher quality than senescent leaves. This aspect is further explored in Chapter 7.

Figure 5.9 Effect of Insect-Induced Leaf Loss on Longevity Distribution of *A. marina* Leaves at Saunders Beach

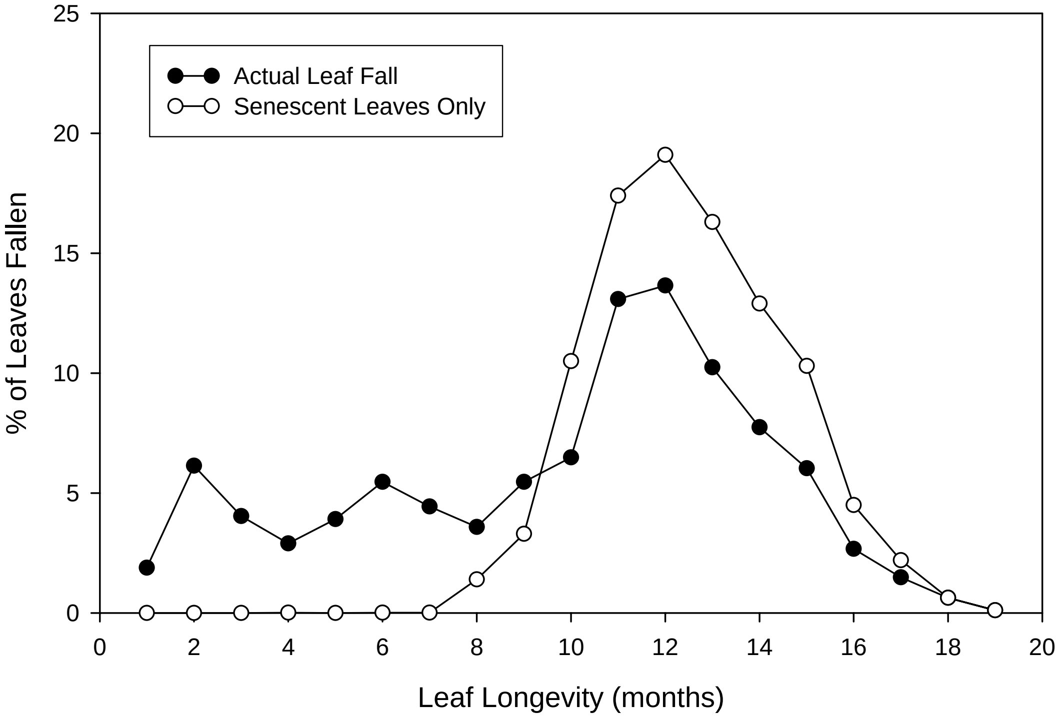
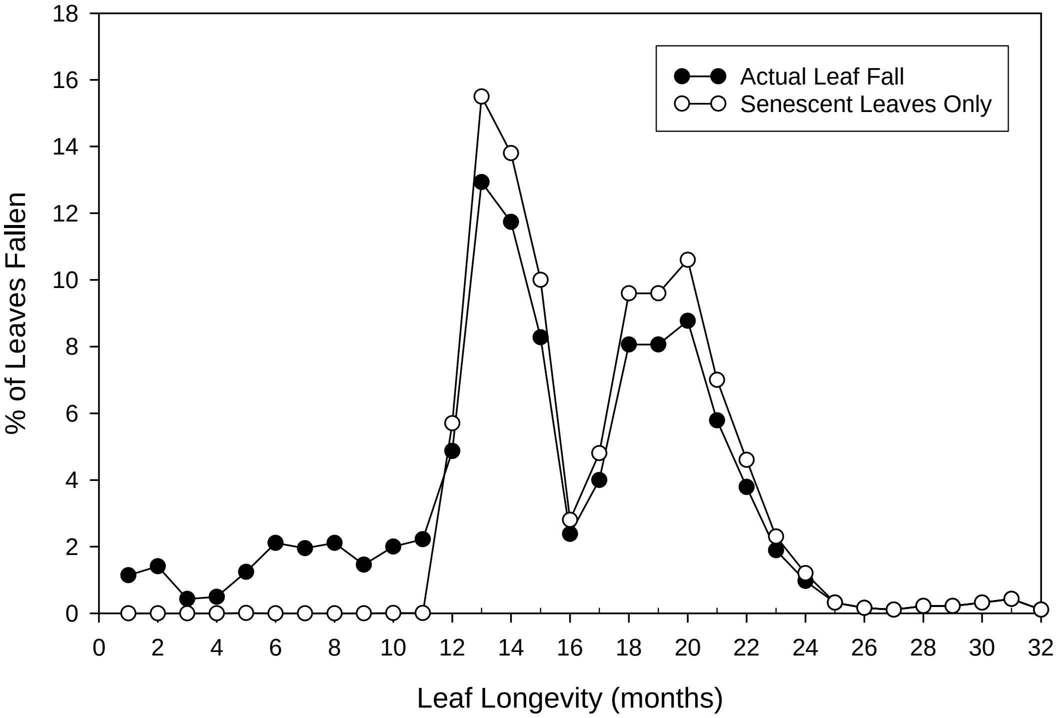


Figure 5.10 Effect of Insect-Induced Leaf Loss on Longevity Distribution of *R. stylosa* Leaves at Saunders Beach



5.4.5 Premature Leaf Loss

Premature leaf loss resulting from insect damage is commonly reported in herbivory studies. Blundell and Paert (2000) reviewed studies on leaf abscission and concluded that damaged leaves are shed more rapidly than undamaged leaves and that the rate of leaf shedding increases with increasing area damaged. Coley (1983) for Panamanian rainforest trees, and Southwood *et al.* (1986) for a variety of British plants (ranging from herbs to shrubs and trees), both found that foliage palatability and herbivore damage were inversely correlated with leaf life expectancy. Stone and Bacon (1983) and Abbott *et al.* (1993), found that leaf longevity decreased with increasing herbivory level for *E. camaldulensis* and *E. marginata* respectively. Premature leaf abscission due to insect damage has also been recognised in mangroves. Lee (1991) found that leaf area damage on *Kandelia candel* mangroves declined with leaf age, indicating premature abscission of more heavily damaged leaves. Murphy (1990) provides qualitative examples of total loss of all leaves on branches in *Excoecaria* and *Sonneratia* due to herbivory. In a recent major defoliation event in Irian Jaya, large areas of *Camptostemon shultzii* were damaged by a leaf-grazing caterpillar. Severely damaged leaves were soon shed from the tree (J. Garrison, pers. comm.). Working with *R. mangle* saplings in Belize, Ellison and Farnsworth (1996) found that herbivory was not correlated with leaf survivorship, except for one cohort at one site where an outbreak of a lepidopteran caterpillar caused higher than usual levels of damage.

Few herbivory studies that have demonstrated insect damage promoting premature leaf loss have documented how many leaves are prematurely shed because of the insect damage. Where leaf loss has been quantified, it has been shown to be significant. Zakaria (1989 in Crawley 1989) found that 17% (range between trees, 0-35%) of birch (*Betula pendula*) leaves either fell prematurely or were entirely consumed. Clark and Clark (1991) found that 21% of new leaves on a rainforest cycad were entirely lost because of insect herbivores. Preszler and Price (1993) found that 24-34% of *Salix lasiolepis* leaves were prematurely abscised because of damage by leaf-mining caterpillars. For *E. marginata*, Abbott *et al.* (1993) found that 10% of *E. marginata* leaves were shed or consumed in the first 12 months. Blundell and Paert (2000) found that the most recently produced leaves were missing from 49% of the seedlings of the Bornean rainforest tree they studied, with insect damage being the most likely explanation for the loss in most cases. Thus, my estimates of 19-30% of *A. marina* leaves and 5-8% of *R. stylosa* leaves prematurely lost from the tree because of insect damage, are comparable with estimates from the limited number of similar studies.

Not only was premature leaf loss a regular occurrence in the current study, but it also frequently affected closely located leaves similarly. For both *A. marina*, and *R. stylosa*, new leaves emerge as opposite pairs, and when one member of a leaf pair was prematurely abscised because of insect damage, the same fate frequently befell the other member of the pair. For any *A. marina* leaf killed by insects, there was a 52-54% chance that its partner leaf would suffer the same fate. For *R. stylosa*, this figure was much higher, at 68-74% probability (Table 5.4).

The correlation of damage levels between members of a leaf pair is not surprising as many leaf herbivores are juveniles with limited mobility (eg, caterpillars) that are more likely to move to the nearest available leaf (often the leaf opposite) when feeding ceases on one leaf. When wood-borers kill a branch, both members of affected leaf pairs die. For both *A. marina* and *R. stylosa*, leaf-grazing caterpillars bind two adjacent leaves together for feeding. In many cases, the adjacent leaves are leaf pairs, especially in *R. stylosa*, but less so for *A. marina* where the nearest leaf is often on an adjoining branch. Most often, both members of a leaf pair are damaged whilst the leaves are young and expanding. This is particularly true for *R. stylosa* whose leaf pairs undergo extensive development around an apical meristem until they unfurl. Caterpillars bore through this leaf-pair spike, usually damaging both leaves. This form of damage is examined in more detail in Chapter 6. The predominance on *R. stylosa* of this form of damage, and that of wood-boring beetle larvae, explains why the frequency of premature loss of both members of an opposite pair is much higher on *R. stylosa* than for *A. marina*.

Premature leaf loss was caused by different types of insects in *A. marina* and *R. stylosa*. For *A. marina*, excessive damage from complete consumption of leaf lamina and grazing of the leaf surface, were equally important as the main causes of premature leaf loss. Many leaves were also lost after suffering very minor amounts of damage but this damage was either to key points (eg, leaf petioles) or during very early stages of leaf development. Galls were more important in causing premature leaf loss at Saunders Beach than at Gordon Creek, reflecting their greater abundance at the former site. Determining the true impact of galls on their host plants requires more specific methods of investigation than was possible here, but they warrant more detailed consideration in future studies.

In contrast to *A. marina*, nearly half of the premature leaf loss recorded on *R. stylosa* did not result from a leaf-feeding insect. Wood-boring beetle larvae caused more leaf loss on *R. stylosa* than did leaf-feeding insects, though this result was dominated by data from Saunders Beach where such damage was more common. For *R. mangle* in Belize, Feller and Mathis (1997) also found that leaf loss due to wood-boring insects was equal to or greater than that of leaf-feeding insects, although their study was based on discrete methods which underestimate true herbivory level (Chapter 4).

5.4.6 The Role of Premature Leaf Loss in Mangrove Herbivory Estimates

One of the major reasons that the long-term method produces higher herbivory estimates than the discrete method is that it can take account of the loss of entire leaves. Despite the examples already cited showing that insect damage promotes leaf loss in mangroves and other ecosystems, loss of entire leaves in mangroves has usually been considered to be a rare or unusual event, although there is little justification for this view. In their highly influential and widely-quoted study on mangrove herbivory, Robertson and Duke (1987) tagged 30 newly opened leaves of *R. stylosa*, *C.tagal* and *A. marina* and found that only zero, one and two leaves respectively were lost over a three-month period. Though not stated, insect damage is a likely cause for the loss of those leaves. This was used as evidence that leaf loss was not sufficiently important to be included in their herbivory estimates. However, in the current study, for *R. stylosa,* though only 3-3.5% of leaves less than three months old (ie, one in 29-33) were lost because of insect damage, this was enough to increase estimates of leaf loss to herbivory 2-3 fold. Because of the short time frame and low numbers of leaves tagged by Robertson and Duke (1987), the true rate of leaf loss for their study cannot be accurately judged. However, given that the level of damage they recorded for *R. stylosa* in their discrete study (5.1-7.6% - Table 4.10) was higher than that recorded for *R. stylosa* in the current study (3.8-4.2% - Table 4.4), it is not unreasonable to assume that the rate of leaf loss due to insects in their study is at least as great as that recorded in the current study.

The loss of two *A. marina* leaves out of 30 over a 3-month period in the study of Robertson and Duke (1987) is similar to the rate of leaf loss obtained in the current study (2 leaves lost within three months from every 23-27 leaves tagged). Inclusion of the missing leaves recorded by Robertson and Duke (1987) would have increased their herbivory estimates on *A. marina* by about 66%. In addition, insect-induced loss of *A. marina* leaves continues at a relatively constant rate (Figure 5.3) until senescence at around 12 months and inclusion of such leaves would have further increased herbivory estimates. Given that the discrete results obtained by Robertson and Duke (1987) for *A. marina* in their study (8.8-12.0% - Table 4.10) were 30-40% greater than in the current study (6.8-8.5% - Table 4.4), it might be assumed that the rate of leaf loss would be at least as great as that recorded in the current study, and possibly even greater. Thus, levels of leaf loss that are considered to be low can actually have a very strong bearing on the overall herbivory result and should not be too easily dismissed. For 21 rainforest species in Panama, Coley (1982) found that although only 2.7% of leaves (1 out of every 37) were entirely consumed by insects, these accounted for 38% of total leaf area lost to insect herbivores.

Whilst Robertson and Duke (1987) at least made some attempt to quantify premature leaf loss, other mangrove herbivory studies have dismissed leaf loss due to insects as being unimportant without even attempting verification. Farnsworth and Ellison (1991) considered that most missing leaves were old and thus excluded them from analysis, assuming their loss to be the result of senescence, not herbivory. For *K. candel*, Lee (1990) found that leaves collected from litter traps under trees had significantly greater herbivore damage than those remaining on the tree and were also smaller. This was attributed to premature detachment of more heavily damaged leaves and younger leaves that had not yet attained full size. Despite this finding, Lee (1990) regarded complete loss of leaf lamina and aborted leaf initiation in *K. candel* to be uncommon and did not account for these factors in his herbivory estimates. Saur *et al.* (1999) quoted Robertson and Duke (1987) and Farnsworth and Ellison (1991) as part of their justification for not including missing leaves in their study.

Given the low levels of average herbivory recorded in the study of Saur *et al.* (1999), (0.2% for *R. mangle*), loss of just 2 leaves in 1,000 would have doubled the herbivory estimates and loss of 2 in 100 leaves would have increased the herbivory estimates 11-fold. The importance but relative rarity of insect-caused leaf loss also illustrates the need for large sample sizes in herbivory studies. Even in forests with low ambient herbivory, occasional loss of heavily-damaged leaves, sufficient to significantly affect overall herbivory estimates, can be created by vagrant herbivores such as grasshoppers and patchily distributed herbivores such as wood-borers. In fact, the distribution of insect damage is commonly skewed toward a large number of leaves with minor damage and a few leaves with extensive damage (see examples in Chapter 4 and Figure 4.3). It is these few leaves with extensive damage that are rarely taken into account in discrete studies, even though they substantially alter the overall result.

5.5 Conclusions

Although it has never been quantified until now, in mangrove herbivory studies, loss of entire leaves because of insect damage has been considered relatively rare and thus not accounted for in herbivory estimates. However, in the current study, 5-8% of *R. stylosa* leaves and 19-29% of *A. marina* leaves were either completely consumed or prematurely abscised because of insect damage, showing not only that this assumption is incorrect, but that the inclusion of just a few such leaves would significantly affect herbivory estimates. Because most insect-killed leaves are young, developing leaves, mean leaf longevity estimates were reduced by 4-5% and 12-13% for *R. stylosa* and *A. marina* respectively. This demonstrates the significant effect that insect herbivores have on the leaf fall patterns of these mangrove species. As regulation of leaf longevity is one of the main mechanisms by which trees optimise their carbon gain and productivity, significant external alteration of optimal leaf longevity could potentially be disruptive to their performance and productivity. In addition, insect-induced leaf loss occurred throughout the year. In the absence of herbivorous insects, there would be reduced leaf fall during the year followed by larger peaks of leaf fall when leaves reached senescence. Given the importance of leaf fall to the productivity of mangrove ecosystems, it could be considered that insect-mediated patterns of leaf fall may have additional, as-yet unexplored roles in mangrove ecology.

CHAPTER 6 – APICAL TIP DAMAGE AND LOSS OF LEAF BUDS

6.1 Introduction

Insect folivory is usually determined by measuring the leaf area damaged or missing from emerged and expanded leaves. Chapter 4 discussed results from discrete studies of mature leaves and compared them to long-term assessments of leaves tagged or marked as juveniles. Both methods involve assessing damage to leaves that had successfully emerged. But what of leaves that do not successfully emerge because of insect damage or are lost when too small to be included in folivory assessments? For most species, *Avicennia marina* included, developing leaves are exposed to herbivory throughout the entire course of their development and are considered to have emerged immediately after budburst. The stage of development at which the leaves are included in herbivory assessments varies between studies. As reported in Chapter 4, only *A. marina* leaves that were at least 5-10 mm in length were generally able to be tagged and recorded for assessment. However, it was observed that many leaves were lost prior to reaching this size.

Like other Rhizophoraceae mangroves, *Rhizophora* spp. are unusual in that leaves are produced from a prominent apical bud located terminally on each shoot. Leaves develop whilst wrapped around this bud, within a pair of stipules, until they reach an advanced stage of development, at which time the stipules are shed and the leaves unfurl as substantially developed leaves (Figure 6.1). Thus all leaves were marked for the herbivory studies in Chapter 4 at a clearly defined point in their development. However, damage to either the leaves or the apical bud prior to shedding of the stipules, commonly results in damage to, or loss of, one or both of the developing leaves (Figure 6.2). There is considerable energy expended in developing leaves, so their loss prior to or during emergence from the stipules, before they have had an opportunity to repay some of that investment, may be significant.

In *Rhizophora* species, the apical meristem is dominant and axillary meristems are rarely viable or are strongly suppressed (Gill and Tomlinson 1969). In most growing shoots, branching does not originate from these suppressed buds but from expansion of lateral shoots that are developed within the stipules of developing leaves and

Figure 6.1 Sequence of new leaves emerging from an apical tip of *R. stylosa*. From left: two stipules enclose two developing leaves; stipules fall away as leaves emerge; and two leaves emerge with apical bud between them

Figure 6.2 Leaf death and damage resulting from insect attack on apical tips of *R. stylosa*. Two dead leaves (black and detached at the petiole base) with stipules (brown)

emerge simultaneously with the leaves (Gill and Tomlinson 1969, Tomlinson 1986). Inflorescences are also produced here at the same time and emerge with the unfurling leaves (Figure 6.3). Thus, in addition to the loss of the developing leaves, damage to the apical bud may also cause the loss of developing lateral branches and new inflorescences. Such effects are usually ignored because the damage to the bud involves a very small area that is not readily assessable by standard techniques. However, the impacts of the damage that is not visible (bud destruction and suppression of leaf and flower production) are potentially more significant than the feeding damage on expanded leaves and flowers.

Where an apical bud has been killed, rather than just damaged, further leaf production and branch growth from that shoot ceases (Figure 6.4). Unless the shoot can regenerate new buds from the suppressed lateral axillary meristems immediately below the terminal bud (Figure 6.5), the shoot will die once the standing crop of leaves has senesced, if not earlier. Dead shoots cannot extend, thus affecting branch architecture. If the suppressed lateral axillary meristems do regenerate, these grow in different directions to what the original shoot would have grown (Figure 6.6), resulting in branch extension becoming more lateral, also an alteration to branch architecture.

Not only are *Rhizophora* species particularly susceptible to damage to their terminal shoots, but they also cannot develop sucker growth when decapitated or epicormic shoots if the trees are knocked over (Gill and Tomlinson 1969). These restricted patterns of new leaf, branch and flower production, are in stark contrast to *Avicennia* spp. which have equipotential node complexes with diffuse branching. New twigs may be produced from all nodes, including those far from the axial meristem and there are often new twigs produced from what appear to be long-dead nodes (Rau and Murphy 1990). *Avicennia* also has the ability to produce numerous new shoots rapidly (ie, coppice growth) after extensive physical damage such as loss of branches (Figure 6.7). Thus *Rhizophora* has considerable investment in each new leaf and limited abilities for compensatory leaf and shoot production from other locations on the plant, but *Avicennia* has less investment in each leaf and well-developed ability to flush new leaves from elsewhere on the plant.

Figure 6.3 Two inflorescences emerging with two developing leaves of *R. stylosa* (stipules have been peeled away for this photo)

Figure 6.4 Comparison of undamaged (right), damaged (centre) and entirely destroyed bud (left) of *R. stylosa*. Note the damaged leaves produced from the damaged bud. The destroyed bud would not be able to produce any more leaves, and unless the suppressed reserve laterals below the terminal node can regenerate new shoots, this branch would die when its current crop of leaves senesce.

Figure 6.5 *Rhizophora stylosa* shoot with destroyed apical bud attempting to compensate by initiating suppressed reserve lateral buds (red colour)

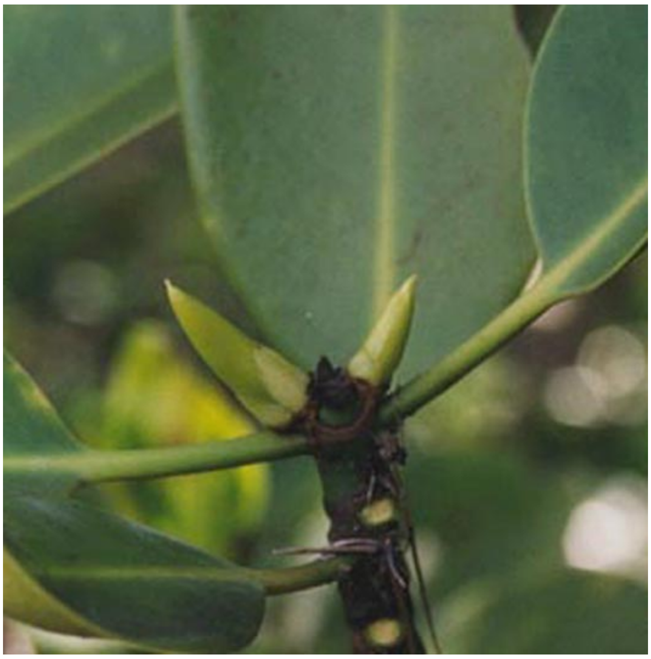


Figure 6.6 *Rhizophora stylosa* reserve lateral buds soon to unfurl new leaves (only ~2cm long). Note suppressed lateral shoots growing in lateral direction compared to the vertical direction the original apical bud would have grown if not destroyed by insects.

Figure 6.7 Numerous branches regenerating (coppice growth) from sawn trunk of *A. marina* along a boardwalk

Feeding on active growing buds and tips is common among insects, though it is rarely assessed in folivory studies (see Onuf *et al.* 1977, Benner 1988, Feller 1995 for exceptions). Damage may occur by direct consumption of the tips and leaves, boring through the tip, galling the tip or sap-feeding on the tip and terminal shoots. Damage and loss of apical buds and tips is common for eucalypts, often by coreid bugs (Landsberg and Cork 1997). In many broad-leaved *Melaleuca* species in northern Queensland, tip-binding moth caterpillars restrict new leaf production, usually through damage to the developing leaves rather than the bud itself (unpub. data). On the same *Melaleuca* species, the coreid bug, *Pomponatius typicus* destroys the entire growing tip, greatly restricting branch extension (Burrows and Balciunas 1998). This substantially reduces the vertical growth of the plant, but promotes lateral branching, resulting in a shorter and more densely branched plant (Balciunas and Burrows 1993). Montagu and Woo (1999) found that the tip-feeding coreid bug, *Mictis profana*, caused the death of 10-15% of the apical tips on *Acacia auriculiformis* trees planted in an orchard, and in another trial, Wylie *et al.* (1997) reported that 25% of *A. auriculiformis* tips were attacked by this bug. Insect galls that develop from apical buds are common on eucalypts, acacias and melaleucas in coastal habitats in northern Queensland, and typically halt all future leaf production, flower production and shoot extension from those buds (unpub. data). In mangroves, damage to apical buds is predominantly caused by moth caterpillars (Onuf *et al.* 1977, Murphy 1990, Feller 1995, this study).

The rate and potential effects of tip damage in mangroves has been commented on by several authors. Primack and Tomlinson (1978) were the first to suggest that insects may play a significant role in damaging buds of *Rhizophora*, even suggesting that the sugary secretions the trees secrete around the base of developing buds are to attract potential predators such as ants and birds. Although they did not assess the rates or effects of tip damage, Murphy (1990) and Rau and Murphy (1990) both commented on the importance of apical bud damage by moth caterpillars on *Rhizophora* and *Sonneratia*, in causing mortality of developing leaves and shoot dieback, suppressing future leaf production, and altering tree architecture by diversion of growth from apical to lateral shoots. Veenakumari *et al.* (1997) reported several hemipteran and coleopteran species feeding on buds of various mangrove trees in the Andaman and Nicobar Islands. They did not specify whether they were referring to flower buds or leaf buds, though in the case of Rhizophoraceae species which produce flowers and leaves from the same buds, this is immaterial. They also reported several species of noctuid and pyralid moth caterpillars boring the terminal shoots of *Sonneratia*, *Rhizophora* and *Avicennia* spp. The rates of insect damage to apical tips and buds in mangroves has only been assessed, albeit briefly, in two studies – Onuf *et al.* (1977) and Feller (1995). Both studied the effects of nutrient enrichment on *R. mangle* in the Neotropics and concluded that insect damage to the developing leaves and tips within the stipules was more significant than insect damage to leaves that had already emerged.

During the conduct of the discrete and long-term studies described in Chapter 4, it was observed that *R. stylosa* apical buds were commonly attacked, and often killed, by 2-3 species of moth caterpillars. Additionally, Curculionidae weevil larvae were collected feeding on *R. stylosa* apical buds on two occasions in the current study, though neither were successfully reared for identification. Many developing leaves died as a result of this damage but were not always included in the herbivory assessments because the leaves were aborted before they could be tagged or marked for assessment. Additionally, it was realised that there were many additional aspects to this type of damage that required separate study.

Developing leaves of *A. marina*, often less than 5mm long (Figure 6.8), are attacked by first-instar larvae of leaf-binding and grazing caterpillars almost as soon as they emerge from the bud. Direct damage to the buds of *A. marina* is not readily visible in the field due to their small size. No insects were found that would specialise in feeding on *A. marina* buds, an observation also noted for *Avicennia* spp. in Singapore by Murphy (1990), though indirect damage to buds probably occurs from larger insects feeding on developing leaves. Loss of developing *A. marina* leaves less than 5mm long due to insect damage was also frequently observed in the current study. No studies have examined damage to developing leaves and leaf buds in any *Avicennia* species. This chapter examines the rates of tip damage and resultant leaf loss and lateral branch production on *R. stylosa* and *A. marina*.

Figure 6.8 Developing leaf buds of *A. marina.* These are often fed upon by leaf-binding caterpillars. Due to their small size, they are not readily located, tagged or incorporated into herbivory measurements.

6.2 Methods

The sites and species studied were those described in Chapter 2.

6.2.1 Discrete Study – Developing *A. marina* and *R. stylosa* Leaves

Discrete surveys for damage to apical tips were carried out for *A. marina* and *R. stylosa* at both Gordon Creek and Saunders Beach. The proportion of developing leaf buds on *A. marina* was surveyed at Saunders Beach in May 2001 and Gordon Creek in June 2001. At each site, 10 trees were selected from various locations representing most habitat types. The proportion of dead, damaged and intact developing leaves was counted on each of 10 branches on each tree. Developing leaves were considered to be those less than 3cm long. For *R. stylosa,* the numbers of undamaged, partly damaged and completely destroyed tips were counted once, on 54 trees at Gordon Creek and 30 trees at Saunders Beach, over the period May-June 2001.

6.2.2 Damage to, and Loss of, Developing *A. marina* Leaves and Buds

In May 2002, 10 branches were tagged on each of 10 *A. marina* trees at both sites. Existing leaves were marked and each branch was assessed every 2-3 weeks until mid-July 2002. These months are part of the period of peak *A. marina* leaf production at both sites. The developing buds are too small to be marked or tagged so adjacent leaves were marked with arrows pointing toward the location of the emerging buds (buds emerge from between the base of two existing leaves). The fate of developing leaves was recorded on each visit as either intact, dead or damaged. Damaged leaves included those damaged by feeding activities such as grazing, existence of galls, or by deformation of leaf shape.

6.2.3 Long-Term Study – *R. stylosa* Developing Leaves

The discrete survey provided a rapid indicator of damage. However, because dead shoots persist for long periods but damaged shoots may recover, it cannot provide accurate data on the rate of tip damage and it also underestimates the proportion of dead versus damaged apical buds. Tagging shoots and recording their fate provides a more accurate means of assessing tip damage rates and the recovery from damage.

For each of 10 *R. stylosa* trees at each site, 30 intact shoots were individually tagged in March 2001. Each shoot was revisited at intervals of 6-12 weeks for 13 months. Sampling intervals were shorter during the summer months, when new leaf production was more frequent. On each sampling trip, the condition of the bud, the number of emerging leaves and their condition were recorded for each shoot.

In addition to the undamaged shoots, 10 shoots whose terminal apical buds had already been damaged by insects were also tagged on each of the 10 trees at each site. This was to evaluate trajectories of recovery from tip damage and effects on leaf production. These shoots were surveyed at the same time as the undamaged shoots.

6.2.4 Gladstone Study

From June 1996 - August 1998, Dr. Norm Duke (then of Australian Institute of Marine Science) studied the effects of oil spills and bioremediation strategies on mangroves at Port Curtis, just north of Gladstone (Duke *et al.* 1999, 2000a). Gladstone has a slightly cooler (mean daily temperature range 18.4-27.5°C) and drier (mean annual rainfall = 896mm) climate than Townsville (Duke 2002). Seasonality of climate and leaf production patterns are similar to those in Townsville, with maximum leaf production also occurring in the summer months (Duke 2002). Measuring the rate of apical bud damage and leaf loss by insects was not the intention of that study but the way in which productivity data were collected (tagging of canopy shoots and counting the emergence of new leaves at regular intervals) made it amenable to such analysis. Dr. Duke kindly provided his raw data on non-oiled treatments for the purposes of analysing rates of damage and leaf loss to apical buds.

Study sites were located in mature stands of 4-9m high *R. stylosa*. Varying numbers of sample plots were located in each of the eight sites but only the control plots, not the experimentally oiled plots, are considered here. They were located either in areas that had not been subject to human disturbance (undisturbed control, n=3), those that were subject to disturbance that simulated the oiled treatments such as cutting of roots to place enclosures around the trees (disturbed control, n=7) and also some sites that were treated with a Osmocote™ fertiliser mix (n=3). Osmocote™ is a slow-release N and P fertiliser applied by shallow burial of the granules under the soil surface.

Within each of the 13 control plots, 21 shoots on a single tree were tagged. Leaf emergence from each shoot was monitored for the duration of the study with either zero, one or two leaves being recorded from each emergence event. Because dead shoots no longer produce new leaves, shoots that died were replaced by tagging a different shoot, so that there were always 21 tagged shoots on each tree. All dead apical tips, and leaves lost at the point of emergence, were considered to have been caused by insect damage. Extensive field observations of mangroves around Townsville (pers. obs.) and Gladstone (N. Duke pers. comm.) support the notion that although loss can sometimes occur via other means, loss of leaves at the point of their emergence is nearly always associated with insect damage. Feller (1995) also considered that damage from bud-boring moths was the primary cause of leaf abscission in unfurling *R. mangle* leaves. It is possible that during the sampling intervals, some leaves successfully emerged and then were lost for other reasons, but this is a sufficiently rare event (as judged from data on hundreds of undamaged shoots in the current study) that it would not affect the results. Thus emergence of no leaves or one leaf on a new node were taken to indicate that shoot damage had occurred.

Damage to the apical shoot that did not result in leaf loss, or that resulted in the emergence of damaged or deformed leaves, was not recorded by this method as leaves were only recorded as being either present or absent. Thus only bud/shoot damage sufficient to cause leaf loss and/or complete death of tips, can be compared between the Townsville and Gladstone data. Fortunately, these are the most significant aspects of tip damage.

The interval between sampling visits in the Gladstone study varied from 1-6 months, becoming greater as the study progressed. Because of the low rate of leaf production, infrequent visits still enable adequate information to be obtained. Table 6.1 sets out information on the study plots used in this analysis, and the duration and frequency of sampling. Further details on the Gladstone study can be found in Duke *et al.* (1999, 2000a) and Duke (2002). Data on the emergence of zero, one or two leaves and the number of dead tips enabled calculation of the number of tips killed, the number of tips damaged badly enough to lose one or two leaves and the proportion of leaves lost at the point of emergence.

Table 6.1 Sampling Regime for Gladstone Study (non-oiled treatments only). See Duke *et al.* (1999, 2000a) and Duke (2002) for further description of study sites and explanation of site codes.

Site Code	Plot No.	State	Duration	Sampling Dates
FLIS	3C	DC	Jun96-Aug98	Every 4-8 weeks Jun96-May97, then Nov97 and Aug98
FLNS	1C	DC	Jun96-Aug98	Every 4-8 weeks Jun96-May98, then Aug98
FLNY	9E	DC	Jun97-Aug98	Every 4-8 weeks Jun97-May98, then Aug98
FLNX	8C	DC	May97-Aug98	Every 4-8 weeks May97-May98, then Aug98
FLIS	3D	DC	Jul96-Aug98	Every 4-8 weeks Jul96-May97, then Nov97 and Aug98
FLSN	2B	DC	Jul96-Nov97	Every 4-8 weeks Jun96-May97, then Nov97*
FLSN	2D	DC	Jul96-Aug98	Every 4-8 weeks Jul96-May97, then Nov97 and Aug98
CISS	5A	UC	Jun96-Aug98	Every 4-8 weeks Jun96-May98, then Aug98
FLNN	6A	UC	Jun96-Aug98	Every 4-8 weeks Jun96-May98, then Aug98
FLSS	7A	UC	Jun96-Aug98	Every 4-8 weeks Jun96-May98, then Aug98
FLNS	1H	F	Aug97-Aug98	Every 4-8 weeks Aug97-May98, then Aug98
FLNX	8F	F	Aug97-Aug98	Every 4-8 weeks Aug97-May98, then Aug98
FLNY	9F	F	Aug97-Aug98	Every 4-8 weeks Aug97-May98, then Aug98

DC=disturbed control, UC=undisturbed control, F=fertilised

* site not sampled in 1998 as it was destroyed for port reclamation works

6.2.5 Panama Study

Dr. Duke conducted a similar study on the effects of oil spills in mangrove forests of Bahias Las Minas, on the Caribbean coast of Panama. This followed a 1986 oil spill from a ruptured refinery tank, which damaged at least 377 ha of mangrove forest (Duke *et al.* 1997). Damage included the death of trees, but sub-lethal effects such as defoliation or reduced canopy leaf biomass were recorded over a much wider area (Duke *et al.* 1997). The same method of tagging shoots and recording leaf emergence events as zero, one or two leaves successfully emerging, was used in this study as in the Gladstone study. Again, Dr. Duke kindly provided the raw data to enable an analysis of tip death and damage that resulted in leaf loss.

In Panama, the study trees were *R. mangle*, which has a similar ecology and growth form to *R. stylosa*. Patterns of seasonality differ between Panama and Australia. Most rainfall occurs in winter, not summer, though the Panamanian winter corresponds to the same time of the year as the southern hemisphere summer. Data were collected from 21 tagged shoots on each of 1-3 trees at each of 26 sites. However, only the data from control (non-impacted) sites are analysed here. These comprised 21 tagged shoots on 17 trees from 13 sites. The sites were located in three areas – coastal mangroves exposed to the ocean, sheltered mangroves along tidal channels or inlets, and mangroves upstream along a river. For one tree at each site, all tagged shoots were examined every month from June 1989 to July 1991. For sites where two or three trees were studied, these extra trees were only sampled from August 1989 to August 1990. The same limitations and assumptions as for the Gladstone dataset apply here. In the Gladstone and Panama studies, tagged shoots were located in the upper canopy only, as opposed to this thesis where shoots were in the lower to middle canopy.

Summary sampling information for the Panama study sites are presented in Table 6.2. Details of the sampling sites and of recovery from the oil spill are given by Duke and Pinzon (1993) and Duke *et al.* (1997, 1998c).

Table 6.2 Sampling Regime for the Panama Study

Location	No. Sites	No. Trees
Exposed	5	7
Sheltered	5	7
Riverine	3	3

6.3 Results

6.3.1 *A. marina* Developing Leaves

In the discrete survey, fewer developing leaves were damaged at Gordon Creek than at Saunders Beach (contingency test, p<0.001, Table 6.3), with 78% of 990 developing leaves being recorded as intact at Gordon Creek and 66% of 838 developing leaves being recorded as intact at Saunders Beach. The death rates of damaged developing leaves were similar at the two sites (79% at Gordon Creek and 75% at Saunders Beach, contingency test, p>0.25).

Table 6.3 Proportion of Developing *A. marina* Leaves Damaged by Insects in the Discrete Survey

Leaf Condition	Gordon Creek	Saunders Beach	p
Undamaged	77.9	66.2	<0.001
Damaged but Alive	4.6	8.6	
Dead	17.5	25.2	>0.25
Total Damaged	22.1	33.8	

In the tagging study, a total of 1,020 and 1,190 developing leaf buds were recorded from Gordon Creek and Saunders Beach respectively. In contrast to the discrete study, in the tagging study, fewer developing leaves were damaged at Saunders Beach than at Gordon Creek (contingency test, p<0.001, Table 6.4). Leaves attacked by insects were more likely to be killed at Gordon Creek than at Saunders Beach (contingency test, p<0.001, Table 6.4).

Table 6.4 Proportion of Developing Leaves Damaged by Insects on Tagged *A. marina* Branches

	% of Leaves Undamaged	% of Leaves Affected		
		Damaged	Dead	Total
Gordon Creek	43.7	21.3	35.0	56.3
Saunders Beach	63.3	18.0	18.7	36.7

At Gordon Creek, the proportion of developing leaves affected by insect attack was significantly greater (contingency test, $p<0.001$) in the tagged study than the discrete study but at Saunders Beach the two methods gave similar results (contingency test, $0.05<p<0.10$). Of the leaves that were attacked by insects at both sites, a greater proportion were damaged rather than killed in the tagging study compared to the discrete study. At Saunders Beach, approximately half of the leaves attacked by insects died, whereas at Gordon Creek, more than 60% of leaves attacked by insects died.

6.3.2 Discrete Study – *R. stylosa*

A total of 7,542 apical tips were assessed for insect damage on the 54 trees at Gordon Creek and 4,859 apical tips on the 30 trees at Saunders Beach. More apical tips were damaged or completely missing at Gordon Creek than at Saunders Beach (contingency test, $p<0.001$, Table 6.5). Initiation of suppressed reserve lateral buds, a surrogate for attempted recovery from apical bud damage, was also greater at Saunders Beach (contingency test, $p<0.001$), where 57% of missing tips had developing reserve lateral buds whereas at Gordon Creek, only 40% of missing tips had reserve lateral buds present.

Table 6.5 Proportion of Tips Damaged by Insects on *R. stylosa*

Site	% of Apical Tips Damaged			% Leaves Lost		
	Damaged Tips	Missing Tips	Total	From Damaged Tips	From Missing Tips	Total
Gordon Creek	11.1	11.4	22.5	8.5	11.4	19.9
Saunders Beach	5.6	6.5	12.1	3.6	6.5	10.1

At both study sites, similar proportions of buds were either completely missing, or damaged but still present. However, as damaged buds may recover, but missing buds do not, the proportion of buds killed will be overestimated in a discrete study such as this.

Only in exceptional circumstances do any leaves remain present on tips where the bud is completely destroyed, so a missing tip can be confidently equated to the loss of both leaves. However, for tips that are damaged but not completely missing, the developing leaves may suffer various fates: having one or both leaves missing; one or both leaves present but damaged; or one or both leaves present but undamaged. For buds that were recorded as damaged (but not completely missing), the proportion of leaves in each category in the discrete survey is presented in Table 6.6.

Table 6.6 Proportion (%) of Leaf Damage and Retention on Damaged *R. stylosa* Buds

	Gordon Creek	**Saunders Beach**
Total no. damaged buds	838	273
% buds with both leaves missing	72	59
% buds with one leaf missing*	9	11
% with both leaves present but at least one leaf damaged	13	24
% with both leaves present and undamaged	6	6

* remaining leaf damaged or undamaged

Even where buds are not completely destroyed, bud damage results in substantial loss of leaves, or damage to surviving leaves. At Gordon Creek, 81% of damaged buds lost at least one leaf and at Saunders Beach, this figure was 70%. Only 6% of damaged buds produced two undamaged leaves. Leaf loss as a result of bud damage was more likely to occur at Gordon Creek than at Saunders Beach (contingency test, p<0.001, Table 6.6).

6.3.3 Long-Term Study – *R. stylosa*

Control Tips

The number of leaf emergence events recorded at Gordon Creek (n=832) was less than at Saunders Beach (n=1032) and therefore so was the number of leaves produced (Table 6.7, noting that each event should consist of two opposite leaves emerging). However, tip damage, and loss of leaves due to tip damage was greater at Gordon Creek (Table 6.7). The lower leaf production but greater leaf loss due to insects at

Gordon Creek further increased the difference between the two sites in the number of new leaves successfully emerging from each tree.

Complete destruction of the apical bud was not significantly more frequent at Gordon Creek, but the number of buds damaged but not killed and the total number of buds attacked by insects (killed+damaged), were (Table 6.7).

The percentage of leaves lost due to tip damage was greater at Gordon Creek than at Saunders Beach. In addition to the loss of leaves, at Gordon Creek, 1.9% of successfully emerging leaves were damaged and 3.0% emerged intact but smaller than normal because of insect damage to the bud. This was not significantly different from Saunders Beach, where 1.1% of successfully emerging leaves were damaged and 0.9% emerged intact but smaller than they would otherwise have been (Table 6.7). The overall proportion of leaves that were in some way affected by insect damage to *R. stylosa* tips was greater at Gordon Creek (14.4% of leaves affected) than at Saunders Beach (6.4% of leaves affected).

Table 6.7 Tip Damage, and Leaf Loss Due to Tip Damage, on *R. stylosa* at Gordon Creek and Saunders Beach (n=10 trees, each with 30 tagged tips, at each site. Proportional data were arcsin transformed and analysed by t-test, df=18 in all cases). Standard errors are provided.

	Gordon Creek	**Saunders Beach**	**t**	**P**
Tip and Bud Damage				
Total No. Emergence Events	853	1032	4.11	P<0.001
% Events Where Buds Killed	4.0±0.8	2.3±0.7	1.41	P<0.17
% Events Where Buds Damaged But Not Killed	7.3±0.9	2.7±0.5	3.77	P<0.001
% of Emergence Events Affected by Insect Damage	11.3±1.2	5.0±1.0	3.85	P<0.001
Leaf Damage				
No. Leaves Produced per Tree	170.6±4.1	206.5±7.7	4.11	P<0.001
% Leaves Lost	9.5±1.4	4.4±1.0	2.88	P<0.005
% Leaves Damaged or Stunted	4.9±0.9	2.0±0.6	1.88	P<0.08
% of Leaves Affected by Insect Damage	14.4±1.9	6.4±1.0	3.41	P<0.003

At Gordon Creek, nearly twice as many tagged tips were damaged in some way by insects over the course of the year, than at Saunders Beach (32% vs 17%; t-test t=3.14, df=18, P<0.006). Between the two sites, 71 lateral branches and 45 flower stalks were produced during the year. All of the new lateral branches and 43 of the 45 new inflorescences recorded in the study emerged from undamaged tips. The remaining two flower stalks were lost as they were on tips killed through insect damage. The true number of flower stalks lost may be higher as their loss would easily go unobserved. The rate of new lateral branch and inflorescence emergence was too low to undertake statistical analysis to determine the expected frequency of such emergences in damaged tips (ie, to estimate the unobserved loss rate).

There was substantial variation in tip damage rates between individual trees at each site, with the percentage of leaves affected by tip damage on each tree varying from 2-22% at Gordon Creek and 1-12% at Saunders Beach (Figures 6.9 and 6.10). The percentage of emergence events affected by insect damage varied from 3.8-16.5% at Gordon Creek and 0.9-12.2% at Saunders Beach (Figures 6.9 and 6.10).

The rank order of trees based on the number of leaves that each attempted to produce versus the number that successfully emerged, was strongly correlated at Saunders Beach (Spearman’s rank correlation, p<0.0005, r_s=0.95, df=2,10) but not at Gordon Creek (Spearman’s rank correlation, p<0.10, r_s=0.50, df=2,10) (Figure 6.11). Thus, because of tip damage caused by insects, trees which initiate the most number of leaves do not necessarily successfully emerge the greatest number of leaves.

Compensatory Leaf Production Due to Tip Death

Where apical growing tips have been completely destroyed, the only means by which that shoot can produce further leaves is to activate the suppressed reserve lateral buds from a previous node on that shoot. Extensive observation of this process in the field indicates that buds are usually generated in the node previous to that destroyed, although they can also occur up to three nodes below the destroyed bud. Only two reserve lateral buds are activated per node, and the maximum number of buds recorded regenerating after tip destruction was six. Emergence of these reserve buds was only observed after complete tip destruction, or on just a few occasions where

Figure 6.9 Damage and Loss of New *R. stylosa* Leaves and Tips Affected by Insect Damage at Gordon Creek

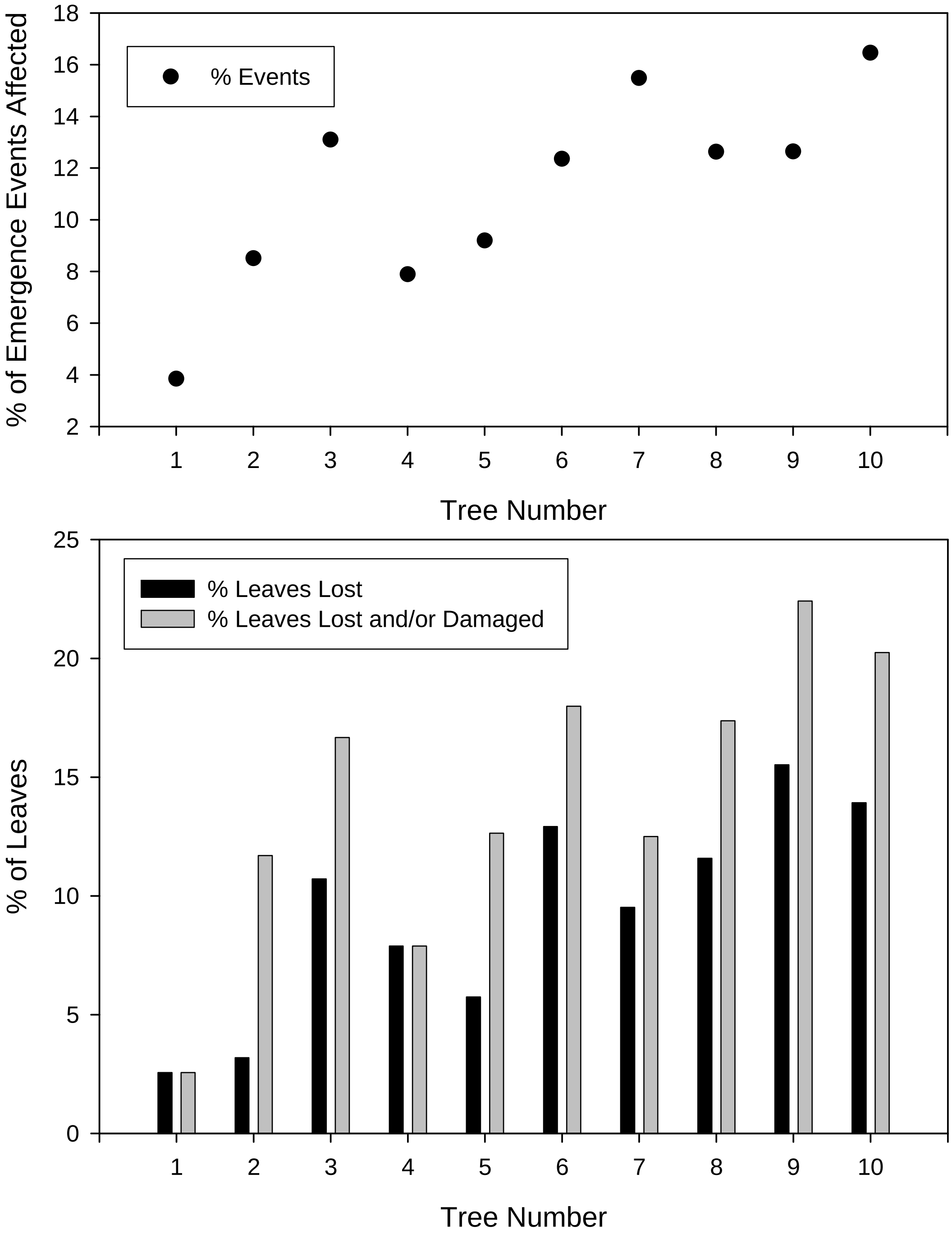


Figure 6.10 Damage and Loss of New *R. stylosa* Leaves and Tips Affected by Insect Damage at Saunders Beach

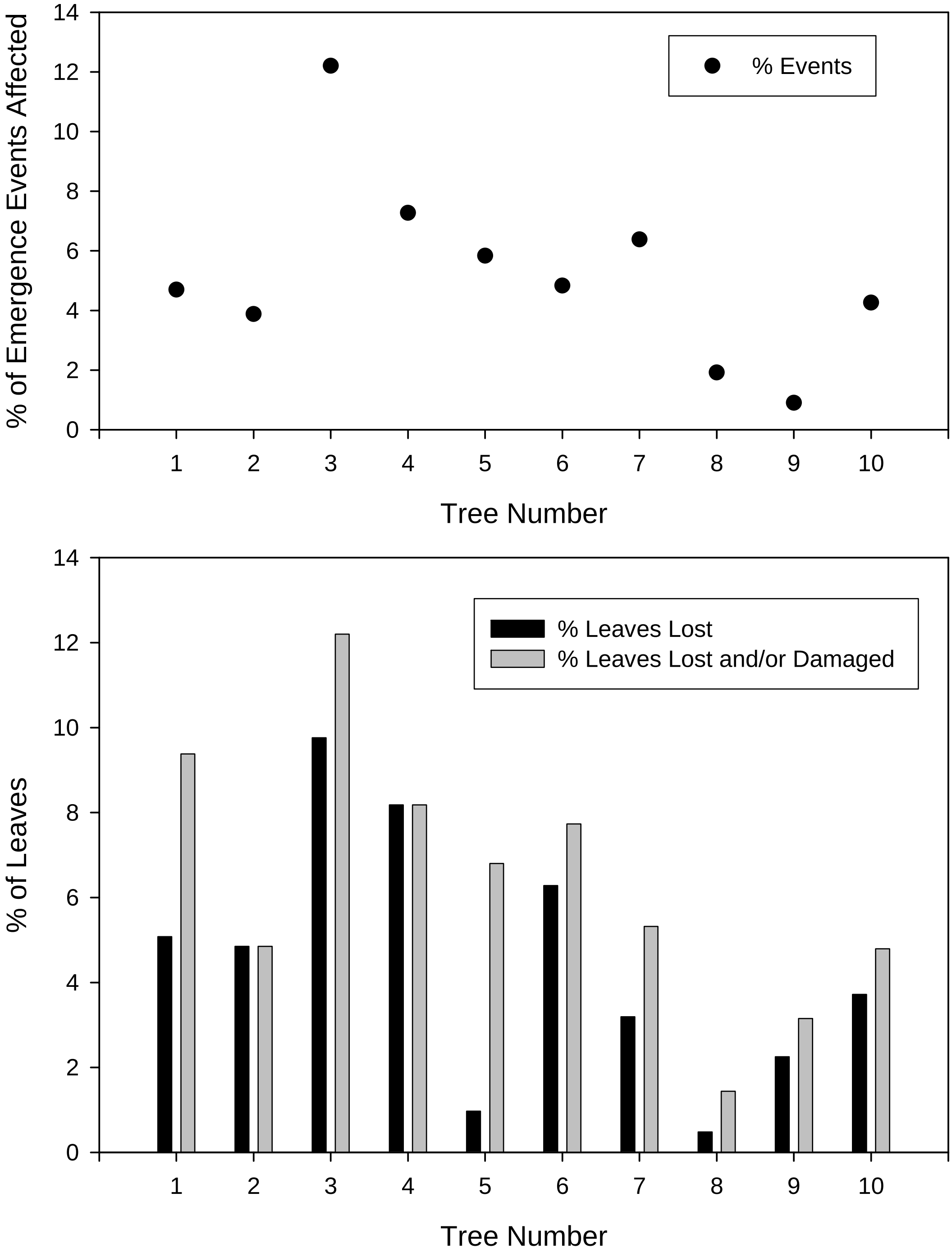
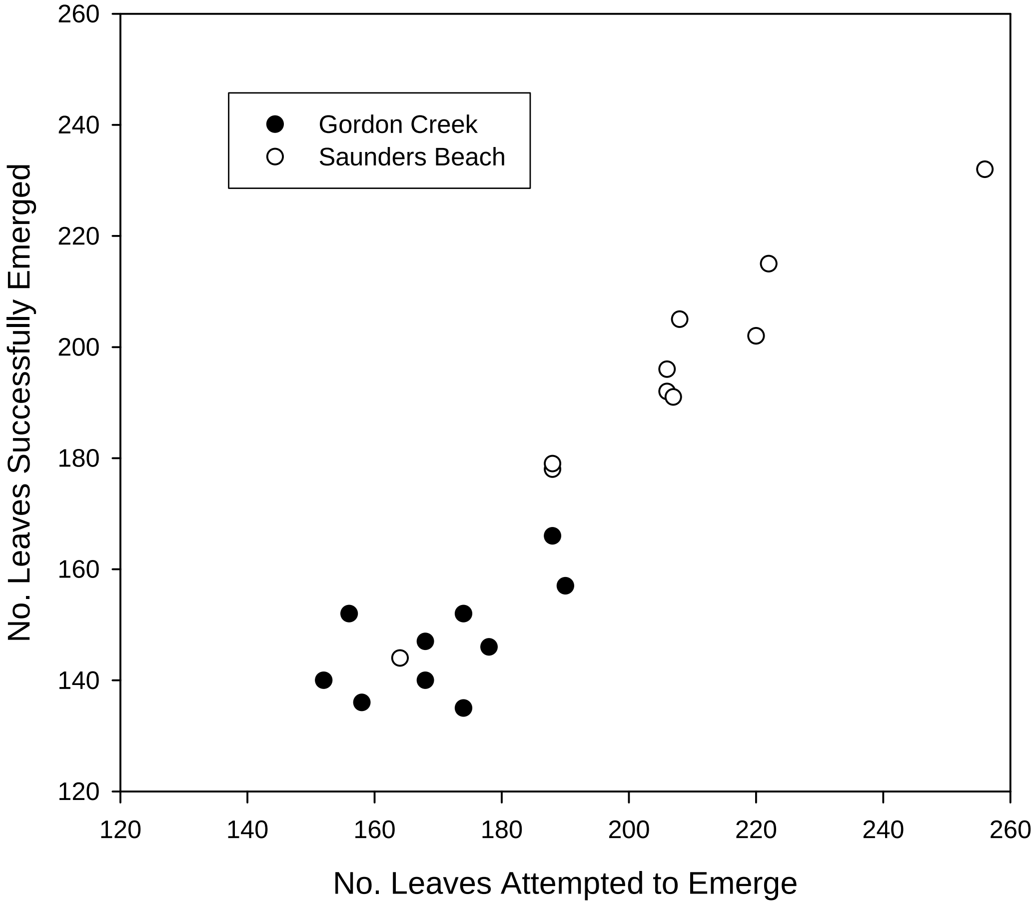


Figure 6.11 Relationship Between the Number of Leaves Produced and the Number That Successfully Emerged From Each of 10 *R. stylosa* Trees



damage to the apical tip was very severe. Thus tip destruction appears to serve as the cue for initiation of reserve buds and insect damage may therefore, if the reserve buds survive, promote formation of new branches.

From the 61 completely destroyed apical tips tagged at Gordon Creek and followed for 13 months, 104 reserve buds emerged, of which 58 died without producing any leaves. From the 75 completely destroyed apical tips tagged at Saunders Beach and followed for 13 months, 118 reserve buds emerged, of which 70 died without producing any leaves. The cause of death of most of these reserve buds is unclear as most died when only 1-2mm long and they perished rapidly. The remaining 56 buds at Gordon Creek and 48 buds at Saunders Beach produced a total of 215 and 304 leaves respectively, though most of these were small (usually 0.5-3cm long compared to 5-6cm for normal leaves). Leaves produced from regenerating buds get progressively larger with each successive pair produced, often taking 3-4 successive pairs to reach an average leaf size.

Given that undamaged tips at Gordon Creek produced, on average, 9.2±0.14 (S.E.) leaves per growing tip over the study period, the 61 destroyed tips could have been expected to have produced 561 full-sized leaves over the same period. Instead, regenerating buds on these tips actually produced only 215, mostly small leaves. Similarly, the 75 destroyed tips at Saunders Beach could have been expected to have produced 10.1±0.12 (S.E.) full-size leaves per tip (total of 756 leaves) over the same period instead of the 304 mostly small-sized leaves produced from the regenerating tips. The reduced number and size of leaves produced from the regenerated buds represent only partial compensation for the loss of potential leaf production due to tip and bud damage.

Branch Death Due to Tip Damage

Each tagged tip also represents a shoot. Of the 800 shoots tagged between the two sites at the beginning of the study, 144 died over the 13 month study. The death of 25 of these was clearly attributable to the activities of wood-boring beetles. Of the remaining 119 shoots, 114 died after their buds were completely destroyed by insects.

It therefore appears that insect damage, via wood-boring and feeding on the apical bud, is also a mechanism that leads to the death of small shoots, and may even be the most common cause of shoot death.

6.3.4 Gladstone Study

Of the 273 shoots initially tagged on 13 trees at the control plots in the Gladstone study, 23 (8.4%) were killed during the two-year study. Of the 1352 leaf emergence events recorded from the tagged shoots, loss of a single leaf was recorded 46 times and loss of both leaves 79 times. Combined with the death of 23 shoots during the study (loss of both leaves in all of these cases), this resulted in an overall loss of 9.2% of emerging leaves due to tip damage caused by insects (Table 6.8). In addition, there would also have been tip damage resulting in damage to leaves that were retained rather than lost, but only complete leaf loss was recorded in that study. If the fertilised sites are excluded from the analysis, then tip damage sufficient to result in leaf loss on the control trees occurred on 12.9% of emergence events resulting in the loss of 10.3% of leaves at the point of emergence.

Table 6.8 Frequency of Tip Damage and Leaf Loss on *R. stylosa* in Gladstone

Sites	No. Trees	% Tips Damaged	% Leaves Lost
Undisturbed control	3	12.0	10.4
Disturbed control	8	12.3	10.2
Fertilised	3	4.4	4.0
Overall	13	10.9	9.2

Proportional data were arcsin transformed for analysis. The differences between the three site groups in the frequency of tip damage resulting in leaf loss, were not statistically significant (One-way ANOVA, $p=0.15$, $df=2,10$, $F=2.32$), probably due to the low level of replication. However, when all the control sites are combined together (ie, as unfertilised sites), then they have a significantly higher damage level than the fertilised sites (t-test, $p<0.05$, $df=11$, $t=2.18$).

6.3.5 Panama Study

The proportion of tips damaged and leaves lost due to tip damage, on *R. mangle* trees in the Panama study, are presented in Table 6.9

Table 6.9 Frequency of Tip Damage and Leaf Loss on *R. mangle* in Panama

Site Aspect	No. Trees	% Tips Damaged	% Leaves Lost
Exposed	7	4.5	2.9
Sheltered	7	4.5	3.7
Riverine	3	11.5	8.7
Overall	17	5.1	4.2

Of the 357 shoots initially tagged on 17 trees at the control sites in, 57 (16%) were killed during the two year study. Of the 1134 leaf emergence events recorded from the tagged shoots, loss of a single leaf was recorded 61 times and loss of both leaves 63 times. Combined with the death of 57 shoots during the study (loss of both leaves in all of these cases), this resulted in an overall loss of 4.2% of emerging leaves due to tip damage caused by insects. There was no significant difference (One-way ANOVA on arcsin transformed data, df=2,14) in the proportion of leaves lost ($p<0.14$, $F=2.28$) or the proportion of tips damaged ($p<0.06$, $F=3.42$) between the trees located in exposed, sheltered or riverine sites.

6.3.6 Comparison of Tip Damage and Loss of Developing Leaves Between Townsville, Gladstone and Panama

Table 6.10 compares rates of tip damage and leaf loss between the Townsville, Gladstone and Panama studies. In order to be fairly compared with the Gladstone and Panama datasets, only tip damage that resulted in loss of one or two leaves has been included from the Townsville dataset for this comparison. All local sites have been combined for each study and only the data from the control sites in Gladstone and Panama are included.

Table 6.10 Frequency of Tip Damage and Leaf Loss on *R. mangle* in Panama and *R. stylosa* in Townsville and Gladstone.

Sites	No. Sites (No. Trees)	% Emergence Events Where Leaf Loss Occurred	% Leaves Lost
Townsville – *R. stylosa*	2 (20)	8.3	6.7
Gladstone – *R. stylosa*	10 (10)	12.9	10.3
Panama – *R. mangle*	13 (17)	5.1	4.2

There were significant differences between the three sites for both the proportion of emergence events where leaf loss occurred and the proportion of leaves lost during such events (One-Way ANOVA on arcsin transformed data, p=0.0002, F=10.44 and p=0.02, F=4.23 respectively, both df=2,44). Tukey's multiple comparison (α=0.05) found all three locations to differ in the proportion of leaves lost but only Panama and Gladstone to differ in the proportion of tip damage events that led to leaf loss. Interestingly, although tip death was twice as frequent in the Panama study compared to the Gladstone study (16% versus 8.4%), loss of leaves due to insect damage was much greater in the latter study (Table 6.10). The current study had the lowest rate of tip death (3.2%, compared to 8.4% and 16% for Gladstone and Panama respectively) but an intermediate rate of leaf loss (Table 6.10).

6.4 Discussion

6.4.1 *A. marina* Developing Leaves

Not surprisingly, a greater proportion of developing leaves were recorded as having suffered insect attack when shoots were tagged and new leaves marked for later inspection, compared to the discrete study where branches were surveyed at one point in time. The difference between the two studies is most likely due to the failure to observe developing leaf buds that were killed and abscised in the discrete study. However, this result is also confounded by the two studies being conducted in different years. Overall, these studies show that damage to developing *A. marina* leaves and leaf buds is very high and that leaves that are attacked are more likely to die than to survive such attacks. Whilst the very high damage rates might suggest that insect attack substantially reduces the leaf production potential of *A. marina*, it is a prolific producer of new leaves from almost anywhere on the branch system, so is probably readily able to compensate for these lost leaves. This study does not address whether the high mortality rates of young, developing leaves results in reduced canopy leaf production. Given that the amount of investment in each bud or developing leaf is likely to be low, loss of such leaves may not be a significant drain upon the energy resources of the plant. This point is further evaluated in Chapter 7.

6.4.2 Apical Tip Damage and Leaf Loss in *R. stylosa* and *R. mangle*

In a discrete study of insect tip damage on dwarf *R. mangle* in Belize, Feller (1995) found that 2-7% of apical buds were damaged and the proportion of aborted leaves ranged from 9-12%. In the discrete surveys in the current study, 22.5% of apical buds were damaged or missing at Gordon Creek and 12.1% at Saunders Beach, and nearly 20% of leaves were aborted from damaged tips at Gordon Creek and over 10% at Saunders Beach.

In the Gladstone study, the rate of apical bud damage and leaf loss was significantly lower in the fertilised plots compared to the control plots. This is in contrast to the results of Onuf *et al.* (1977) and Feller (1995) for *R. mangle* in the Neotropics, which show substantial increases in both parameters in response to nutrient enrichment. Whether this is due to failure of the fertilisation treatment or a genuine lack of response to fertiliser is not known. In both the Gladstone and Belize studies (Feller 1995), fertiliser was applied in granular form and in the Florida study (Onuf *et al.* 1977), fertiliser was naturally applied via guano from a roosting bird colony.

There were significant differences in the frequency of damage to tips and leaf loss resulting from insect damage, between Townsville, Gladstone and Panama, with Gladstone being the highest for both parameters and Panama the lowest. The Panama study involved *R. mangle* whereas the Townsville and Gladstone studies were based on *R. stylosa*. In Florida, Onuf *et al.* (1977) also tagged and followed growing tips to record their rate of damage by bud-feeding caterpillars. They found that 7.8% (range 4.8-10.9%) of leaves were lost due to tip damage in low nutrient mangroves and

21.1% (range 14.0-28.0%) in high nutrient areas (these being underneath bird colonies). The former value is similar to the values found here.

The high proportion of dead compared to damaged tips recorded in the Panama study contrasts with the current study, the Gladstone study and Feller (1995) who reported the frequency of damaged buds on *R. mangle* to be 4-5 times that of completely killed buds on control trees. Onuf *et al.* (1977) who also studied *R. mangle* (in Florida), reported that complete destruction of the growing tip was less frequent than damage from which the bud could recover.

Not all the tip damage and leaf loss at the point of emergence recorded in the Panama and Gladstone studies can be definitely attributed to insect damage although most such damage is probably the result of insect feeding activities. The rate of tip damage that did not result in any leaf loss is not recorded in these datasets but results from the Townsville study suggest that it is likely to be low. The differences between the two Townsville sites indicate that even sites in the same area can have substantially different levels of damage. Although the differences between individual Panama sites were similarly variable, division of the Panama control sites into sheltered, riverine and exposed habitats found no significant differences in the proportion of leaves lost or tips damaged.

6.4.3 Other Aspects of Apical Tip Damage

As flowers and lateral branches are produced alongside new leaves within the apical growing tip, they are also susceptible to damage and loss from insect herbivores. The low frequency of occurrence of flowers on tagged branches did not enable assessments of their loss to be calculated. For instance, flowers were present in only 16 emergence events at Gordon Creek and two at Saunders Beach. Similarly, low rates of normal lateral bud production also preclude their consideration here. Many more shoots would have had to be tagged and monitored to collect enough data to answer these questions. However, from the available data, it is likely that the percentage of normal lateral buds and flowers lost because of bud damage is at least that of leaves (ie, ~4-7%).

The size of a leaf depends on the length of the apical bud from which it develops. Shortening of the apical bud by removal of its distal portions was a common form of insect damage these buds suffered. When such damage occurred, the next pair of leaves produced, though appearing to be normally formed, were shorter than they would otherwise have been. Successive leaves get larger until the pre-damaged bud length is reached. This usually took 3-4 pairs of leaves depending on the extent of initial bud damage. This impact of insect apical bud damage on the size of future leaves (and potentially also inflorescences and lateral shoots), was also observed by Onuf *et al.* (1977) for *R. mangle*.

Resources that would otherwise have gone into dead buds could be reallocated to intact shoots, thus maintaining overall leaf productivity. This could not be comprehensively tested in this study as reallocation of resources, if it occurs, may occur at a variety of temporal and spatial scales. There was no significant difference in the number of leaves produced from intact shoots directly adjoining, and not directly adjoining, killed shoots, at either study site. Thus there was no evidence for resource reallocation and compensatory leaf production at the local shoot scale at least.

Species of the Rhizophoraceae that are mangroves exude a sticky solution (usually a milky colour in *R. stylosa*) from the base of the stipules that covers the organs being produced within the stipules. Primack and Tomlinson (1978) analysed this substance and found it to be a concentrated galactose sugar solution. They also noted several bird species routinely visiting these buds feeding on the secretion. As the birds observed are opportunistic foragers known to also take insects, they postulated that these birds would also take insects when they were encountered and that the secretion may aid in reducing herbivory on the vulnerable buds. Ants that may predate upon insect herbivores have also been observed feeding on the exudate of *R. stylosa* (pers. obs.) and *K. candel* (J. Lee pers. comm.) and may offer a similar service. This interesting aspect of plant-insect relationships has not been investigated in any study.

6.4.4 Architectural Effects

As apical buds are the site from which branch extension and emergence of new lateral branches occurs, damage to these buds could alter the architecture of the trees. This could result from a combination of shoot death and compensation via initiation of suppressed reserve buds below the dead apical bud.

A significant additional effect of apical bud damage is the death of the shoot that results from its inability to produce any further leaves once the apical buds have been destroyed. Over the 12-month course of the present study, nearly 15% of shoots died following the death of their apical buds. A further 3% died as a result of wood-boring beetle larvae. Thus 18% of shoots died because of herbivorous insects over a 12-month period. Similar results have been recorded elsewhere. Of 357 shoots tagged in a study of *R. stylosa* on Hinchinbrook Island, 20% were dead within 12 months (Bunt and Duke unpub. data in Primack and Tomlinson 1978).

Over the course of one year, 11.3% and 8.0% of shoots were killed by tip-feeding insects at Gordon Creek and Saunders Beach respectively. Over two years, 8.4% of shoots were killed in the Gladstone study and 15.7% in the Panama study. That the rate of shoot death is higher at Panama than Gladstone, yet the rate of leaf loss due to tip damage is much lower there, is because of the greater propensity for tip damage to result in total destruction in the Panama study. In the Panama study, 53% of tip damage events that resulted in leaf loss also resulted in death of the tip. In Gladstone, only 15% of tip damage events resulted in death of the tip. At Gordon Creek and Saunders Beach 35% and 46% of tip damage events, respectively, resulted in death of the tip.

Recent research has shown that wood-borers are important sources of branch death in mangroves and that such branch death has significant repercussions for mangrove ecology, including the provision of canopy gaps that allow for recruitment into otherwise uniformly-aged stands of trees (Feller and Mathis 1997, Feller 2002). Shoot death and reduced leaf production because of apical bud damage may also affect canopy dynamics, though with a different spatial pattern (eg, canopy thinning instead of canopy gaps).

The ability of *R. stylosa* to compensate for apical bud damage and destruction via initiation of suppressed lateral buds, will depend on the frequency with which the suppressed lateral buds emerge and the proportion which successfully regenerate new leaves. Though this form of new bud production is prolific, 50-60% of buds died without successfully producing any leaves. The suppressed laterals that did successfully produce leaves, produced them more rapidly than undamaged buds, but the first few pairs of leaves were very small. In the 12 months of this study, from the many tips that were killed, only six regenerated lateral buds produced full-sized leaves. Thus it appears that although there is significant potential for initiation of suppressed lateral buds to compensate for lost apical and lateral buds, this potential is rarely realised. This supports the views of Tomlinson (1986) for *R. mangle*, who observed that the suppressed reserve buds did not contribute to crown development, this only being achieved by the apical and lateral buds.

Although the architectural impacts of damage by apical bud and tip-feeding insects have not been measured in this study, they have been shown in other plant species. Whitham and Mopper (1985) showed that feeding of a moth larva on the terminal shoots of the pinyon pine, *Pinus edulis*, altered the architecture from that of an upright open-canopy tree to a prostrate, closed-canopy tree. Balciunas and Burrows (1993) found a significant difference in height growth between insecticide-treated and control *M. quinquenervia* within three months. Despite the large difference in height, there was no difference in the number of leaves or branches on the treated and control plants. The large difference in height was attributed to a tip-feeding coreid bug that destroys apical growing tips. This promoted lateral rather than vertical growth, resulting in the control trees taking on a shorter but bushier growth from compared to the taller and less bushy insecticide-treated saplings. Thus the major insect herbivore effect was not one of consumption of plant material but of reduced vertical shoot extension and suppression of potential plant growth. Although not examined in the current study, a similar effect may occur for *R. stylosa*.

The potential for tip-feeding insects to affect the architecture of mangrove trees has been suggested previously. Murphy (1990) noted that *Sonneratia* subjected to high levels of attack from caterpillars that damaged apical meristem tips appeared to have a “twiggy” growth form compared to its growth form at a site with lower levels of attack. Rau and Murphy (1990) also speculated on how similar damage to *Rhizophora* in Thailand would have the same effect on tree architecture. They found that apart from damaging emerged leaves, the leaf-rolling pyraustine moth *Pleuroptya* also destroys the apical meristem causing complete dieback of the axial shoot and suggested that this should have a significant effect on tree architecture.

Apical damage may have more impact in dense populations where there is strong competition for light, such as commonly occurs in mangroves. Thus damage to apical buds on leading shoots of the upper canopy in *R. stylosa* and other Rhizophoraceae may be more significant than damage to apical buds on lower branches. Absence of such bud-feeding insects could also alter the ecology of some species. Changes in tree growth form due to ecological release from insect herbivores are well known. For example, *Melaleuca quinquenervia* grows taller in its introduced range in Florida than it does in its native range in Australia, possibly due to a lack of insect tip-feeders in Florida (Balciunas and Burrows 1993). Jacobs (1955) recognised that eucalypts grown outside of Australia have a different crown shape from that of their Australian counterparts, due to the absence of insect bud damage. *Rhizophora mangle* has been introduced to Hawaii from Florida but the insects that feed on their tips in Florida are apparently absent there (or at least low in abundance) (N. Duke and K. Krauss pers. comm.). The Hawaiian trees grow taller and straighter and have less branching than their Florida counterparts (N. Duke pers. comm.), though the role that the lack of tip-feeders may play in this has not been investigated.

Traditional methods of assessing herbivory only include assessing damage to existing leaves. Suppression of leaf production by tip-feeding insects is rarely considered, but may be substantial, especially in trees that invest heavily in new leaves and that have poor powers of tip regeneration (eg, *Rhizophora* and other members of the Rhizophoraceae).

6.4.5 Significance of Tip Damage for Leaf Herbivory Estimates

Assessment of the importance of loss of developing leaves and leaf buds on *Avicennia* spp. has not been undertaken in any study. Presumably, most researchers consider such losses to be unimportant for *Avicennia* spp. However, tip damage has now been shown to be a significant herbivory mechanism on *Rhizophora* spp. in Florida (Onuf *et al.* 1977), Belize (Feller 1995), Panama, Gladstone and Townsville (this study) and is also believed to be significant in SE Asia (Murphy 1990, Rau and Murphy 1990). It thus appears to be a widespread trait for *Rhizophora* spp. The occurrence of this type of damage appears to be common on *Bruguiera* spp. and *Ceriops* spp. around Townsville (pers. obs.) and this is likely to be true elsewhere, so this appears to be a general feature of herbivory on mangrove Rhizophoraceae species.

Onuf *et al.* (1977) determined that on *R. mangle* in Florida, leaf abortion caused by bud-feeding caterpillars comprised 86-96% of total foliage loss due to insects. Feller (1995) determined that the amount of leaf tissue lost because of bud damage and loss of developing leaves in response to bud damage on *R. mangle* in Belize, was 3-4 times greater than that consumed directly by all other folivores. Although that study only utilised a discrete method of assessing direct consumption which probably underestimated true folivory loss, this would be unlikely to entirely account for the difference. For example, in the current study, Table 6.11 shows how loss of developing leaves due to bud damage compares to the discrete and long-term folivory estimates obtained from already emerged leaves (data from Chapter 4).

Table 6.11 Comparison of Folivory Estimates (% Leaf Area Lost) on Developing and Emerged Leaves. Discrete and Long-Term Data come from Chapter 4, Table 4.4).

	% Leaf Area Damaged		
Site	**Discrete**	**Long-Term**	**Bud/Tip Damage***
Gordon Creek	3.8	7.5	9.4
Saunders Beach	4.2	13.2	4.4

* this estimate only includes leaves that were aborted and does not include damage to leaves that were not aborted.

At Saunders Beach, most damage occurred after leaves emerged. At Gordon Creek, the greatest damage occurring whilst leaves were in the developing bud phase. The larger difference between the two measures at Saunders Beach can be attributed to a lower rate of bud damage there and the higher rate of leaf loss due to the activities of wood-borers (Chapter 4). It also needs to be considered that 1.9% and 1.1% of juvenile leaves tagged for the long-term study at Gordon Creek and Saunders Beach respectively, already had some form of insect damage when marked for the first time. Much of this damage probably occurred whilst the leaves were emerging, rather than after they had emerged, thus further increasing estimates of the proportion of insect damage that occurs prior to leaf emergence. Combining estimates of leaf loss of emerged leaves (from Chapter 4) with that of developing leaves (this Chapter), the total loss of leaf material due to herbivorous insects approaches 20% for *R. stylosa*.

Productivity studies based on leaf litter traps are common in mangroves. In such studies, leaf production of Rhizophoraceae species is determined by the number of stipules collected within litter traps. This is reliable because there is only one stipule produced per leaf and the stipules fall at the point of leaf emergence (Duke *et al.* 1984). As stipules fall even when the leaves are destroyed by tip damage, they really only reflect the number of leaves that the tree attempted to produce, not those that successfully emerged to form part of the canopy standing crop. As demonstrated in the current study, and by Onuf *et al.* (1977) and Feller (1995), the number of leaves that successfully enter the canopy standing crop may be up to 20% less than the number of stipules produced. As also demonstrated in the current study, trees that attempt to produce the greatest number of leaves (ie, have the highest stipule fall) do not necessarily have the highest number of new leaves entering the canopy standing crop. In such situations, stipule counts will not reliably reflect which trees had the most new leaves entering the canopy standing crop. Additionally, trees with the higher proportion of damaged tips do not necessarily have the highest proportion of leaves lost due to tip damage. This is because greater leaf production from undamaged apical buds can partly compensate for the high rate of tip damage. Thus assessments of the impact of insect damage to apical buds need to measure leaf production rates as well as tip/bud damage rates. This can be achieved using long-term rather than discrete assessment methods.

As shown in the current study and by Onuf *et al.* (1977) and Feller (1995), leaves lost to bud damage are not yet fully developed, being smaller and lighter than leaves lost to folivore damage after they have emerged (see Chapter 7 for data on changes in leaf biomass with age). Hence, insect damage to, and loss of, leaves after they emerge, may cause greater leaf biomass loss than loss of leaves due to bud damage. On the other hand, leaves that do successfully emerge are able to pay back at least part, if not all, of the investment in their construction. Leaves that are lost before they have a chance to emerge do not pay back any of the tree's investment in them (ie, construction costs) and may thus represent a greater loss to the tree.

6.4 Conclusions

Insect damage to apical buds and tips, resulting in the damage or loss of developing young leaves, is common on both *A. marina* and *R. stylosa*. However, for *A. marina*, investment in each developing leaf is likely to be low and this species can produce new leaves from many places. In contrast, there is considerable investment in each developing *R. stylosa* leaf and new leaves may only be produced from apical buds on each shoot. Thus, loss of developing leaves at or before the point of emergence from the protective stipules is likely to be more significant for *R. stylosa*.

Damage or loss of developing leaves at or just prior to their emergence, has rarely been considered in herbivory studies, though such losses may be just as significant as damage that occurs after leaf emergence. In the current study, bud damage by insects caused the loss of 5-9% of *R. stylosa* leaves; which is a similar amount of leaf area to that lost to insects after the leaves emerge. Although the amount of leaf area lost is similar, leaves lost at the point of emergence have different physical and chemical characteristics to older leaves and this is the subject of the next chapter.

In addition to loss of leaf material, bud damage and destruction by insects also affects total leaf production potential, branch architecture, flower production and lateral branching and may be the most significant single consequence of herbivory for *Rhizophora* spp. and probably other mangrove Rhizophoraceae as well. This type of tip damage has been reported from other Rhizophoraceae species around the world, and appears to be universally associated with these species. Thus, this aspect of insect herbivory and its role in the ecology of Rhizophoraceae mangroves in particular, deserves more attention. Of special interest would be to determine the leaf and flower production, and the growth from of Rhizophoraceae mangroves, grown in the presence and absence of tip-feeding insects.

CHAPTER 7 – ONTOGENIC CHANGES IN SELECTED CHEMICAL AND PHYSICAL LEAF COMPONENTS

7.1 Introduction

Differences in the herbivory level of leaves are often attributed to differences in their nutrient status, which affects their nutrititive value to herbivores, and to secondary compounds that may act as chemical deterrents to herbivores (Schoonhoven *et al.* 1998). However, physical properties of leaves such as their thickness and toughness may be equally significant determinants of herbivory levels (Hochuli 1996). Both the chemical and physical properties of leaves will vary as they age, with major changes expected to occur as the young leaves develop and as mature leaves senesce.

In many species, especially in tropical forests, there is a clear ontogenic pattern of susceptibility to herbivore damage and leaf loss to herbivore damage (Lowman 1985, Coley and Aide 1991, Kursar and Coley 1991). Chapters 4-6 demonstrated that, for both *R. stylosa* and *A. marina*, herbivory was much greater on young, developing leaves and that these leaves were also susceptible to herbivore-induced premature leaf abscission. In Panama, Coley (1983) found herbivory rates on 24 shade-tolerant species to be 25 times greater on young rather than mature leaves. It is commonly suggested that young leaves are more heavily damaged because they are less tough than older leaves and have higher nutrient contents (Kursar and Coley 1991). Toughness is an effective anti-herbivore defence that makes leaves more difficult to chew and digest (Coley 1983, Kursar and Coley 1991). For example, Coley (1983) found that leaf toughness of 46 rainforest canopy tree species in Panama was a better predictor of herbivory rate than was nutritive value. Increased leaf toughness (eg, cell wall lignification) is not an option for young leaves as it is incompatible with leaf expansion (Coley 1983, Kursar and Coley 1991). Once full leaf size is achieved, leaves can harden and toughen, resulting in rapid decreases in herbivory (Coley 1983, Kursar and Coley 1992).

Leaf toughness is commonly assessed by penetrometer tests that provide a proxy indicator of toughness by measuring the force required to push a rod through a leaf. Although penetrometers do not actually measure leaf toughness or any other mechanical property of a leaf (Wright and Vincent 1996, Aranwela *et al.* 1999, Sanson *et al.* 2001), they provide a useful indicator of leaf toughness and have been found to correlate with herbivory in many studies (eg, Feeny 1970, Coley 1983, Lowman and Box 1983, Reich *et al.* 1991, Feller 1995, Jackson 1995). Another proxy measure of leaf toughness is leaf mass per unit area (LMA) or its inverse – specific leaf area (SLA – leaf area per unit mass). Both LMA and SLA provide reliable measures of leaf physical properties (Choong *et al.* 1992, Edwards *et al.* 2000). In particular, they have been widely used as an indicator of leaf toughness in studies of insect herbivory (Landsberg 1990, Stone and Bacon 1995, Landsberg and Gillieson 1995, Abbott *et al.* 2000, Steinbauer 2001). Lucas and Pereira (1990) developed a scissoring technique that measures leaf fracture toughness (the work done to fracture a leaf surface). This provides a means of determining the true mechanical property of leaf toughness and how it changes across a leaf. Choong *et al.* (1992) compared results from the scissoring technique, penetrometer tests and SLA for 42 tree species from Singapore, including 16 mangrove species. They found that both penetrometer tests and SLA were useful indicators of leaf fracture toughness. The scissoring technique is a laboratory-based technique that requires specialised equipment so is not commonly used. Although often correlated with herbivory in individual studies, penetrometer tests vary substantially with the diameter of the rod used, the rate at which force is applied and the degree of control of the operator, potentially giving it poor comparability between studies.

Young leaves may also be more susceptible to herbivory because of their greater nutrient and water content, which increases their nutritional value. Young leaves typically have 2-4 times the nitrogen content of older leaves (Mattson and Scriber 1987, Coley and Aide 1991, Kursar and Coley 1991) which can increase herbivore fitness. Also, leaf nitrogen content and leaf photosynthetic rate are generally positively correlated (Kikuzawa 1995). Leaf water content is also related to herbivory and larval growth rates (Scriber 1977, Slansky and Feeny 1977, Reese and Beck 1978, Schroeder and Malmer 1980, Coley and Aide 1991) and photosynthetic rate (Gulmon and Chu 1981). Leaf water content may be crucial to leaf palatability (Coley 1983) and insect herbivore nutrition (Scriber and Feeny 1979, Scriber and Slansky 1981) and is readily derived when drying leaves for determination of LMA.

In ecological herbivory studies, it is important not only to understand how herbivory varies with leaf age but also to recognise that leaves of different age have different values to the plant and different roles in ecosystem productivity. Chapter 4 explored herbivory on leaves on the basis of percentage leaf area damaged, a standard measure in herbivory studies. Chapter 5 provided evidence that more heavily damaged leaves are more likely to be prematurely abscised, thus reducing their longevity and their ability to return energy to the plant and to pay back their construction and maintenance costs. It is well known that plants retranslocate significant proportions of their nutrient content prior to senescent leaf loss. However, Chapter 5 demonstrated that a significant percentage of leaves, especially for *A. marina*, never reach senescence because of damage by insect herbivores. In most herbivory studies, leaves are all considered as equivalent. However, the age at which abscised leaves fall, the mechanism of their loss and whether there was any opportunity for retranslocation of nutrients and other compounds from the leaves, will have a substantial bearing on the impact of their loss on the plant. Merely considering the proportion of leaf area missing without any further consideration of the values and ecological role of the affected leaves, misses the true impact of this herbivory. For instance, Chapters 4-6 showed that the greatest herbivory and leaf loss is suffered by young leaves that have received less investment by the plant (ie, they are still growing) but offer high potential for future returns through photosynthesis (ie, foregone opportunity cost). Additionally, although herbivory and herbivore-caused leaf loss is greater on *A. marina* than on *R. stylosa*, leaves of the latter appear to be larger and thicker than *A. marina* leaves and are thus likely to represent a much greater energy investment. Therefore, herbivory on leaves of different ages will have different implications for the plants and the loss of any individual leaf may be more significant to *R. stylosa* than to *A. marina* even where the proportion of area damaged is the same.

Litter fall in mangroves has been studied extensively (Duke *et al.* 1981, Saenger and Snedaker 1993) and is considered a crucial mechanism of energy transfer because it is a major carbon and energy source for mangrove and estuarine fauna (Robertson 1986, Robertson and Daniel 1989). Litter fall is predominantly measured in terms of dry weight biomass (i.e. quantity of litter fall) but there are also a number of studies that have looked at the quality of the litter fall. However, no previous studies have investigated the ways in which insect herbivores may influence the quality of the litter fall. Given that insect herbivores have a significant influence on the leaf fall pattern (Chapter 5), and that the biomass and nutrient content of leaves can be expected to vary with the age at which they fall, it is likely that these are additional mechanisms by which insect herbivores influence the ecology of mangroves.

The purpose of this chapter is two-fold: firstly, it examines some of the factors that may explain why herbivory is concentrated on younger leaves; secondly, it explores how the nutrient and energy investment of leaves varies through their development from emergence to senescence, and determines how insect herbivores may influence the rate of nutrient return from trees to the ecosystem through their effect on the quality of litter fall. These goals are achieved by examining changes in nutrient content, water content, chlorophyll content, leaf thickness and LMA with leaf age. These provide relevant information on both the susceptibility to herbivory of leaves and also reflect the value of the leaf to the plant and its quality as leaf litter.

7.2 Methods

The variables used to describe leaf condition were nitrogen, phosphorus, chlorophyll, water content, LMA and leaf thickness. Leaves analysed for these variables were collected from *A. marina* and *R. stylosa* at Gordon Creek and Saunders Beach (see Chapter 2 for details on sites and plant species).

7.2.1 Leaf Developmental Stages

Five stages were identified for examination of leaf developmental changes. These were furled/recently emerged, immature, recently mature, old leaves and senescent leaves. Note that the five stages each occupy varying lengths of time. Leaves pass through the first two stages relatively quickly (a few weeks) as they develop, but the progression from recently mature to old leaf occupies most of the total lifespan. These stages were readily identifiable in the field, based on size, texture, toughness, nodal position and colour (Figure 7.1 and 7.2):

Figure 7.1 The five developmental stages of A*. marina* leaves defined in this study. From left, these are: furled, immature, recently mature, old and senescent. Note the changes in leaf colour as well as texture.

Figure 7.2 The five developmental stages of *R. stylosa* leaves defined in this study. From left, these are: furled, immature, recently mature, old and senescent. Note the changes in leaf colour, even between recently mature and old leaves, as well as changes in texture.

> Furled/Recently Emerged Leaves – For *R. stylosa* these leaves were still wrapped within their stipules and were considered to be about to unfurl. In *A. marina* they were leaves that were in the early stages of development, all being less than 3cm long.
>
> Immature leaves (IM) – For both species, these were leaves that had attained at least 75% of their full size, but that still had a soft, flexible texture, pale green colour and were located in the apical nodal position.
>
> Recently mature leaves (RM) – For both species, these were leaves that had a strong green colour with a polished sheen on the upper surface, that had recently hardened and that were generally either in the apical or second nodal position.
>
> Old leaves – For both species, these leaves were hard and had lost their polished sheen and usually occupied at least the 4th nodal position.
>
> Senescent leaves – For both species, these leaves were yellow or sometimes partly brown. The oldest leaves, lacking any green colouration, were selected provided that they were still attached to the tree. Leaves in late senescence that fell from the tree when lightly touched were preferred.

These stages can be approximated to leaf age, based on extensive observations of thousands of tagged newly-emerged leaves (Chapter Four). For *R. stylosa* (based on the time elapsed since shedding of the leaf stipule), immature leaves are around one month old, recently mature leaves 2-3 months old, and old and senescent leaves are at least six months old. Although *A. marina* leaves have shorter longevity than *R. stylosa* leaves, the age structure is similar as the leaves undergo development at a similar rate and it is the proportion of leaf life occupied by the old leaf stage that varies. Where possible, leaves with low levels of damage were selected. For *R. stylosa*, this was commonly the case, but for *A. marina*, damage was often prevalent on most leaves, necessitating the use of damaged leaves in some cases. When this occurred, damaged areas were cut from the leaf and discarded prior to chemical analysis. *R. stylosa* leaves were collected during March 2002 and *A. marina* leaves were collected during May-June 2002, to coincide with their respective major periods of new leaf production.

7.2.2 Water Content and Nutrient Analysis

For both species at both sites, 10 leaves from each developmental stage on each of 10 trees were collected and transferred to paper bags. The exception was for recently emerged leaves of *A. marina* where at least 20 leaves were collected in order to ensure enough leaf material had been collected for analysis. Only one leaf out of any pair of opposite leaves was chosen and the selection of leaves from adjacent branches was avoided to maximise the distribution of collected leaves around the plant. All collected leaves were returned to the laboratory as soon as possible after collection (within hours), and weighed. They were then oven-dried at 60°C for 7 days and reweighed after cooling to room temperature for at least one hour, to determine their dry weight and water content.

For each developmental stage, the leaves from each tree were combined together for chemical analysis. For each composite sample, the leaf material was ground in a mechanical mill and 0.2 g of ground leaf tissue was digested for analysis. Analysis followed the methods of Baethgen and Alley (1989) for nitrogen and Anderson and Ingram (1989) for phosphorus. Nutrient content was expressed both as a percentage of leaf dry weight (this being common in the literature) and as the absolute amount of nutrient per leaf using the mean dry weight of leaves for each leaf developmental stage.

7.2.3 Leaf Size and Physical Attributes

Before leaves were ground for nutrient analysis, five leaves from each tree at each site were individually weighed and measured for length, area and thickness. Length of fresh leaves was measured to the nearest millimetre using a ruler placed along the leaf midrib, and excluded the petiole. For *A. marina*, leaf area was determined by tracing leaf outlines on to 1mm-grid graph paper. For the larger *R. stylosa* leaves, leaf area was determined from the allometric equation: leaf area = 43.23 x length – 1240.83, derived from measurement of 60 leaves (r^2=0.949). Fresh and dry leaf weights were measured with a balance accurate to 0.001g.

Leaf thickness was measured with a screw-gauge micrometer with ±0.002mm accuracy. Prior testing indicated that leaf thickness varied across each leaf, being thicker near the midrib and thinner near the outer edge. The lower half of the lamina was generally thicker than the upper half. Leaf thickness was standardised to measurements taken in the middle of the either the left or right half of the leaf lamina of dried leaves. LMA was used in this study because it is a useful indicator of leaf physical properties, it is comparable across numerous studies where it has been used and it also relates to many other aspects of leaf ecology, including construction costs (Kikuzawa 1995, Reich *et al.* 1992) and the relative value of a leaf (*sensu* Harper 1989). As is standard, LMA, which is a product of leaf density and thickness, was calculated from the weight of dried leaves and the area of the same leaves before they were dried.

7.2.4 Chlorophyll Content

Chlorophyll concentration was used as a measure of potential photosynthetic activity and because chlorophyll is a nutritious molecule, it also increases leaf attractiveness to herbivores (Turner 2001). Field collection followed the same protocols as for nutrient analysis, though separate leaves were collected. Leaves were quickly (<3hrs) returned in paper bags to the laboratory, and placed into a freezer to preserve the chlorophyll content. Analyses followed a modified version of Porra *et al.* (1989) whereby 10 discs totalling 2 cm^2 of leaf tissue were cut from a leaf using a hole punch and mechanically ground for two minutes with 4 ml of ice-cold 80% acetone. The ground material was then transferred to a test tube, made up to 10ml and placed in a fridge for one hour before being centrifuged at 3,000 rpm for 10 minutes. Absorbance was read at 646.4 and 663.6nm on a spectrophotometer. Chlorophyll concentrations were calculated according to the following formulae (Porra *et al.* 1989).

Chlorophyll *a* (nmol/ml) = 13.71 A663.6 – 2.85 A646.6
Chlorophyll *b* (nmol/ml) = 23.39 A646.6 – 6.542 A663.6

Only two minutes of grinding was required for *R. stylosa* leaves. Preliminary testing found that longer grinding time was required for *A. marina* leaves but this heated the samples and may have caused some chlorophyll loss. For these leaves, leaf discs were soaked in 5 ml of 80% acetone overnight to leach out the chlorophyll before being ground for two minutes, made up to 10ml and then centrifuged. Comparative testing showed that for *A. marina*, this method provided higher chlorophyll values (ie, greater chlorophyll extraction efficiency). The converse was true for *R. stylosa*. Chlorophyll content (chlorophyll *a* and *b* combined together) was expressed both as a percentage of leaf dry weight and as the absolute amount of nutrient per leaf using the mean dry weight of leaves for each leaf developmental stage.

7.2.5 Role of Insect Herbivores in Nutrient and Biomass Loss

As in most herbivory studies, the data from Chapters 4-6 only relate to the proportion of leaf area damaged and the proportion of leaves lost due to herbivore damage. Given that biomass and nutrient content of leaves vary between leaf developmental stages, how do losses of leaves and leaf area measured in previous chapters, equate to losses of nutrients and leaf biomass? Using data from Chapters 4, 5 and 6, estimates of herbivore damage to leaves, the proportion of leaves that fell from the tree at each stage of development, and the proportion whose loss was due to insect damage, is known. This can be compared to data on the average nutrient content for leaves of the same developmental stage in this chapter, to determine the relative amounts of nutrient returned to the mangrove forest floor in senescent leaves and in leaves that were consumed or prematurely abscised because of insect damage (ie, non-senescent leaves). Similarly, herbivore damage in Chapter 4 was based on percent of leaf surface area damaged. By incorporating data on mean biomass of leaves of different developmental stages from this chapter, the overall effect of herbivory of loss of leaf biomass can be estimated.

7.2.6 Statistical Analysis

Proportional data on water, nutrient and chlorophyll content were arcsin transformed. For water, nutrient and chlorophyll content and leaf size and physical attributes, three-way fixed effects ANOVA's were used to compare differences between leaf developmental stages, sites and species and the interaction between these terms. Where significant differences were found, Tukey's multiple comparisons procedures (Zar 1982) based on α=0.05, were used to determine where the differences occurred.

7.3 Results

Results of statistical analysis of the change in leaf physical parameters and water content over five leaf developmental stages are shown in Table 7.1 and for nutrient and chlorophyll parameters in Table 7.2.

Table 7.1 Summary of Three-Way ANOVA's Comparing Leaf Area, Leaf Dry Weight, LMA, Leaf Thickness and % Water Content for Two Species (*A. marina* and *R. stylosa*) at Two Sites (Gordon Creek and Saunders Beach) Across Five Leaf Developmental Stages. For % water content, there were 5 samples (=trees) per leaf stage per site per species with 10 leaves combined together for each sample. For all other parameters, measurements were taken on 5 replicate leaves for each developmental stage, from each of 10 trees at each site (ie, total n=50 for each sample group). Values provided are the *F* statistics. Full details of the ANOVA's are presented in Appendix B.

Source of Variation	**df**	**Leaf Area**	**Leaf Dry Weight**	**LMA**	**Leaf Thickness**	**% Water Content^1**
Species	1	3320***	2908***	695***	71***	315.39***
Site	1	52***	40***	9.88**	13.74***	8.07**
Leaf Stage	4	818***	674***	200***	40***	62.85***
Species x Site	1	3.00	0.82	8.26**	0.30	2.15
Species x Stage	4	90***	160***	17.82***	3.44**	83.82***
Site x Stage	4	7.04***	7.14***	0.98	0.80	2.55*
Species x Site x Stage	4	5.73***	3.56**	5.74***	0.50	1.24

1 Based on ARCSIN transformed data

**P*<0.05, ***P*<0.01, ****P*<0.001

7.3.1 Leaf Area and Weight

Leaf area (Figure 7.3) and leaf dry weight (Figure 7.4) showed almost identical patterns between sites, species and leaf developmental stages. At all stages of leaf development, *R. stylosa* leaves were significantly larger and had significantly more biomass than *A. marina* leaves. For both species, the consistent differences in mean leaf area between the two sites across all developmental stages were not statistically significant, except for old and senescent *R. stylosa* leaves. For both species, leaves continued to increase in size and biomass after reaching the stage designated as maturity. The lack of significant species x site interaction term indicates the patterns illustrated by the two species were the same at both sites.

7.3.2 Leaf Thickness

R. stylosa leaves were thicker than *A. marina* leaves for all leaf developmental stages at each site (Figure 7.5), though this difference was not significant for furled/recently emerged leaves at either site. Interestingly, the thickness of furled *A. marina* leaves from Gordon Creek was not significantly different (and were actually slightly greater) than furled *R. stylosa* leaves from Saunders Beach. For both species, leaves were consistently thicker at Gordon Creek than at Saunders Beach for all developmental stages except senescence, though Tukeys test only revealed this to be statistically significant for old *R. stylosa* leaves. Species by site interactions were not significant for leaf thickness; that is, differences between species were similar at each site.

Leaf developmental stage had a significant effect on leaf thickness for both species at both sites but the two species showed different patterns of change. For both species, leaf thickness increased as the leaves aged but this occurred at different stages for the two species (Figure 7.5). At both sites, *R. stylosa* leaf thickness increased gradually as the leaves aged, with no individual step being significant. Mean leaf thickness decreased with senescence at Gordon Creek but increased at Saunders Beach, although the latter result is likely to be a sampling artefact as suggested by the unusually large standard error of that result. In contrast, for *A. marina* at both sites, leaf thickness showed little change as the young leaves developed and the greatest increase in leaf thickness occurred after the leaves had matured.

Figure 7.3 Surface Area (mean ± S.E.) of Fresh *A. marina* and *R. stylosa* Leaves at Each Developmental Stage

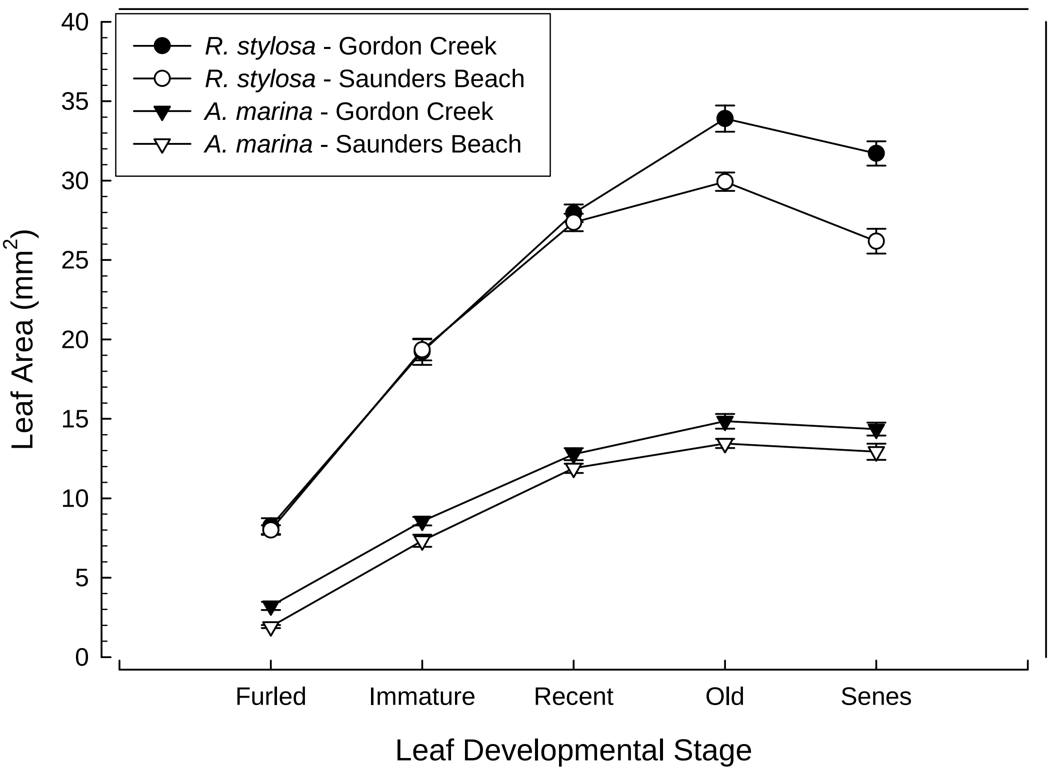


Figure 7.4 Dry Weight (mean ± S.E.) of *A. marina* and *R. stylosa* Leaves at Each Developmental Stage

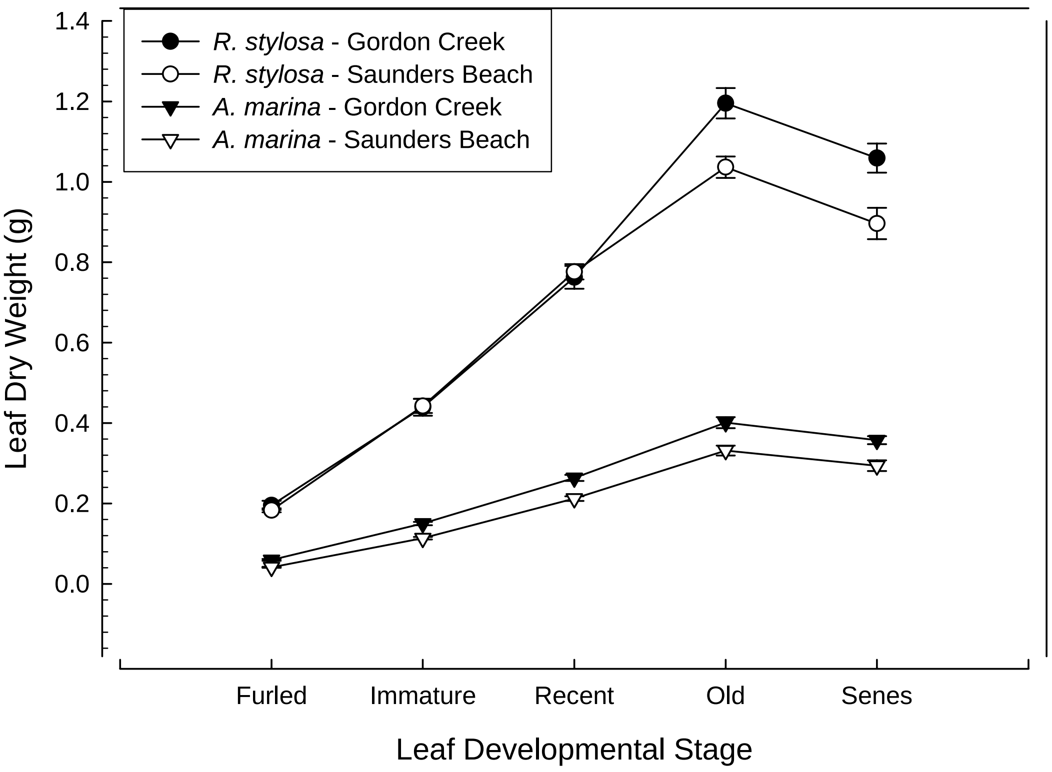


Figure 7.5 Lamina Thickness (mean ± S.E.) of *A. marina* and *R. stylosa* Leaves at Each Developmental Stage

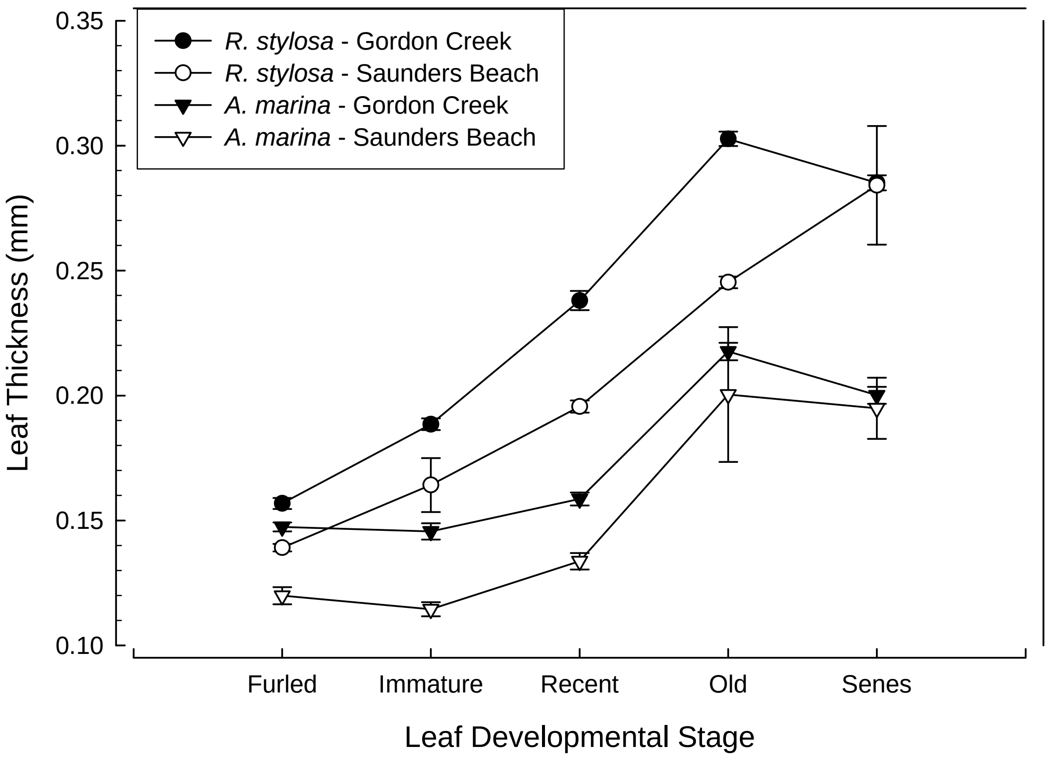
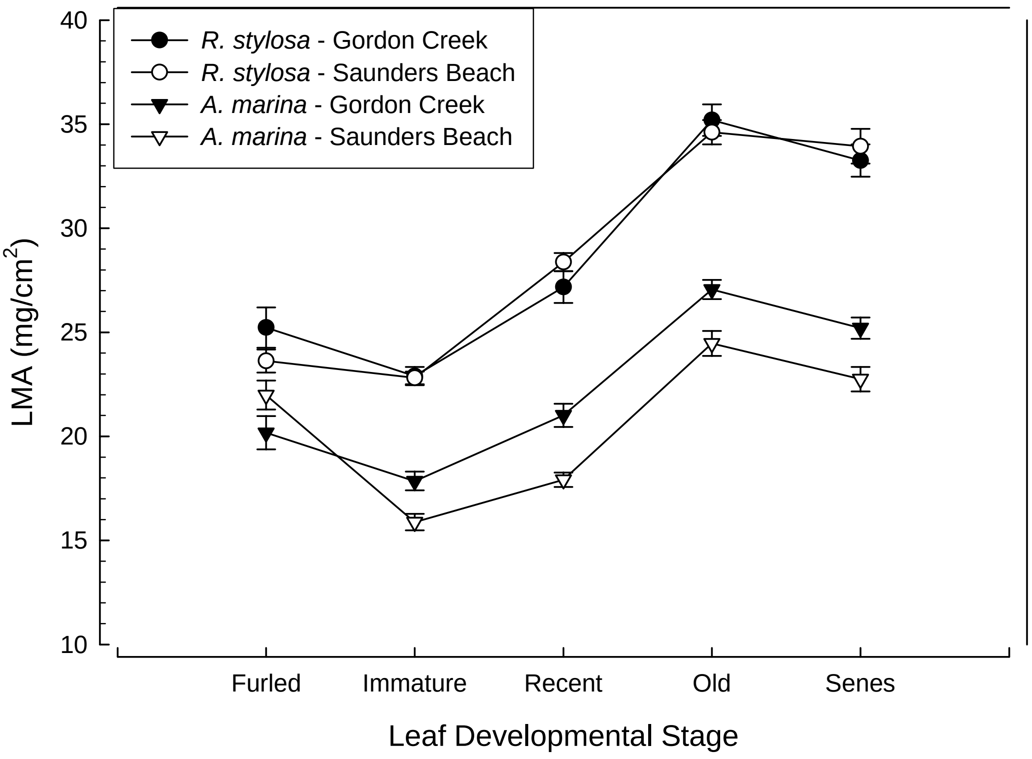


Figure 7.6 Leaf Mass per Unit Area (mean ± S.E.) of *A. marina* and *R. stylosa* Leaves at Each Developmental Stage



7.3.3 Leaf Mass per Unit Area (LMA)

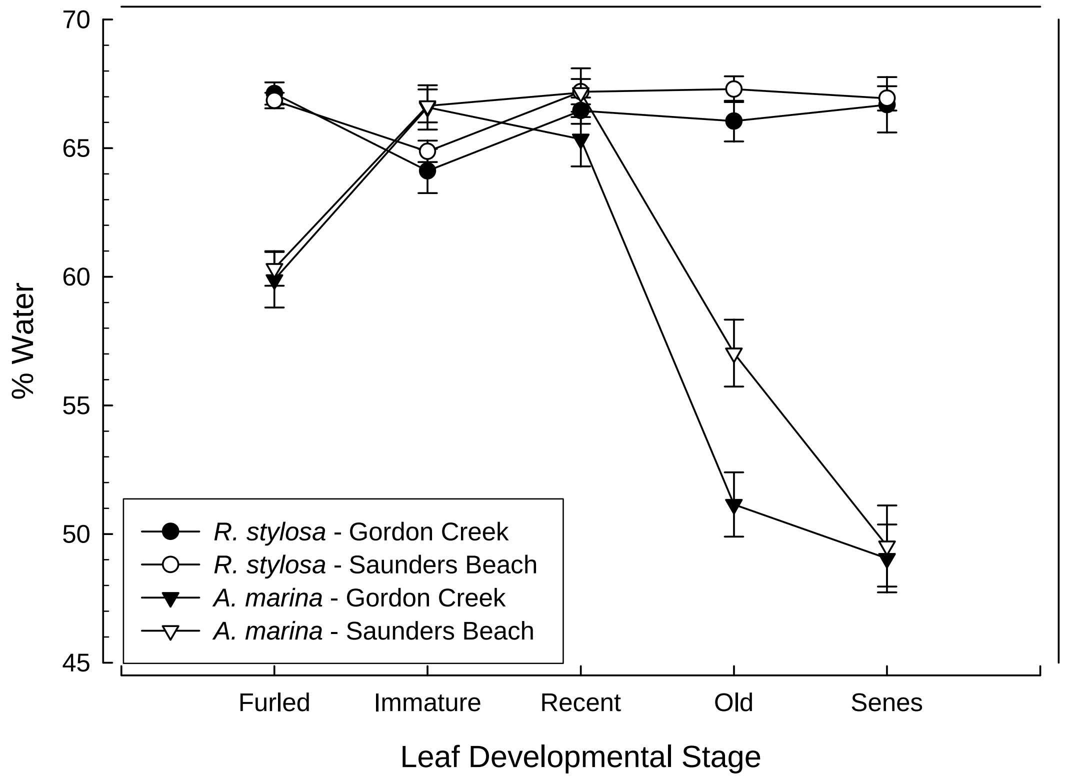
LMA was significantly greater for *R. stylosa* leaves than for *A. marina* leaves at both sites and for all leaf developmental stages except for furled leaves at Saunders Beach (Figure 7.6). For *A. marina,* LMA was significantly higher at Gordon Creek than at Saunders Beach, but for *R. stylosa*, there were no differences between sites. There were significant differences in LMA between leaf developmental stages (Table 7.1) with both species at both sites showing the same the pattern of change with developmental stage (Figure 7.6). LMA decreased from furled to IM leaves but thereafter increased gradually through RM and old leaves before declining slightly with senescence. The decrease between recently emerged and immature leaves was significant for *A. marina* at both sites but not significant for *R. stylosa* at either site. For both species, the increase in LMA from IM to RM to old leaves was significant but the decrease in LMA during senescence was not.

7.3.4 Water Content

There were significant differences between percentage water content for species, sites and the various stages of leaf development (Table 7.1). *R. stylosa* had a higher overall water content than *A. marina*, though this was essentially due to the significant decrease in water content in old and senescent *A. marina* leaves (Figure 7.7). Otherwise, the maximum water content values were similar for the two species. For *R. stylosa* leaves, there was no significant difference in water content between sites. For *A. marina*, leaves from Saunders Beach had significantly greater water content than leaves from Gordon Creek, though the only individual developmental stage for which this was significant was for old *A. marina* leaves.

The two species showed contrasting patterns of water content (Figure 7.7). Water content was constant across all leaf developmental stages for *R. stylosa*, with a slight drop for immature leaves. Reanalysis of the data after removal of immature leaves eliminated the significant effect of leaf developmental stage for this species. In contrast, for A. *marina*, water content varied significantly with leaf development stage. At both sites, water content of *A. marina* leaves increased from furled to IM leaves, peaked at the IM and RM stages and then declined between RM and old leaves

Figure 7.7 Percent Water Content (mean ± S.E.) of *A. marina* and *R. stylosa* Leaves at Each Developmental Stage



and between old and senescent leaves. Significant interaction effects indicated that the differences in water content of leaf developmental stage were different for *A. marina* and *R. stylosa* (as evidenced by the different pattern observed in those species) but that both species behaved similarly at both sites (as illustrated in Figure 7.7). Thus the observed patterns appear to be related to water conservation mechanisms of the species rather than differences related to the sites studied.

7.3.5 Chlorophyll Content

Chlorophyll concentration (Table 7.2) was significantly greater for *R. stylosa* at Gordon Creek but at Saunders Beach there was no significant difference between the two species. Though chlorophyll concentration was consistently higher across all leaf developmental stages at Gordon Creek for *R. stylosa* and at Saunders Beach for *A. marina*, site differences were not significant for either species. For both species, chlorophyll concentration differed significantly across leaf developmental stages (Figure 7.8). For *A. marina* at both sites, Tukeys tests revealed significant differences only between old leaves and the youngest leaves and old leaves and senescent leaves. For *R. stylosa* at Saunders Beach, the only significant differences detected were for senescent leaves compared to all other leaf stages. For *R. stylosa* at Gordon Creek, significant differences were found between all leaf stages from immature to senescent. For both species at both sites, chlorophyll concentration showed a generally increasing trend as the leaves matured but a significant decrease during senescence.

On a per leaf basis, differences in total chlorophyll content were more readily apparent across leaf developmental stages and between sites and species. For both species, total chlorophyll content increased with each successive leaf developmental stage, peaking in old leaves before rapidly declining during senescence (Figure 7.9). For *A. marina* at both sites, chlorophyll content of old leaves was significantly greater than all other leaf developmental stages and senescent leaves were not significantly different from immature or recently mature leaves. For *R. stylosa* at both sites, significant differences were detected between immature and recently mature leaves and between old and senescent leaves, though senescent leaves were not significantly

Table 7.2 Summary of Three-Way ANOVA's for Nutrient and Chlorophyll Content for Two Species (*A. marina* and *R. stylosa*) at Two Sites (Gordon Creek and Saunders Beach) Across Five Leaf Developmental Stages. There were 10 samples (=trees) per leaf stage per site per species with 10 leaves combined together for each sample. Values provided are the *F* statistics. Full details of the ANOVA's are presented in Appendix B.

Source of Variation	**df**	**Chlorophyll**	**μg Chl/leaf**	**% Nitrogen**^{1}	**% Phosphorus**^{1}	**mg N/leaf**	**mg P/leaf**
Species	1	9.82**	258***	1007.08***	282.99***	316.84***	605.95***
Site	1	0.11	2.39	4.11*	103.75***	80.165***	298.65***
Leaf Stage	4	109***	135***	521.15***	287.68***	242.80***	97.96***
Species x Site	1	12.43**	6.23*	26.56***	60.89***	43.55***	138.11***
Species x Stage	4	4.07**	43***	16.15***	12.90***	18.97***	9.93***
Site x Stage	4	0.72	1.36	3.72**	0.26	1.76	6.36***
Species x Site x Stage	4	2.24	2.60*	1.13	1.52	2.208	3.97**

1 Based on ARCSIN transformed data

*P<0.05, **P<0.01, ***P<0.001

different from immature leaves. For both species, the differences between the various leaf developmental stages were consistent between the two sites studied as evidenced by the lack of a site by stage interaction. Though chlorophyll content was generally higher at Gordon Creek for *R. stylosa* and Saunders Beach for *A. marina,* site differences were not significant. Total chlorophyll content per leaf was significantly greater for *R. stylosa* than for *A. marina* for all leaf stages, except senescent leaves and young leaves. Though chlorophyll concentration was very low in the senescent leaves (Figure 7.8), the amount of chlorophyll per leaf was similar in senescent leaves to young leaves, especially for *A. marina* (Figure 7.9).

7.3.6 Nutrient Concentration

Nitrogen concentration (Table 7.2) was significantly greater for *A. marina* than *R. stylosa* for all leaf developmental stages except senescent leaves (Figure 7.10). Phosphorus concentration of *A. marina* leaves was significantly greater than *R. stylosa* leaves for all leaf developmental stages except old and senescent leaves (Figure 7.11).

Figure 7.8 Total Chlorophyll Concentration (mean ±S.E.) of *A. marina* and *R. stylosa* Leaves at Each Developmental Stage

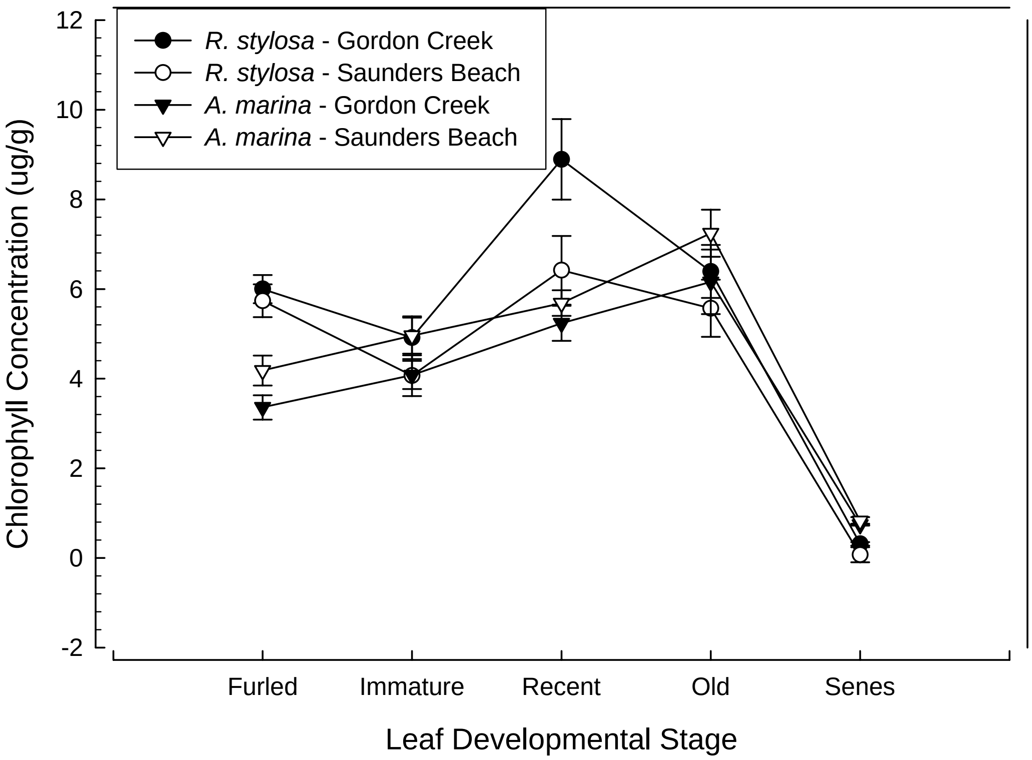
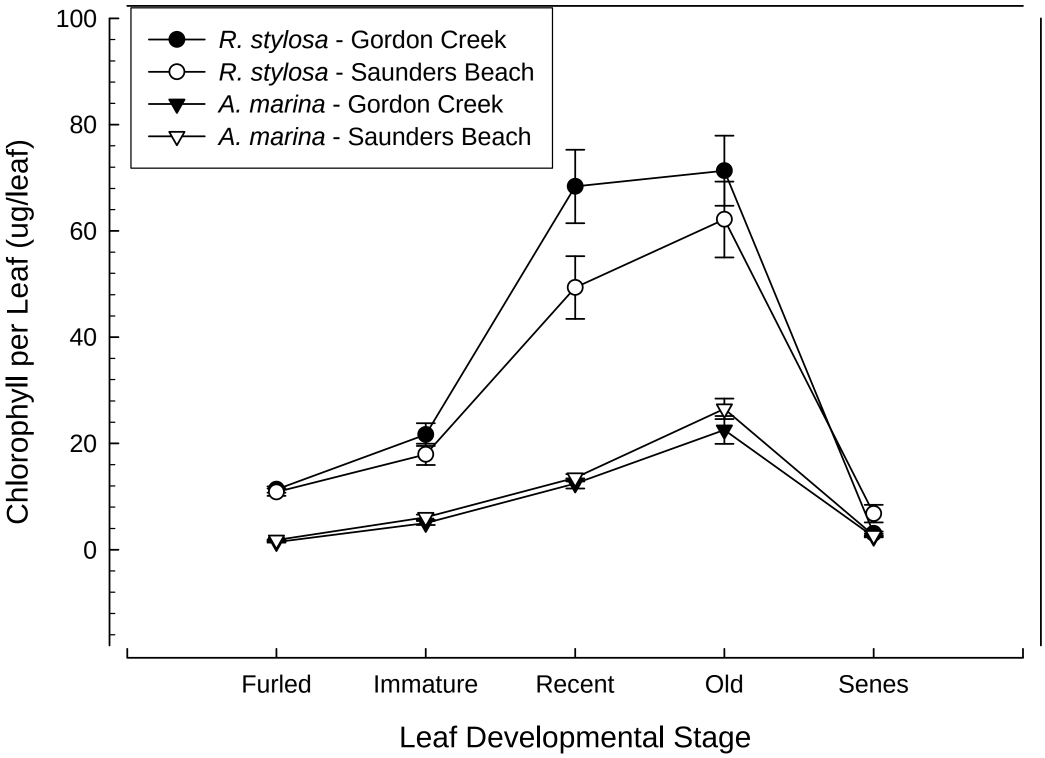


Figure 7.9 Total Chlorophyll Content (ug/leaf) of *A. marina* and *R. stylosa* Leaves Versus Leaf Developmental Stage



There was a significant difference between sites for both N and P concentration. For N concentration in *A. marina*, Tukeys test revealed significantly greater N concentration at Saunders Beach for recently mature, old and senescent leaves, but for P concentration in *A. marina,* Tukeys test failed to identify any differences between sites for any leaf developmental stage. For N concentration in *R. stylosa,* Tukeys test failed to identify any differences between sites for any leaf developmental stage but in direct contrast, P concentration in *R. stylosa* was significantly greater at Gordon Creek for all five leaf developmental stages.

There were significant differences in both N and P concentrations for different stages of leaf development. This effect remained significant for both species and at both sites, indicating the general applicability of this feature. The concentrations of both nutrients in leaves of both plant species at both sites were greatest in the newest leaves and steadily declined as the leaves aged (Figure 7.10 and 7.11). For N concentration, there were larger declines between old and senescent leaves than between earlier leaf developmental stages; however, for P concentration, the rate of decline was gradual between all leaf developmental stages (Table 7.3).

Overall decrease in N concentration from leaf emergence to senescence was similar for both species at both sites, although decline in P concentration was greater for *A. marina* than for *R. stylosa*. For both species, there was a significant decline in N and P concentration with leaf developmental stage. Decline in nutrient concentration occurred for both species at both sites across all leaf developmental stages. In no case did the concentration between successive leaf developmental stages increase. Decline in nutrient concentration was usually significant between furled and IM leaves, rarely significant between IM and RM leaves, but was always significant between RM and old leaves and between old and senescent leaves (Table 7.3), indicating a greater rate of decline as old age and senescence progressed. For N concentration, the greatest decline occurred between old and senescent leaves but for P concentration, the greatest decline occurred between RM and old leaves.

Figure 7.10 Percent Nitrogen Content (mean ± S.E.) of *A. marina* and *R. stylosa* Leaves at Each Developmental Stage

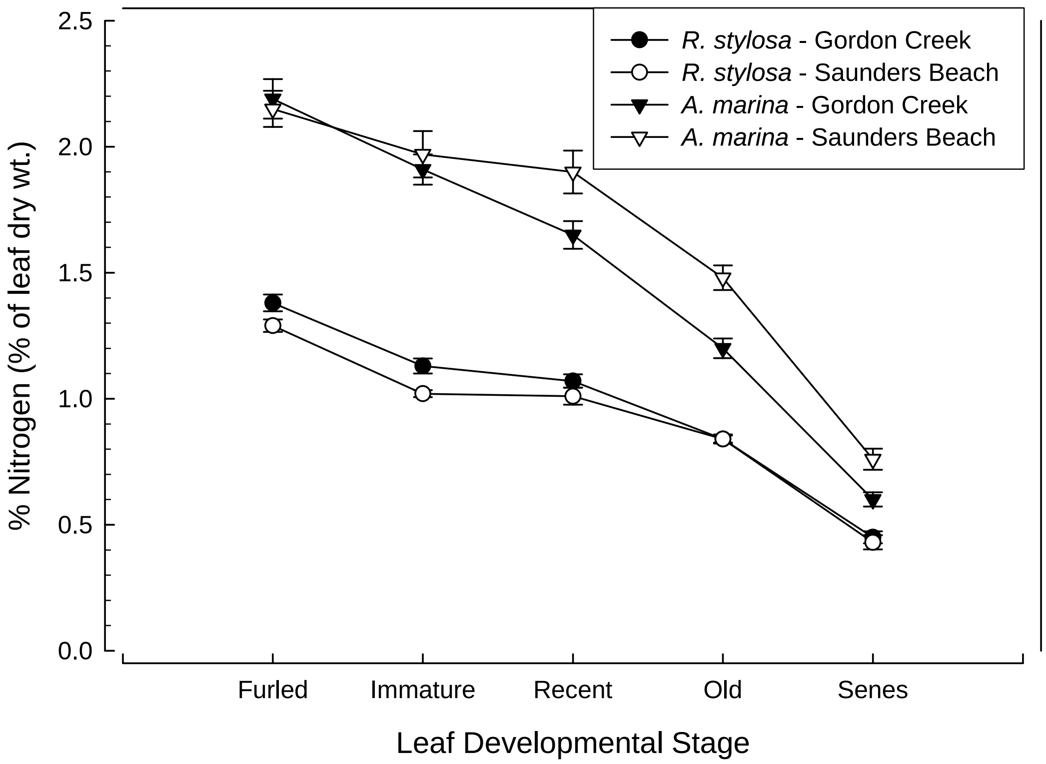


Figure 7.11 Percent Phosphorus Content (mean ± S.E.) of *A. marina* and *R. stylosa* Leaves at Each Developmental Stage

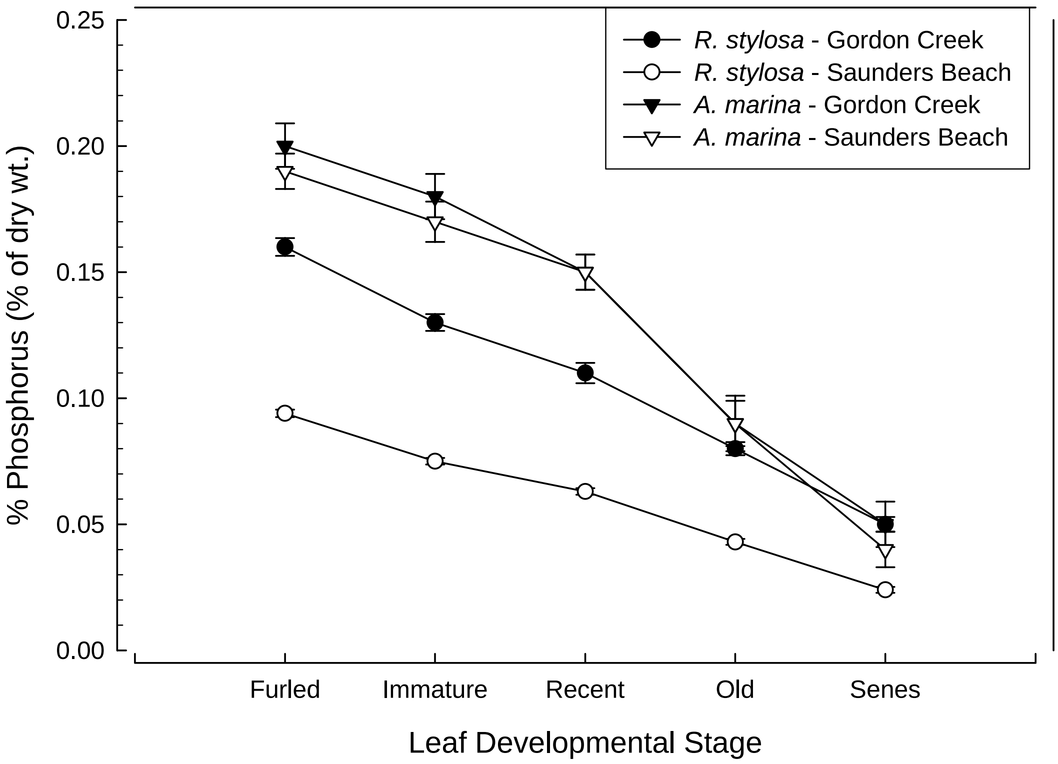


Table 7.3 Percentage Decline in Nutrient Concentration Between Each Successive Leaf Developmental Stage and Overall Decline From Youngest to Oldest Leaves

Species	Site	Furled-IM	IM-RM	RM-Old	Old-Senescent	Furled-Senescent[1]
% Nitrogen						
A. marina	Saunders Beach	8.6	3.1	19.5*	33.7*	65
	Gordon Creek	12.9*	11.7*	20.7*	27.6*	73
R. stylosa	Saunders Beach	21.5*	0.4	13.0*	32.1*	67
	Gordon Creek	18.6*	4.1	16.6*	28.3*	68
% Phosphorus						
A. marina	Saunders Beach	11.6	9.0	33.2*	26.2*	80
	Gordon Creek	11.9	13.3	27.5*	22.1*	75
R. stylosa	Saunders Beach	20.6*	12.4	21.5*	19.7*	74
	Gordon Creek	21.8*	9.6	20.5*	19.8*	72

* marks leaf developmental stages which were significantly different (Tukeys multiple comparison test, α=0.05). Comparisons are made horizontally across the rows. In all cases, differences across more than one leaf developmental stage (eg. Furled-RM or IM-Old etc.) were significantly different.

[1] overall decline across all leaf developmental stages from emergence to senescence

7.3.7 Total Nutrient Content

The total nutrient content of a leaf depends on both its nutrient concentration and the biomass of the leaf. At both sites, nitrogen and phosphorus content were higher in *R. stylosa* than *A. marina* (Table 7.2). For *R. stylosa*, both nitrogen and phosphorus content were significantly higher at Gordon Creek than at Saunders Beach (Table 7.2). Phosphorus content of *A. marina* leaves was generally greater at Gordon Creek, but this was only significant for RM leaves. For nitrogen, the differences were significant only for RM and IM *A. marina* leaves.

For both *A. marina* and *R. stylosa* at both sites, there was a significant difference in both nitrogen and phosphorus content for different stages of leaf development (Figure 7.12 and 7.13). Nitrogen content for both *A. marina* and *R. stylosa* was greatest in old leaves. Phosphorus content was either greatest in old leaves or, in two cases, it was slightly greater in RM leaves than old leaves. Although nutrient content sharply declined during senescence, in several cases, senescent leaves still contained greater absolute amounts of nutrient than the youngest leaves (Figure 7.12 and 7.13). This

Figure 7.12 Total Nitrogen Content (mean ± S.E.) of *A. marina* and *R. stylosa* Leaves at Each Developmental Stage

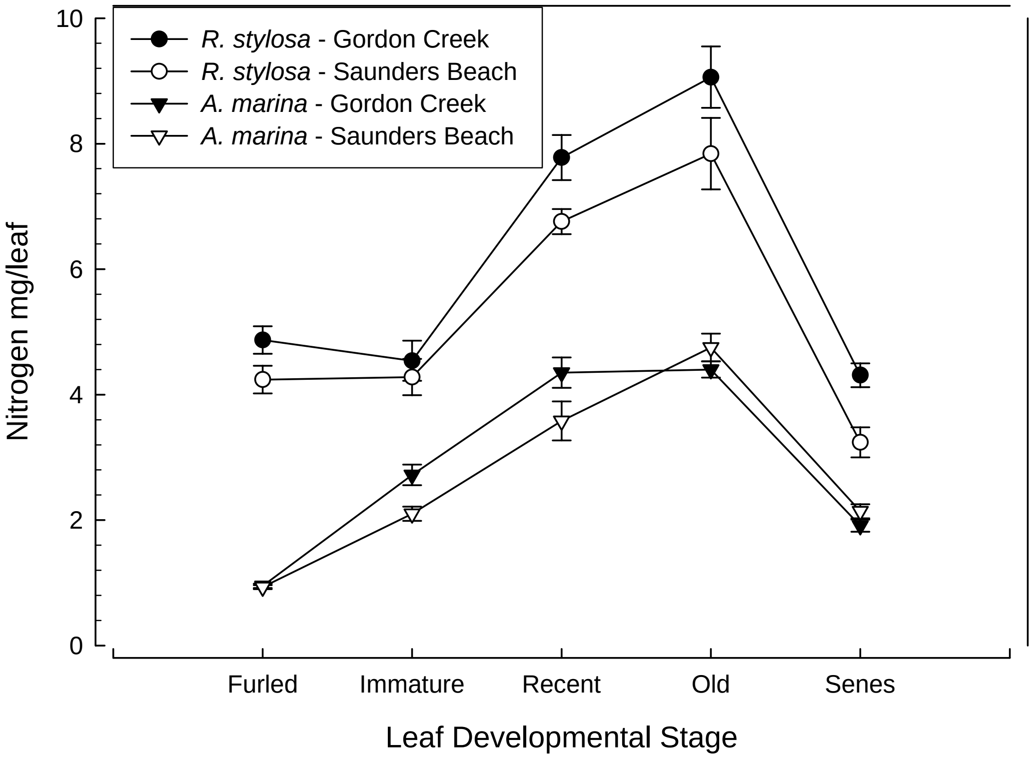
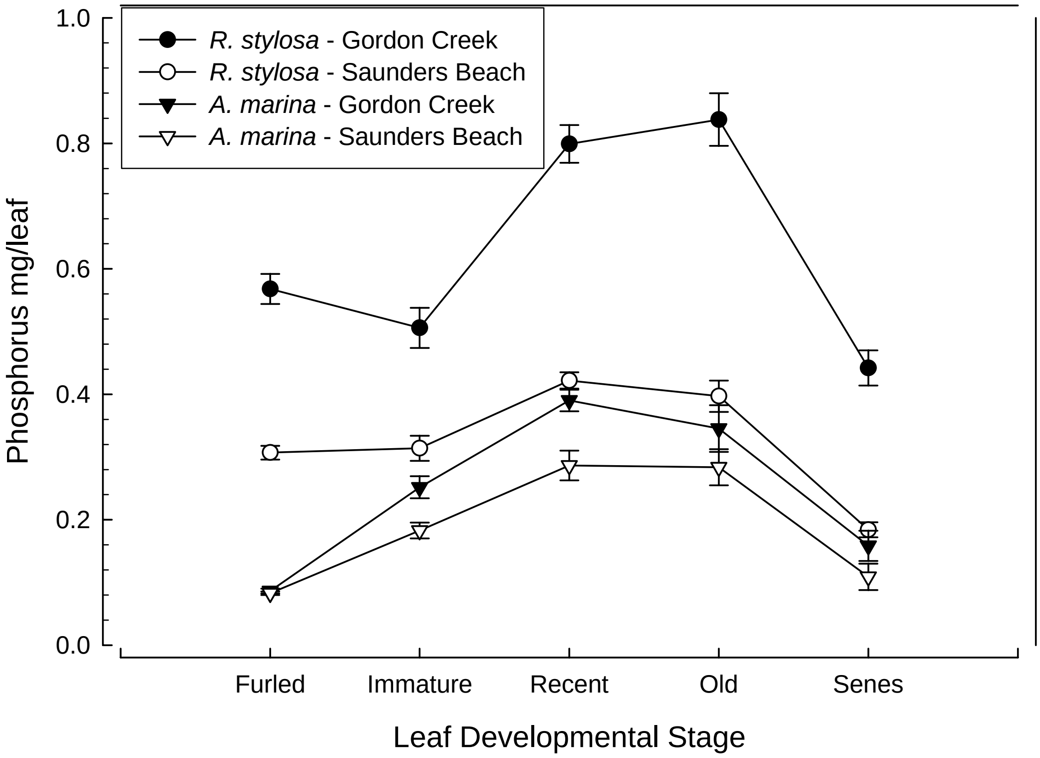


Figure 7.13 Total Phosphorus Content (mean ± S.E.) of *A. marina* and *R. stylosa* Leaves at Each Developmental Stage



contrasts strongly with the pattern of nutrient concentration where the youngest leaves had the highest concentration and the senescent leaves had the lowest concentration.

A. marina had a different pattern of nitrogen and phosphorus content change between each leaf developmental stage than *R. stylosa*. For *A. marina*, both nutrients increased gradually with each successive stage from furled to RM. Nutrient content for RM and old leaves were generally similar and there was a decrease to senescent leaves, though senescent leaves held greater nutrient content than furled leaves. For *R. stylosa*, there was very little difference between furled and IM leaves. Nutrient content increased through RM leaves, peaking in old leaves before declining with senescence, with senescent leaves, in contrast to the situation for *A. marina*, having lower nutrient content than furled leaves.

For both plant species, there were, in all cases, significant increases in nitrogen and phosphorus content between IM and RM leaves and significant decreases in nitrogen and phosphorus content between old and senescent leaves. Overall decrease in nitrogen and phosphorus content from the maximum value to senescence was similar for *A. marina* at both sites, but for *R. stylosa*, decline in nutrient and phosphorus content was greater at Saunders Beach than at Gordon Creek (Table 7.4).

Table 7.4 Percent Change (either increase or decrease) in Nutrient Content Compared to the Maximum Amount, Between Each Successive Leaf Developmental Stage and Decline Between Maximum Value and Senescent Leaves

Species	Site	Furled-IM	IM-RM	RM-Old	Old-Senescent	Max. Content-Senescent Content[1]
Nitrogen (mg/l)						
A. marina	Saunders Beach	+24.7*	+31.3*	+24.5*	-54.9*	-54.9
	Gordon Creek	+40.4*	+36.9*	+1.2	-56.6*	-58.8
R. stylosa	Saunders Beach	+0.01	+31.7*	+13.7*	-58.7*	-58.7
	Gordon Creek	-0.04	+35.8*	+14.1*	-52.4*	-52.4
Phosphorus (mg/l)						
A. marina	Saunders Beach	+34.9*	+36.3*	-0.01	-61.1*	-61.1
	Gordon Creek	+42.3*	+35.4*	-11.5	-47.9*	-59.4
R. stylosa	Saunders Beach	+1.7	+25.6*	-5.9	-50.7*	-56.6
	Gordon Creek	-7.4	+34.9*	+4.6	-47.2*	-47.2

* marks leaf developmental stages which were significantly different (Tukeys multiple comparison test, α=0.05). Comparisons are made horizontally across the rows.

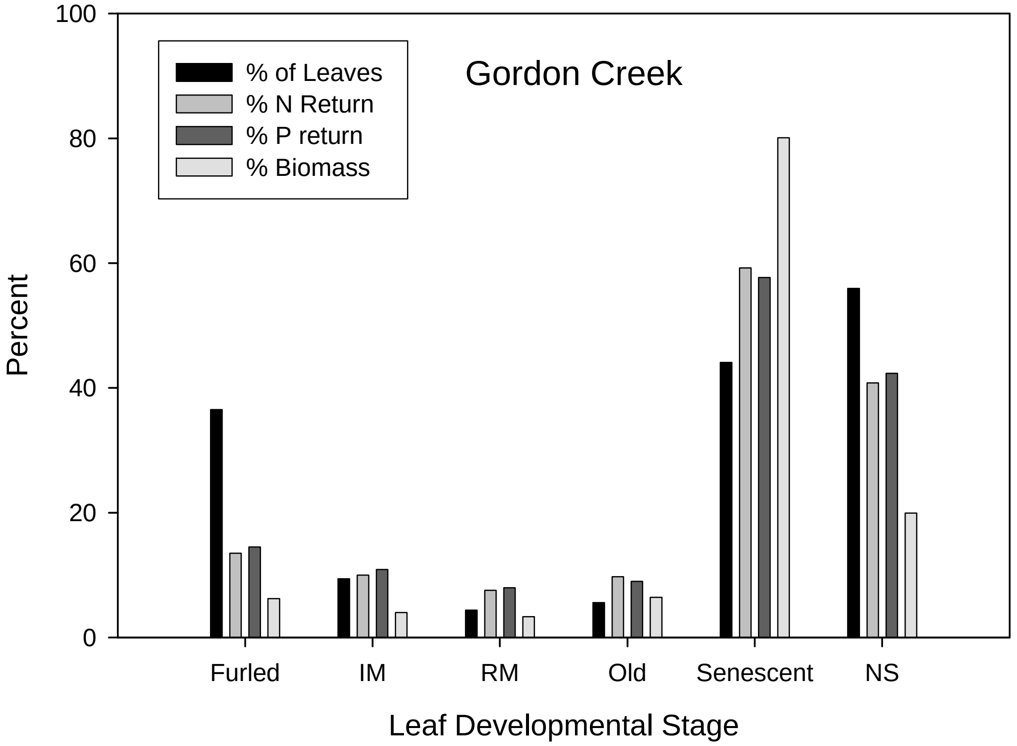
[1] difference between the maximum leaf nutrient content and the nutrient content after senescence.

7.3.8 Role of Insect Herbivores in Nutrient and Biomass Loss

For *A. marina*, all leaf developmental stages substantially contributed to nutrient return and leaves prematurely abscised because of insect damage returned similar total amounts of nutrients as did leaves that reached senescence (Figure 7.14). In contrast, for *R. stylosa* most nutrient returned in senescent leaves (Figure 7.15). For *R. stylosa* at Gordon Creek, nutrient return in prematurely-abscised leaves was dominated by furled leaves, with little nutrient returning in IM, RM or old leaves (Figure 7.15). A similar result occurred at Saunders Beach, although because of wood-borers, loss of older leaves was more common there.

For *A. marina*, the number of leaves prematurely lost because of insect damage was much greater than the biomass or nutrient content lost in those leaves because most such leaves were still in their developing phase and therefore low in absolute nutrient content and biomass. This pattern is less apparent for *R. stylosa* because, although the loss of developing leaves was also prevalent, in this case, the leaves were already well-developed before they were lost, thus representing greater biomass and nutrient content. Nutrient return to the forest floor via prematurely abscised insect-damaged leaves was greater than would be predicted from return of leaves alone (Figures 7.14 and 7.15). The role of herbivorous insects in nutrient return is much greater for *A. marina* than for *R. stylosa* and for both species, was greater at Saunders Beach than at Gordon Creek (Figures 7.14 and 7.15). For *A. marina* at Saunders Beach, more than half of the nutrient returned in leaf litter is returned in leaves prematurely abscised because of insect damage.

Figure 7.14 Effect of Insect-Caused Leaf Drop on Nutrient Return to the Forest Floor and Leaf Biomass Loss of *A. marina* Leaves. NS = the four non-senescent leaf categories (Furled, IM, RM and Old) combined together



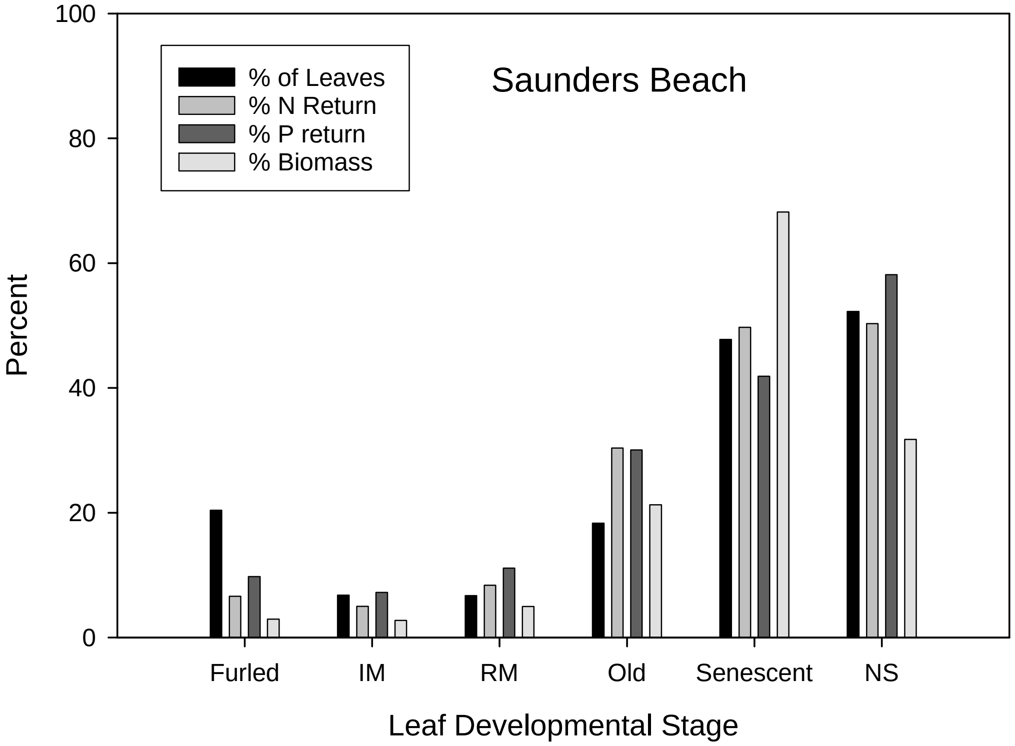
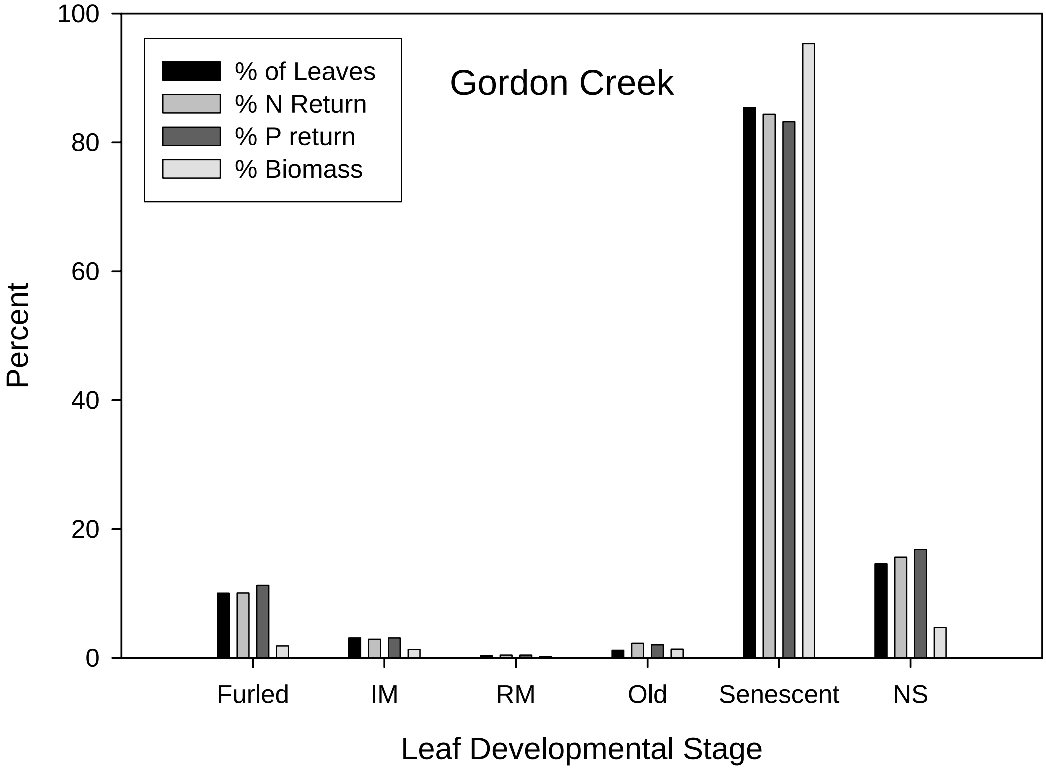
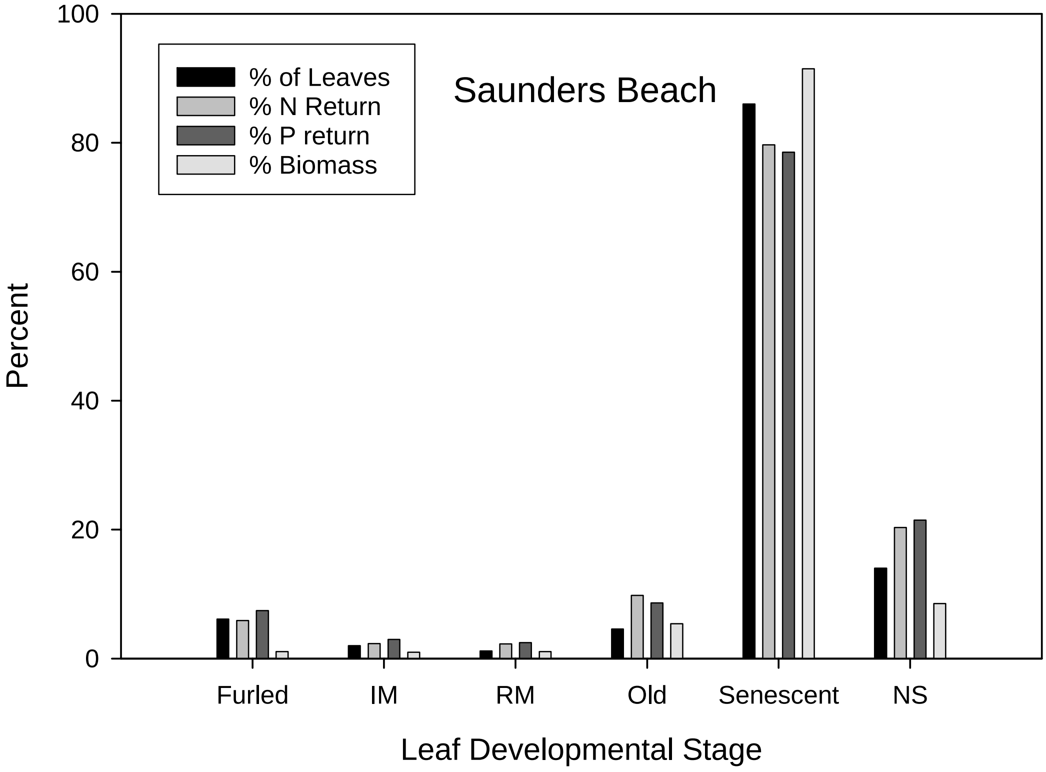


Figure 7.15 Effect of Insect-Caused Leaf Drop on Nutrient Return to the Forest Floor and Leaf Biomass Loss of *R. stylosa* Leaves. NS = the four non-senescent leaf categories (Furled, IM, RM and Old) combined together





Because most leaves lost due to insect damage were still developing, the biomass of leaf material lost due to insects was less than that suggested by leaf area losses. In this sense, insect herbivory results in less loss of leaf biomass than would be suggested by measurements of proportional leaf area loss, as occurs in most studies. This effect was greater for *A. marina* than for *R. stylosa*, reflecting the greater number of leaves that failed to reach senescence. Overall, for *A. marina*, insect herbivores caused the loss of 20-32% of leaf dry weight biomass but 40-58% of leaf nutrients (N and P). For *R. stylosa*, insect herbivores caused 5-9% of leaf dry weight biomass loss and 16-21% of leaf nutrient (N and P) loss.

7.4 Discussion

7.4.1 LMA and Leaf Physical Characteristics

Leaf mass per unit area (LMA, or its inverse – SLA) are associated with many critical aspects of plant ecology and herbivory. They are correlated with photosynthetic rate (Field and Mooney 1986, Reich *et al.* 1997, Shipley and Lechowicz 2000, Niinemets 2001), water stress (Niinemets 2001, Lamont *et al.* 2002), leaf lifespan (Reich *et al.* 1992, Wright *et al.* 2002) and palatability to herbivores (Lucas and Pereira 1990). For mangroves, LMA has been correlated with salinity (Camilleri and Ribi 1983) and exposure to sunlight (Ball *et al.* 1988, Lovelock *et al.* 1992). Along with leaf longevity (examined in Chapter 5), both traits are strongly related to a plant's carbon-fixation strategy (Wright and Westoby 2002) and LMA is a useful index of leaf construction cost and carbon balance (Jurik 1986, Reich *et al.* 1992). Plants with high LMA have long leaf lifespans, mainly because LMA is related to leaf strength, so high LMA leaves are more tolerant of physical damage and suffer less herbivory (Chabot and Hicks 1982, Grubb 1986, Coley 1988, Reich *et al.* 1991, Wright and Cannon 2001). Mooney and Gulmon (1982) also noted the general trend for longer-lived leaves to have higher ratios of leaf specific weight (ie, LMA) to N-concentration. Both patterns are supported in this study where the longer-lived *R. stylosa* leaves had higher LMA but lower N-concentration than the shorter-lived *A. marina* leaves.

Neither *A. marina* nor *R. stylosa* showed any increase in LMA as young leaves developed, with *A. marina* in fact showing a decrease between recently emerged and immature leaves. This probably reflects the rapid proportional increase in leaf area expansion during this time that outstrips increase in leaf biomass. For *A. marina*, this effect may have been further exacerbated by the biomass dominance of the prominent leaf mid-vein in the small newly-emergent leaves. After this initial decrease, LMA for both species rapidly increased as the leaves matured, and then continued to increase at a slower rate after full leaf area had been attained, reflecting a continued increase in leaf thickness (and possibly density as well). Feller (1995, 1996) calculated the LMA of *R. mangle* leaves from Belize using mature penapical and basal leaves, which, in the context of this study, would most likely correspond to IM/RM and old leaves, respectively. The values obtained for LMA (mean approximately 29mg/cm^2 for penapical leaves and 32 mg/cm^2 basal leaves, as judged from Figure 8 of Feller 1995 and Figure 5 of Feller 1996, respectively) were similar to this study. For *R. stylosa* leaves collect from four sites in north Queensland, Lovelock *et al.* (1992) found LMA to vary from 12 to 30mg/cm^2 (estimated from Figures 8 and 9 of Lovelock *et al.* 1992 – leaf stage was not stated but presumably they were mature leaves). Five species of Rhizophoraceae mangroves from north Queensland had LMA ranging from 9-19mg/cm^2 (Ball *et al.* 1988). Choong *et al.* (1992) compared SLA for various tree species in Singapore. Conversion of these values to LMA shows that the 16 mangrove species tested had a mean LMA of 15.2mg/cm^2 (range 8.1-27.5) compared to 10.9mg/cm^2 (range 5.0-18.5) for 12 secondary forests species on degraded infertile soils and 5.6mg/cm^2 (range 2.9-8.7) for 9 secondary forest species on non-degraded soils. Reich *et al.* (1999) found mean LMA of 111 plant species from North and South America to be 13.7 mg/cm^2 (range 2.1-82.6), and this included 21 tree species from tropical Venezuela with a mean LMA of 12.1mg/cm^2. In a comprehensive review of published LMA values for several hundred plant species, Niinemets (1999) reported mean LMA to be 11.5mg/cm^2 (range 1.2-56.0, SD=9.0). Thus the values reported for *A. marina, R. stylosa* and several related mangrove species, are higher than the reported mean of many literature values. This suggests that these mangrove leaves may be denser and tougher than leaves of many other plant species, though more data is required for verification. Ellison (2002), though also lamenting the lack of LMA data for mangroves, presented data indicating that mangroves have slightly higher LMA than other plant species in general, but similar to that of evergreen broad-leaved trees.

Although newly emerged *R. stylosa* leaves were larger than recently emerged *A. marina* leaves, they did not have a significantly greater thickness or LMA. However, as the leaves developed, the *R. stylosa* leaves rapidly become thicker and higher in LMA. Interestingly, leaves continued to get larger, thicker and to have higher LMA values well after they first reached a stage visually recognised as representing maturity. Leaf size, thickness and LMA all decreased slightly during senescence reflecting withdrawal of leaf materials during this phase. In the only comparable study in mangroves, Wang and Lin (1999) found that area of *B. gymnorrhiza* leaves did not increase after maturity and decreased by 15% during senescence, though LMA only decreased by 6%, due to concurrent decreases in leaf mass during senescence. Loss of leaf mass during senescence is not uncommon. Chapin and Kedrowski (1983) found a mean of 18% loss in leaf mass for 43 taiga tree species.

7.4.2 Water Content

Young leaves tend to have higher water content than older leaves (Scriber and Slansky 1981, Kursar and Coley 1992) and this was borne out in the current study for *A. marina* but not for *R. stylosa*. The maximum water content of the two species was the same with the major difference being the decline of water content in old and senescent leaves of *A. marina* compared to the constant values obtained for all age classes in *R. stylosa*. Leaf water content has only been measured in a few studies for mangroves and these are summarised in Table 7.6. The values for percentage water content found in *R. stylosa* in the current study (64-67%) are generally similar to reported literature values which are mostly between 57-71%, though with a few notable exceptions. The only other literature value for *R. stylosa* is the questionably low 29% reported by Choong *et al.* (1992). There are no published literature values for *A. marina* and the water content reported for other *Avicennia* spp. covers a wide range, even at the one location (Singapore – Choong *et al.* 1992).

Table 7.6 Summary of Literature Values for % Water Content in Avicenniaceae and Rhizophoraceae Mangrove Leaves

Species	Location	Result	Comment	Reference
Rhizophoraceae				
R. apiculata	Singapore	57%	Mature leaves	Choong *et al.* 1992
R. apiculata	Nth. Qld.	70-73%	Combined age classes	Ball *et al.* 1988
R. x *lamarkii*	Nth. Qld.	68-70%	Combined age classes	Ball *et al.* 1988
R. mangle	Brazil	69%	Leaf stages not stated	De Lacerda *et al.* 1986
R. mangle	Belize	63%	Leaf stages not stated	Feller 1995
R. mangle	Florida	64-75%	Leaf stages not stated	Camilleri and Ribi 1983
R. mangle	Venezuela	69%[1]	Leaf stages not stated	Sobrado 2000
R. mucronata	Nth Qld.	56-69%	6 age classes	Atkinson *et al.* 1967
R. mucronata	Singapore	57%	Mature leaves	Choong *et al.* 1992
R. mucronata	Kenya	65.8±8.1%(s.d.)	Mature leaves	Slim *et al.* 1996
R. stylosa	Singapore	29%	Mature leaves	Choong *et al.* 1992
R. stylosa	Townsville	64-67%	All age classes	This study
R. stylosa	Nth. Qld.	69-71%	Combined age classes	Ball *et al.* 1988
B. cylindrica	Singapore	67%	Mature leaves	Choong *et al.* 1992
B. gymnorrhiza	Singapore	56%	Mature leaves	Choong *et al.* 1992
B. gymnorrhiza	Nth. Qld.	66-72%	Combined age classes	Ball *et al.* 1988
C. tagal	Kenya	63.1±3.6%(s.d.)	Mature leaves	Slim *et al.* 1996
C. tagal	Singapore	41%	Mature leaves	Choong *et al.* 1992
C. tagal	Nth. Qld.	70-72%	Combined age classes	Ball *et al.* 1988
Avicenniaceae				
A. alba	Singapore	32%	Mixed mature leaves	Choong *et al.* 1992
A. germinans	Venezuela	62%[1]	Leaf stages not stated	Sobrado 2000
A. marina	Townsville	49-67%	All age classes	This study
A. officinalis	Singapore	75%	Mixed mature leaves	Choong *et al.* 1992
A. rumphiana	Singapore	45%	Mixed mature leaves	Choong *et al.* 1992
A. schaueriana	Brazil	71-73%	Leaf stages not stated	De Lacerda *et al.* 1986

[1] percent water content calculated from area/dry weight ratio presented in Sobrado (2000)

The only study that has compared water content of mangrove leaves of different age classes is that of Atkinson *et al.* (1967) who sampled leaves of six age classes from *R. mucronata* at Princess Charlotte Bay in northern Queensland. The age classes were stated to range from furled to senescent, though the exact stages in between were not specified. They found that water content increased from 56% in furled leaves to 65% in the second age class and 69% in senescent leaves. Though the values for the mature leaves are similar to those for *R. stylosa* in the current study (66-67%), the value for the furled leaves is lower (also 66-67% in the current study). For *R. stylosa* in the current study, the water content was stable across the different leaf developmental stages. Atkinson *et al.* (1967) only used five leaves in total for each leaf age class compared to 10 leaves from each of 10 trees at two sites (ie, 200 leaves for each leaf developmental stage) in the current study, thus leaving them more prone to variation.

Atkinson *et al.* (1967) suggested that, for *R. mucronata,* increased moisture content of the older leaves helped dilute the sodium and chloride ions that accumulate in senescing leaves of *Rhizophora* spp. Jamale and Joshi (1976) found that the leaf water content of the mangroves *Sonneratia acida* and *Excoecaria agallocha* in India increased during senescence from 74 to 82% in the former and 74 to 84% in the latter species. They also attributed this to the increased concentration of sodium and chloride ions that they found, though no statistics were used and no information was provided on the range of data values obtained or the number of replicates sampled. *R. stylosa* also accumulates salt with age, but in the current study, there was no increase in water content with senescence. However, given that it did not decrease its water content with age as did *A. marina*, which excretes salt from its leaves, this may in itself be a mechanism of maintaining dilution in senescing leaves. Cram *et al.* (2002) has recently reviewed several datasets and showed that mangroves do not actually increase salt concentration into leaves that are senescing and that the increased amount of salt in older leaves is merely a result of increased leaf thickness. Thus salt concentration remains the same and there is no need to increase the percentage water content of senescent leaves, as maintaining water concentration with leaf development will by itself maintain sufficient ion dilution. In the current study, *R. stylosa* leaves continued to increase in thickness well after reaching maturity, only ceasing to increase leaf thickness during senescence. In contrast, in plants like *A. marina* which excrete salt on to leaf surfaces, there is actually a reduction (up to 50% - Cram *et al.* 2002) in Na+ levels in older leaves, thus allowing the plant to reduce water content in older leaves and conserve fresh water, a limited resource in mangrove environments.

Coley (1983) examined the water content of young and mature leaves of 22 pioneer and 24 persistent canopy tree species in a Panamanian rainforest and found a significantly greater water content for young leaves of both groups (74 vs 70% in the former and 76 vs 62% in the latter). These values are generally higher than those obtained for *R. stylosa* and *A. marina*. Leaf moisture content for mature leaves of 13 rainforest species at Paluma, north of Townsville ranged from 37-64% (Jackson 1995) but from 84-90% for two species of stinging tree in rainforests and moist forests near Cardwell (Hurley 1995). In Singapore, Choong *et al.* (1992) found that the 16 mangrove species they tested had a mean water content of 59% compared to 51% for the 26 non-mangrove tropical forest species they tested. That dataset displayed substantial variation, even between closely related species that grow in similar locations (eg, the three *Avicennia* spp. tested had average water contents of 32, 75 and 45% and the three *Rhizophora* spp. tested had average water contents of 29, 57 and 57% - Table 7.6). Rather than using whole leaves as was the case for Coley (1983) and the current study, Choong *et al.* (1992) used a hole punch to cut discs from leaves which were then weighed and dried. This process may have caused reduced water content values. Additionally, for many species, only as few as five individual leaves were sampled. Steinbauer (2001) found that old *Eucalyptus globulus* leaves had significantly lower water content than young, developing leaves (60.4±0.3% versus 63.0±0.6% respectively). These values are also lower than those obtained by Coley (1983) and the current study, but again involved discs cut from a leaf, which may underestimate water content.

Comparison with the comprehensive data of Coley (1983) would suggest that mangroves have lower water content than rainforest species, though the data of Choong *et al.* (1992) and Jackson (1995) would suggest the opposite. The summary presented in Table 7.6 also show no evidence for any differences between *Rhizophora* spp. and *Avicennia* spp. although the data collected for the current study indicate that the main difference between the two species is not in the actual water content of the young and recently mature leaves but how it changes with leaf age.

7.4.3 Chlorophyll Content

Gross changes in chlorophyll can be visually determined by leaf colour. Young leaves are generally light green, become darker with maturity and then yellow during senescence due to a loss of chlorophyll. Many tree species also delay greening of their young leaves until leaf development is more advanced. Coley and Kursar (1996) (in Turner 2001) surveyed 250 tropical tree species and found that 33% had delayed greening. Chlorophyll is a nutritious molecule that enhances leaf attractiveness to herbivores (Turner 2001). Kursar and Coley (1992) and Coley and Kursar (1996) suggested that the role of delayed greening was to reduce losses of chlorophyll and other resources until the developing leaves, that are vulnerable to high levels of herbivory, were tougher and better protected. They suggested that such a strategy would be more advantageous in light-limited environments where the foregone costs of reduced photosynthesis rate due to low chlorophyll levels would be less than in high light environments. Neither *A. marina* or *R. stylosa,* both of which grow in high light environments, showed any evidence of delayed greening in the current study, and have not been reported to have this trait elsewhere. In fact the relatively high chlorophyll concentration of the youngest leaves and the small degree of increase in chlorophyll concentration between furled and mature leaves suggests that both species have high photosynthetic rates from a very early age.

Few studies of chlorophyll in mangrove leaves have been made and these show considerable variation in total chlorophyll concentration. The current study found total chlorophyll concentrations of 5.6-6.4μg/g for *R. stylosa* and 6.2-7.2μg/g for *A. marina*. No literature values of any *Rhizophora* spp. were found for comparison with *R. stylosa*. In South Africa, Naidoo *et al.* (2002) found total chlorophyll concentrations in *A. marina* of 4.2-6.3μg/g and in *B. gymnorrhiza* to be 4.8-5.6μg/g. In India, total chlorophyll levels reported by Jamale and Joshi (1977) and Joshi and Bhosale (1982) include 6.5-9.0μg/g for *Avicennia officinalis* and 10.3-11.4μg/g for *Avicennia alba* which is generally higher than for *A. marina* in the current study. Those same authors also reported values ranging from 3.7μg/g to 13.9μg/g for four other mangrove species (*Sonneratia alba*, *Aegiceras corniculatum*, *Excoecaria agallocha* and *Acanthus ilicifolius*). In four studies from India summarised by Karmarkar (1982), total chlorophyll levels in mature leaves of the mangrove species *Sonneratia* spp., *A. ilicifolius*, *Lumnitzera racemosa* and *Thespesia populnea* (a mangrove associate), ranged from 2.2μg/g to 21.0μg/g and decline during senescence ranged from 76-92%, which compares with 92% for *R. stylosa* and 88% for *A. marina* in the current study.

Patterns of chlorophyll content were clearer when considered on a total chlorophyll per leaf basis rather than as a concentration. Because of its larger leaves, *R. stylosa* had greater chlorophyll content per leaf than *A. marina*, but a greater chlorophyll concentration only at Saunders Beach.

Total chlorophyll content per leaf differed across all leaf developmental stages for *A. marina* and across most leaf stages from immature to senescent for *R. stylosa*. There were consistent differences in chlorophyll concentration across the various stages of leaf development for both species, but these were only significant when comparing senescent leaves to other leaf stages. Both species showed increasing chlorophyll concentration until leaf maturity and then a large decline in chlorophyll concentration with senescence, though the decline was larger on a per leaf basis for *R. stylosa*. Wang and Lin (1999) also found that chlorophyll concentrations of *B. gymnorrhiza* leaves increased with leaf development and then decreased substantially (by about 70%) during senescence. Although chlorophyll concentrations in senescent leaves were very low, there were similar total amounts of chlorophyll per leaf found in senescent leaves as there were in young leaves, especially for *A. marina* where senescent leaves had more total chlorophyll than all leaves except old leaves.

7.4.4 Nutrient Content

Leaf nitrogen content is generally highest in young, developing leaves and declines as the leaves age (Mattson 1980, Scriber and Slansky 1981, Kursar and Coley 1991, 1992). Leaves import nitrogen during their developing phase and when they are mature, the nutrients that are present become diluted as leaf dry matter content continues to increase (Mooney and Gulmon 1982). During later leaf stages and during senescence, nitrogen is exported from the leaf to support new growth elsewhere in the plant (Mooney and Gulmon 1982). In the current study, the changes in nitrogen and phosphorus concentration across the five stages of leaf development generally followed this pattern, though the greatest proportional decline in phosphorus concentration occurred between RM and old leaves rather than during senescence. In contrast, changes in absolute nutrient content per leaf followed a different pattern. For both species, maximum nutrient content per leaf was found in the recently mature or old leaves, with the youngest leaves having a similar nutrient content to the senescent leaves. The differences in nutrient concentration versus nutrient content are due to changes in the size of the leaves as they develop and senesce. Although nutrient concentration declines as the leaves age, older leaves actually contain a greater amount of nutrient per leaf. This suggests that nutrient resorption only occurs during senescence itself whereas most studies examining nutrient resorption assume this process begins after the leaves reach maturity (see section 7.4.5).

The differences between the two methods of expressing leaf nutrients has relevance to different aspects of ecology. Nutrient concentration represents the amount of nutrient an insect herbivore would receive per unit of leaf consumed and is one of the main reasons why herbivores prefer young leaves to older leaves (Coley 1983, Kursar and Coley 1991). Absolute nutrient content per leaf is more relevant to evaluating impacts of leaf loss. From a nutrient ecology perspective, loss of larger, mature green leaves, despite their lower nutrient concentration, represents a greater loss of nutrient from the tree. For *A. marina*, even the loss of senescent leaves represents a greater loss of nutrient than does the loss of young, developing leaves.

Species with low LMA tend to have higher leaf nitrogen concentration (Field and Mooney 1986, Choong *et al.* 1992, Reich *et al.* 1997, Wright *et al.* 2001). The lower LMA but higher N-concentration of *A. marina* compared to *R. stylosa* in this study supports this notion. *A. marina* had greater nitrogen and phosphorus concentration than *R. stylosa* across most leaf developmental stages and this provides one reason why this plant was more heavily damaged by insects than *R. stylosa*. However, because of their greater leaf size, each *R. stylosa* leaf contained more nitrogen and phosphorus than each *A. marina* leaf. Thus, such leaves would be worth defending more heavily, because the loss of an individual leaf could be more costly in terms of nutrient loss for *R. stylosa* than for *A. marina*.

Differences between leaf developmental stages had the greatest effect on nutrient content, followed by species differences. Differences between the two sites were minor by comparison. Thus, insufficient attention paid to the age/developmental stage of leaves selected for analysis in nutrient studies (a very common problem) will obscure differences between sites and species. A search of the literature revealed a total of 34 studies that have assessed nutrient content of Rhizophoraceae and/or Avicenniaceae leaves from the canopy (Table 7.7 for nitrogen and Table 7.8 for phosphorus). This total excludes numerous papers that analysed the nutrient content of fallen leaves collected from leaf litter traps or on the ground. The results show considerable variation but are in general agreement with the values found in the current study. As can be noted from Tables 7.7 and 7.8, most studies have selected leaves for nutrient analysis on the basis of being mature or by their nodal position, both of which could encompass a wide variety of leaf ages and developmental stages. Several studies also failed to state what leaf stage they analysed.

Though a number of studies have compared nutrients in mature and senescent leaves to measure nutrient resorption (Table 7.9), of these 34 studies, only four (Onuf *et al.* 1977, Snedaker and Brown 1981, Wang and Lin 1999, Ochieng and Erftemeijer 2002) have examined changes in nutrient concentration from young developing leaves to senescent leaves. Onuf *et al.* (1977) determined N concentration for three stages of *R. mangle* leaf development (bud, new leaves, yellow leaves). The stages represented appear to correspond with furled, IM/RM and senescent. Although they only used six leaves for each category sampled, they found that the youngest leaves had the highest N concentration. Onuf *et al.* (1977) recorded a 66 and 77% decrease in N concentration from the bud to senescent leaf stage in their high and low nutrient sites respectively. In the current study, N concentration of *R. stylosa* leaves decreased by 67-68% from the bud stage to the senescent stage. Snedaker and Brown (1981) studied changes in P concentration with leaf age for *R. mangle* in Florida. Relative age was assessed by selecting leaves at varying positions along a stem from the bud to the 6th node from the bud. They found that P concentration increased slightly from the bud to the first position but, thereafter, decreased at a fairly constant rate through to leaves from the 6th node (whether these were senescent was not stated, neither was the level of replication that was used). Wang and Lin (1999) examined changes in N and P concentration of *B. gymnorrhiza* leaves from China, each month from shortly after emergence, to senescence (only about 9-10 months in that study).

As occurred in the current study, they found that nutrient concentration was greatest in the youngest leaves and declined as the leaves aged. Ochieng and Erftemeijer (2002) analysed N and P concentration in nine different age classes of *A. marina* leaves. For both nutrients, there was little decline across the six non-senescent age classes, then an abrupt decline through the three senescent age classes. Resorption

Table 7.7 Summary of Literature Values for Nitrogen Concentration in Leaves of Rhizophoraceae and Avicenniaceae Mangroves. Where necessary, data have been converted to % format for ease of data comparison.

Species	Location	Nitrogen Concentration	Leaf Stage	Comments	Reference
Rhizophoraceae					
***Rhizophora* spp.**					
R. apiculata	Singapore	1.14%	M	Leaf stage not stated	Choong *et al.* 1992
R. apiculata	Thailand/Philippines	1.05±0.05%[1]	M	Seedlings	Duarte *et al.* 1998
R. apiculata	Malaysia	1.02%	M		Ong *et al.* 1985
R. apiculata	SW India	0.68%	S		Wafar *et al.* 1997
R. mangle	Belize	1.020±0.04%[1]	M	Dwarf trees	Feller 1995
R. mangle	Brazil	1.0%	M	Leaf stage not stated	Rodin and Bazilevich 1967 in Lugo 1990
R. mangle	Florida	0.98%	M		Heald 1971
R. mangle	Florida	1.10±0.04%[2]	M		Twilley *et al.* 1986
R. mangle	Florida	1.3%	M	Leaf stage not stated	Snedaker 1975 in Lugo 1990
R. mangle	Brazil	4.5±1.4%[2]	M		De Lacerda *et al.* 1986
R. mangle	Puerto Rico	1.5±0.02%[1]	M	Leaf stage not stated	Lugo 1990
R. mangle	Belize	0.95±0.29%[1]	V	Greenfall	Feller 2002
R. mangle	French West Indies	2.21-3.10%	V	Randomly collected leaves	Saur *et al.* 1999
R. mangle	Belize	0.50±0.3%[1]	S		Feller 2002
R. mangle	Belize	0.51%	S	Dwarf trees	Feller *et al.* 1999
R. mangle	Florida	0.50%	S	Dwarf trees	McKee and Feller 1995
R. mangle	Belize	0.32%	S	Fringe trees	Feller *et al.* 1999
R. mangle	Florida	0.47%	S	Basin trees	McKee unpub. data in Feller *et al.* 1999
R. mangle	Florida	0.34-0.61%	S	Various forest types	Steyer 1988
R. mangle	Florida	1.42±0.46%	F	High nutrient site	Onuf *et al.* 1977
R. mangle	Florida	1.60±0.10%	IM	High nutrient site	Onuf *et al.* 1977
R. mangle	Florida	0.48±0.03%	S	High nutrient site	Onuf *et al.* 1977
R. mangle	Florida	1.55±0.16%	F	Low nutrient site	Onuf *et al.* 1977
R. mangle	Florida	1.20±0.04%	IM	Low nutrient site	Onuf *et al.* 1977
R. mangle	Florida	0.36±0.03%	S	Low nutrient site	Onuf *et al.* 1977
R. mucronata	China	1.3%	M	Leaf stage not stated	Rodin and Bazilevich 1967 in Lugo 1990
R. mucronata	Singapore	1.29%	M	Leaf stage not stated	Choong *et al.* 1992
R. mucronata	SW India	0.62%	S		Wafar *et al.* 1997
R. mucronata	Kenya	0.65±0.13%[2]	M		Slim *et al.* 1996
R. mucronata	Kenya	0.56±0.02%[2]	O		Slim *et al.* 1996
R. mucronata	Kenya	0.27±0.02%[2]	S		Slim *et al.* 1996
R. mucronata	Kenya	0.7±0.1%[2]	IM		Rao *et al.* 1994
R. mucronata	Kenya	0.3±0.1%[2]	S		Rao *et al.* 1994
R. stylosa	Singapore	1.48%	M	Leaf stage not stated	Choong *et al.* 1992
R. stylosa	Darwin	1.2%	M		Woodroffe *et al.* 1988
R. stylosa	Townsville	0.78±0.05%[2]	M		Spain and Holt 1980
R. stylosa	Mackay	1.07-1.38%	M	Leaf stage not stated	Duke *et al.* 2000b
R. stylosa	Western Australia	0.99%	V	Leaf stages mixed together	Alongi *et al.* 2003
R. stylosa	Townsville	~0.6%[4]	S		Robertson 1988
***Bruguiera* spp.**					
B. cylindrica	Singapore	1.55%	M	Leaf stage not stated	Choong *et al.* 1992
B. exaristata	Darwin	1.0%	M		Woodroffe *et al.* 1988
B. gymnorrhiza	Kenya	0.8±0.1%[2]	IM		Rao *et al.* 1994
Cont'd overleaf					

Table 7.7 cont'd

B. gymnorrhiza	Kenya	0.3±0.1%[2]	S		Rao *et al.* 1994
B. gymnorrhiza	Singapore	1.25%	M	Leaf stage not stated	Choong *et al.* 1992
B. gymnorrhiza	Okinawa	~0.4%[4]	S		Mfilinge *et al.* 2002
B. gymnorrhiza	China	~1.05-~0.35%[5]	V	Leaf stages mixed together	Wang and Lin 1999
B. parviflora	Darwin	0.8%	M		Woodroffe *et al.* 1988
B. parviflora	Mackay	1.13%	M	Leaf stage not stated	Duke *et al.* 2000b
***Ceriops* spp.**					
C. australis	Mackay	0.72-1.07%	M	Leaf stage not stated	Duke *et al.* 2000b
C. tagal	Townsville	0.86±0.10%[2]	M		Spain and Holt 1980
C. tagal	Darwin	0.8±0.2%[2]	M		Woodroffe *et al.* 1988
C. tagal	Singapore	0.83%	M	Leaf stage not stated	Choong *et al.* 1992
C. tagal	Kenya	0.63±0.16%[2]	M		Slim *et al.* 1996
C. tagal	Kenya	0.44±0.02%[2]	O		Slim *et al.* 1996
C. tagal	Kenya	0.29±0.01%[2]	S		Slim *et al.* 1996
C. tagal	Kenya	0.8±0.1%[2]	IM		Rao *et al.* 1994
C. tagal	Kenya	0.2±0.1%[2]	S		Rao *et al.* 1994
C. tagal	Townsville	~0.45%[4]	S		Robertson 1988
***Kandelia* spp.**					
K. candel	China	1.39%	M		Li *et al.* 1999
K. candel	Okinawa	~1.7%[4]	S		Mfilinge *et al.* 2002
Avicenniaceae					
***Avicennia* spp.**					
A. alba	Singapore	3.03%	M	Leaf stage not stated	Choong *et al.* 1992
A. alba	India	0.79-1.04%	M	Leaves coll. seasonally	Jamale and Joshi 1977
A. germinans	Florida	1.82±0.03%	M		Twilley *et al.* 1986
A. germinans	Florida	1.40%	S		McKee and Feller 1995
A. germinans	Florida	0.97%	S		McKee unpub. data in Feller *et al.* 1999
A. germinans	Florida	0.51-0.66%	S		Steyer 1988
A. marina	Kenya	1.7-1.9±0.3%[2]	IM		Rao *et al.* 1994
A. marina	Kenya	0.5-0.7±0.1%[2]	S		Rao *et al.* 1994
A. marina	Kenya	1.66±0.08%[2]	M		Ochieng and Erftemeijer 2002
A. marina	Kenya	0.54±0.02%[2]	S		Ochieng and Erftemeijer 2002
A. marina	Brisbane	1.74±0.1-2.92±0.25%[2]	M		Law 1995
A. marina	Mackay	1.23-2.57%	M	Leaf stage not stated	Duke *et al.* 2000b
A. marina	Darwin	1.3%	M		Woodroffe *et al.* 1988
A. marina	Townsville	1.76±0.18%[2]	M		Spain and Holt 1980
A. marina	Townsville	~0.85%[4]	S		Robertson 1988
A. marina	Zanzibar	0.63±0.07%[3]	S		Skov and Hartnoll 2002
A. marina	Western Australia	1.44 %	V	Leaf stages mixed together	Alongi *et al.* 2003
A. officinalis	Singapore	1.46%	M	Leaf stage not stated	Choong *et al.* 1992
A. officinalis	India	2.51-2.77%	M	Leaves coll. seasonally	Joshi and Bhosale 1982
A. officinalis	India	2.51-2.77%	M		Joshi and Bhosale 1982
A. officinalis	SW India	0.81%	S		Wafar *et al.* 1997
A. rumphiana	Singapore	1.18%	M	Leaf stage not stated	Choong *et al.* 1992
A. schaueriana	Brazil	2.3±0.7%; 1.9±1.0%[2]	M		De Lacerda *et al.* 1986

Leaf Stages: F=furled, IM=immature, M=mature, O=old, S=senescent, V=various leaf ages used. Note that in many studies, no indication of the leaf stages used was given. These are noted in the comments column and it is assumed for them that most, if not all leaves, were mature.

1 (±1 Standard Error)

2 (±1 Standard Deviation)

3 (± 95% Confidence Interval)

4 value estimated from graphical data presentation

5 range of values estimated from graphical data presentation, from maximum associated with young, developing leaves to minimum associated with senescent leaves

Table 7.8 Summary of Literature Values for Phosphorus Concentration in Leaves of Rhizophoraceae and Avicenniaceae Mangroves. Where necessary, for ease of comparison, data have been converted to % format.

Species	Location	Phosphorus Concentration	Leaf Stage	Comments	Reference
Rhizophoraceae					
***Rhizophora* spp.**					
R. apiculata	SW India	0.06%	S		Wafar *et al.* 1997
R. apiculata	Malaysia	0.11%	M		Ong *et al.* 1985
R. apiculata	Thailand/Philippines	0.075±0.004%[1]	M		Duarte *et al.* 1998
R. mangle	Brazil	0.22%	M	Leaf stage not stated	Rodin and Bazilevich 1967 in Lugo 1990
Rhizophora sp.	Brazil	0.15%	M	Leaf stage not stated	Lamberti 1969 in Lugo 1990
R. mangle	Florida	0.05%	M	Leaf stage not stated	Snedaker 1975 in Lugo 1990
R. mangle	Belize	0.036±0.003%[1]	M		Feller 1995
R. mangle	Panama	0.09%	M	Leaf stage not stated	Golley *et al.* 1975 in Lugo 1990
R. mangle	Puerto Rico	0.082±0.001%[1]	M	Leaf stage not stated	Lugo 1990
R. mangle	Belize	0.01%	S		Feller *et al.* 1999
R. mangle	Belize	0.013±0.002 %[1]	S		Feller 2002
R. mangle	Belize	0.046±0.003%[1]	V	Greenfall	Feller 2002
R. mangle	French West Indies	0.10-0.l4%	V	Randomly collected leaves	Saur *et al.* 1999
R. mucronata	China	0.08%	M	Leaf stage not stated	Rodin and Bazilevich 1967 in Lugo 1990
R. mucronata	SW India	0.12%	S		Wafar *et al.* 1997
R. stylosa	Darwin	0.09%	M		Woodroffe *et al.* 1988
R. stylosa	Townsville	0.10±0.02%[2]	M		Spain and Holt 1980
R. stylosa	Western Australia	0.080 %	V	Leaf stages mixed together	Alongi *et al.* 2003
***Bruguiera* spp.**					
B. exaristata	Darwin	0.08%	M		Woodroffe *et al.* 1988
B. gymnorrhiza	China	~0.125-~0.06%[5]	V	Leaf stages mixed together	Wang and Lin 1999
B. gymnorrhiza	Okinawa	~0.055%[4]	S		Mfilinge *et al.* 2002
B. parviflora	Darwin	0.07%	M		Woodroffe *et al.* 1988
***Ceriops* spp.**					
C. tagal	Townsville	0.09±0.02%[2]	M		Spain and Holt 1980
C. tagal	Darwin	0.06±0.01%[2]	M		Woodroffe *et al.* 1988
***Kandelia* spp.**					
K. candel	China	0.13%	M		Li *et al.* 1999
K. candel	Okinawa	~0.14%[4]	S		Mfilinge *et al.* 2002
Avicenniaceae – all *Avicennia* spp.					
A. marina	Kenya	0.059±0.005%[2]	M		Ochieng and Erftemeijer 2002
A. marina	Kenya	0.023±0.006%[2]	S		Ochieng and Erftemeijer 2002
A. marina	Darwin	0.17%	M		Woodroffe *et al.* 1988
A. marina	Brisbane	0.169±0.01-0.190±0.02%[2]	M		Law 1995
A. marina	Townsville	0.16±0.03%[2]	M		Spain and Holt 1980
A. marina	Western Australia	0.135 %	V	Leaf stages mixed together	Alongi *et al.* 2003
A. officinalis	SW India	0.06%	S		Wafar *et al.* 1997

Leaf Stages: F=furled, IM=immature, M=mature, O=old, S=senescent, V=various leaf ages used. Note that in many studies, no indication of the leaf stages used was given. These are noted in the comments column and it is assumed for them that most, if not all leaves, were mature.

1 (±1 Standard Error)

2 (±1 Standard Deviation)

3 (± 95% Confidence Interval)

4 value estimated from graphical data presentation

5 range of values estimated from graphical data presentation, from maximum associated with young, developing leaves to minimum associated with senescent leaves

during senescence in that study was 68% for N and 61% for P, with the result for N being comparable to the result obtained for *A. marina* in the current study but the result for P being lower than that obtained for *A. marina* in the current study (Table 7.9).

For the 34 studies listed in Table 7.7, mean nitrogen concentration (± S.E.) for mature Rhizophoraceae leaves (converted to % by noting that 10mg/g=1%) was 1.26±0.13% (n=34) though some studies had consistently higher values (eg, de Lacerda *et al.* 1986 and Saur *et al.* 1999). Mean nitrogen concentrations for mature *Avicennia* leaves from Table 7.7 are 1.88±0.18% (n=17) though some studies had much higher values (eg, Joshi and Bhosale 1982, de Lacerda *et al.* 1986 and Choong *et al.* 1992).

Phosphorus has been measured much less frequently than nitrogen. The values for phosphorus obtained in the current study (0.06-0.11% for RM leaves and 0.043-0.078% for old leaves) encompass the range obtained in most studies of mangrove leaves listed in Table 7.8.

The results of nutrient analyses are usually presented in terms of concentration. All of the mangrove papers listed in Tables 7.7 and 7.8, except two, have used this method of expressing nutrient content. Slim *et al.* (1996) and Wang and Lin (1999) are the only studies that present nutrient data in terms of total nutrient content per leaf, taking into account the different biomass of different-aged leaves. Slim *et al.* (1996) only examined mature, old and senescent leaves, not young developing leaves. For nitrogen in *R. mucronata* (they did not analyse for phosphorus), they found that absolute nitrogen content increased as the mature leaves became old and then declined abruptly during senescence. This is the same pattern observed for *R. stylosa* in the current study. Slim *et al.* (1996) found that *Ceriops tagal* behaved slightly differently, with absolute nitrogen content declining slightly as the leaves aged, though with a sudden decline once senescence began. The fact that absolute nutrient content is generally highest in mature and old leaves is very important to many aspects of ecology and should be presented more often, especially as it can be calculated from nutrient concentration values via leaf dry weight. For *B. gymnorrhiza* in China, Wang and Lin (1999) found that N and P content per leaf increased markedly as the leaves developed, was relatively stable after they matured, then decreased rapidly during senescence. This is broadly similar to the current study, except that in Wang and Lin (1999), the final absolute nutrient content in senescent leaves was much lower than that of recently emerged leaves, whereas in the current study, senescent leaves had a similar absolute nutrient content to recently emerged leaves.

7.4.5 Nutrient Resorption

Prior to leaf-fall, plants translocate nutrients from the leaf back to the plant (Kikuzawa 1995). Resorption or retranslocation of nutrients during leaf senescence is a major nutrient-conservation mechanism for plants (Killingbeck 1996). As leaves contain a large proportion of the nutrient capital of plants (Chapin 1980), and are also the major component of forest litter, especially in mangroves, resorption of nutrients from leaves before they are shed represents an important ecological process. Several authors have concluded that because leaf longevity can be extended considerably but nutrient resorption is limited by nutrient mobility, that leaf longevity variation has greater potential for improving nutrient conservation than does increasing resorption (Aerts 1996, Reich *et al.* 1995, Aerts and Chapin 2000). Thus, even though *R. stylosa* has lower nutrient resorption efficiency than *A. marina* (Table 7.9), its longer leaf life span would enable greater nutrient-use efficiency.

The relative amount of N and P resorbed during senescence (termed resorption efficiency) varies between species and there are few or only weak, patterns between growth forms and leaf nutrient status (Aerts 1996). Phosphorus is generally resorbed more efficiently than nitrogen (Turner 2001) and this was the case for both *A. marina* and *R. stylosa* in the current study. Killingbeck (1996) examined nutrient resorption data for 88 woody species and concluded that nutrient resorption proficiency (the minimum level to which nutrient concentration is taken during senescence) was high in any plant that can reduce the N and P levels in senescing leaves to <0.7% and 0.05% respectively. In the current study, *R. stylosa* reached these levels for both nutrients, but *A. marina* did not for either nutrient. Thus *R. stylosa* had a lower nutrient resorption efficiency but greater resorption proficiency than *A. marina*. Resorption efficiency is a measure of the relative degree to which plant can conserve nutrients whereas resorption proficiency is a measure of the degree to which selection pressure has led to minimisation of nutrient loss (Killingbeck 1996).

In most studies (see Aerts 1996 for a comprehensive review), including in mangroves (eg, Feller *et al.* 1999), only nutrient concentration, not absolute nutrient content, is reported. In those studies, nutrient resorption is taken to be the difference between nutrient concentration in mature leaves and senescent leaves. However, the current study, along with that of Snedaker and Brown (1981), Wang and Lin (1999), and Ochieng and Erftemeijer (2002), show that maximal nutrient concentration occurs in the youngest leaves before maturity, so this procedure does not record the true decline between maximum and minimum nutrient concentration. Also, the leaf growth and nutrient results from the current study suggest that both *A. marina* and *R. stylosa* leaves continue growing after reaching maturity and that the reduction in nutrient concentration of young, developing leaves as they mature (previous section) is probably due to dilution by additional leaf biomass, rather than reduction of the total amount of nutrient present. The absolute nutrient content of the leaves indicates that resorption only occurs when old leaves senesce. Thus, many studies have overestimated nutrient resorption by not taking differences in leaf developmental stages, and dilution of nutrients by increasing leaf biomass, into account. Additionally, the comparability of nutrient levels and resorption efficiencies between studies will depend significantly upon the stage of development of the leaves sampled in the various studies.

Table 7.9 lists published data for nutrient resorption in mangrove leaves, which for the above reasons, can only be considered to be reductions in nutrient concentration rather than true resorption. Several other studies have compared nutrient content in non-senescent leaves in the canopy with leaves collected in litter traps that are usually only emptied on a monthly basis. These are not included. To facilitate comparisons, all of the results listed in Table 7.9 are based on decline in nutrient concentration between mature and senescent leaves. Snedaker and Brown (1981) found that decline in P between the youngest and senescent leaves was ~67%. In the current study, decline in N between the youngest and senescent leaves was 67-68% for *R. stylosa* and 65-73% for *A. marina* and decline in P was 72-74% for *R. stylosa* and 75-80% for *A. marina*.

Table 7.9 Summary of Published Data on Proportional Decline in Nutrient Concentration Between Mature and Senescent Leaves of Rhizophoraceae and Avicenniaceae Mangroves.

Species	Location	N-decline	P-decline	Reference
Based on concentration				
B. gymnorrhiza	Kenya	63%		Rao *et al.* 1994
B. gymnorrhiza	China	49%	36%	Wang and Lin 1999
C. tagal	Kenya	54%		Slim *et al.* 1996
C. tagal	Kenya	69%		Rao *et al.* 1994
R. mangle	Belize	45-50%	>70%	Feller *et al.* 1999
R. mangle	Florida		~50%[1]	Snedaker and Brown 1981
R. mucronata	Kenya	58%		Slim *et al.* 1996
R. mucronata	Kenya	59%		Rao *et al.* 1994
R. stylosa	Northern Territory	66%	44%	Woodroffe *et al.* 1988
R. stylosa	Townsville	55-58%	59-62%	This study (RM leaves)
R. stylosa	Townsville	46-49%	40-44%	This study (old leaves)
A. marina	Northern Territory	61%	65%	Woodroffe *et al.* 1988
A. marina	Kenya	69%		Rao *et al.* 1994
A. marina	Kenya	68%	61%	Ochieng and Erftemeijer 2002
A. marina	Townsville	60-64%	67-75%	This study (RM leaves)
A. marina	Townsville	49-50%	47-56%	This study (old leaves)
Based on absolute content				
B. gymnorrhiza	China	60%	48%	Wang and Lin 1999
C. tagal	Kenya	50%		Slim *et al.* 1996
R. mucronata	Kenya	51%		Slim *et al.* 1996
R. stylosa	Townsville	52-59%	47-57%	This study
A. marina	Townsville	55-59%	59-61%	This study

1 estimated from graphed data

As the nutrient declines listed in Table 7.9 will depend on the exact stage of leaf development sampled, comparison between studies should be done cautiously. In the current study, the mature leaves were categorised as either recently mature or old (ie, leaves that had been mature for some time were used for comparison). The amount of nutrient decline varies substantially between the two. Most other studies have only compared two age groups – mature and senescent leaves. In those studies, the mature leaves may have included a variety of stages from early to late maturity, thus producing more of an average result. In a literature review covering nutrient resorption for a variety of plant growth forms, Aerts (1996) found that mean resorption for phosphorus was 52% (n=287) and for nitrogen, it was 50% (n=226). From Table 7.9, average nitrogen decline was 60% and average phosphorus decline was 57%.

For absolute nutrient content (instead of nutrient concentration), Slim *et al.* (1996) found that, on average, the absolute N content of senescent leaves of *R. mucronata* and *C. tagal* leaves in Kenya were 50 and 51% lower respectively than the oldest green leaves of these species. These figures more accurately represent resorption, and are similar to that obtained for *R. stylosa* in the current study (52-59% reduction in absolute N content from old to senescent leaves). However, when using % concentration, Slim *et al.* (1996) found that resorption between old and senescent leaves was 34% for *C. tagal* and 52% for *R. mucronata*, and in the current study, the figures for *R. stylosa* were 46-49% (Table 7.9). Thus, because of the different leaf developmental stages at which nutrient concentration and absolute nutrient content reach their maximum, they provide different estimates of nutrient resorption.

7.4.6 Relationship of Leaf Ontogeny to Herbivory Patterns

The patterns of leaf development and changes in leaf constituents are reflected in the patterns of herbivory for both *A. marina* and *R. stylosa*. For both species, herbivory was greatest on the youngest leaves, which had the highest concentrations of nutrients and so would be more nutritious for most herbivores. The youngest leaves also had lower density (LMA) and leaf thickness than mature leaves which would further contribute to their palatability. The youngest leaves of *A. marina* and *R. stylosa* had relatively similar LMA but, as the leaves developed, the LMA of *R. stylosa* leaves increased rapidly, becoming significantly greater than that of the *A. marina* leaves. Herbivory did continue on mature *A. marina* leaves, but at a reduced level compared to herbivory on younger leaves. However, herbivory was very rare on mature *R. stylosa* leaves with most loss of mature *R. stylosa* leaves actually resulting from branch death caused by wood-borers. Although other factors such as anti-herbivore chemical deterrents may affect herbivory, the increased LMA of mature *R. stylosa* leaves compared to mature *A. marina* leaves may also play a significant role in deterring herbivory on mature *R. stylosa* leaves. In addition to its thinner leaves and lower LMA, the greater nutrient content of *A. marina* leaves throughout all leaf development stages would make them more desirable for herbivores than *R. stylosa* leaves.

Neither *A. marina* nor *R. stylosa* have delayed greening but there are still delays in full importation of nutrients and chlorophyll which would aid in reducing losses to herbivores until the leaves can be better defended against such damage. *A. marina* imports nitrogen and phosphorus to developing leaves at a relatively even rate as they develop. In contrast, the absolute N and P content of immature *R. stylosa* leaves is the same as for newly unfurled leaves, but the import rate increases dramatically after this point. This same pattern is repeated, although to a lesser extent for chlorophyll. Thus, *R. stylosa* delays the importation of nutrients and chlorophyll more than does *A. marina*. Given that increasing leaf toughness is not an available anti-herbivore defense when young leaves are expanding, this may be a strategy to reduce herbivory losses on young *R. stylosa* leaves by delaying maximum nutrient and chlorophyll import rates until the leaves are better developed and better protected.

7.4.7 Nutrient Cycling and Retention

In mangrove ecosystems, the main source of nutrient return from trees to the forest floor is litterfall (Robertson *et al.* 1992). Litter production and its subsequent decomposition has major effects on microfauna, macrofauna and organic carbon accumulation (Gleason and Ewel 2002). They are also key processes contributing to estuarine and wetland food webs (Odum and Heald 1975b, Rodelli *et al.* 1984, Robertson *et al.* 1992). Thus the potential impacts of insect herbivory on ecosystem productivity go beyond considerations of the amount of leaf area eaten or abscised because of insect damage. Because insects efficiently convert leaf tissue into frass and promote premature loss of leaves with higher nutrient contents than would be the case if those leaves underwent normal senescent processes, they contribute to greater nutrient losses from trees and may also promote nutrient cycling within mangrove ecosystems. The nutrient content of prematurely abscised leaves will depend on the type of damage they incur and the rate of their abscission. The abscission process may involve some resorption of nutrients, though probably not to the same extent as during senescence. The loss from the canopy of younger leaves with a higher nutrient concentration, and in the case of *A. marina*, higher water concentration, should represent a superior quality food resource for benthic consumers such as crabs, compared to senescent leaves. They should also breakdown and decompose faster (Robertson 1988, Robertson *et al.* 1992. Twilley *et al.* 1997).

Additionally, leaf material that is consumed is predominantly converted to insect frass (Duke 2002) which is enriched in nutrients and easily incorporated into food chains (Schowalter *et al.* 1986, Lovett *et al.* 2002). Frass also leaches nutrients more readily and decomposes more rapidly, than leaf litter (Hollinger 1986, Emmerson and McGwynne 1992). Herbivores such as caterpillars turn leaf material into frass efficiently. For a Limacodidae caterpillar feeding on *R. stylosa* near Gladstone, Duke (2002) found that the amount of frass produced was approximately equal to the weight of leaf material consumed with the difference being the relatively small weight gains of the caterpillars. Anderson and Lee (1995) found that frass from caterpillars fed *A. marina* leaves was enriched in nitrogen compared to uneaten leaf material.

Prematurely abscised leaves, insect frass and insect remains may constitute a significant proportion of total nutrient return to the forest floor. In a California oak forest with herbivory of around 25-35% of annual production, Hollinger (1986) found that up to 37% of the N returning to the forest floor in litterfall consisted of insect frass and body parts. Insect frass plays a strong role in regulating nutrient cycling and productivity in temperate forests, such that it may even benefit overall forest productivity (Mattson and Addy 1975, Seastedt and Crossley 1984). Whether this holds true for mangroves has not been tested. In the current study, 40-50% of *A. marina* leaf material was either consumed (much of which would be returned as frass) or prematurely abscised with those leaves being of superior nutritional quality to senescent leaves. Thus insect-mediated loss of nutrients is almost as great as that occurring in normal litterfall. In addition, under similar or even lower levels of herbivory in other forests, plants shift their carbon allocation strategies to replace the lost foliage and reduce allocation to wood production (Morrow and LaMarche 1978, Seastedt and Crossley 1984, Balciunas and Burrows 1993), resulting in a greater pool of nutrients available in leaf form.

7.5 Conclusions

In a comprehensive review of leaf characteristics, including lifespan, leaf-N and SLA (the inverse of LMA), Reich *et al.* (1992) compiled published data from more than 100 studies covering a variety of habitat types. They found that leaves with short lifespans generally have a high SLA (ie, low LMA), high N-concentration and high photosynthetic rates. The two species in this study conformed to this pattern. *A. marina*, with a leaf lifespan of 12 months compared to the 18 months of *R. stylosa* (see Chapter 5) had significantly lower LMA and higher N-concentration. Photosynthetic rate was not measured but chlorophyll concentration was similar for both species. Leaves with lower LMA and higher nutrient concentration would be expected to have higher herbivory (Coley 1988) and that is the case here. Although N and P concentration is lower in *R. stylosa* leaves compared to *A. marina* leaves, because of their greater biomass, they contained greater absolute amounts of N and P. Based on plant-herbivore theory and the data collected in this study, it appears that *A. marina* invests relatively less in each individual leaf than does *R. stylosa,* and suffers much greater herbivory and herbivore-induced leaf loss than *R. stylosa*. However, with the copious leaf production of *A. marina*, which is in stark contrast to the constrained leaf production of *R. stylosa*, it would is likely to be able to tolerate much greater levels of herbivory. Because of the restricted leaf production capabilities of *R. stylosa*, the loss of individual leaves could be more costly to this plant and increased leaf longevity would enable it to gain maximum benefit from each leaf. The higher LMA of *R. stylosa* may enable it to achieve such long-lived leaves (Coley 1988, Reich *et al.* 1991).

The nutrient content, chlorophyll content, leaf biomass and investment into a leaf varies significantly with its developmental stage. This affects the ontogeny of herbivore damage and the relative importance of the loss of leaves of various ages to the plant and to the recycling of nutrients and other leaf materials, in the mangrove ecosystem. In the current study, nutrient concentrations were highest when the leaves first emerged and gradually declined throughout their lives but the greatest absolute leaf nutrient content occurred in leaves that had been mature for some time but not yet begun senescence. Thus, although younger leaves represent a more concentrated nutrient source for herbivores and are therefore most heavily attacked (Chapter 5), because of their greater weight, the loss of mature leaves actually represents the greatest loss of nutrients and tissue mass per unit area. For *A. marina*, even the loss of senescent leaves represents a greater absolute loss of nutrient content compared to the loss of developing leaves. Clearly, leaves are not all of equal value to the plant and do not contribute equally to overall nutrient cycling in the ecosystem. The relationships between herbivore damage estimates (based on leaf area), and changes in nutrient content and biomass with leaf age, suggest that herbivorous insects promote a greater and more rapid return of nutrients to the mangrove ecosystem, but a lesser return of leaf biomass, than would be suggested by estimates of leaf area damage alone. Thus the true ecological role of insect herbivores in mangroves is much more than their effect on leaf area loss.

CHAPTER 8 – GENERAL DISCUSSION AND CONCLUSIONS

8.1 Herbivore Fauna and Herbivory Level

The aim of this thesis was to evaluate the level and importance of insect folivory in mangrove ecosystems using the common and widespread mangroves *Avicennia marina* and *Rhizophora stylosa* as examples. This investigation was stimulated by the widespread but mostly untested belief that mangrove ecosystems do not support specialised or diverse insect herbivore faunas and that insect herbivory, and therefore the ecological role of insect herbivores, is less in mangroves than in other forest ecosystems.

This study revealed the diversity of the folivore faunas of *A. marina* and *R. stylosa* to be comparable to other tropical tree species for which information could be located. Additionally, it was found that the folivore fauna shows a high degree of specialisation and adaptation to the mangrove environment and to their mangrove host plants. The two tree species supported distinct faunas with little overlap between them. Even the functional groups differed, with gall-forming species comprising nearly one-third of the fauna on *A. marina* but entirely absent on *R. stylosa*. A review of the literature suggests that this pattern may be similar across *Avicennia* and *Rhizophora* spp. worldwide, as may be the notable lack of beetle species on both mangroves. Several other similarities between the faunas reported on mangroves in other parts of the world indicate intriguing similarities that would be worthy of investigation. Several lines of evidence also point to a limited overlap in faunas reported over different parts of the geographical ranges of *A. marina* and *R. stylosa* in Australia. It is suggested that the true number of folivores feeding on mangroves within Australia could run to several thousand species, indicating the large task ahead in documenting this fauna.

Although herbivory has been assessed many times in mangroves, it has nearly always relied on discrete assessment methods. In this study, the long-term assessment method produced herbivory estimates 2-3 times higher for *R. stylosa* and 4-5 times higher for *A. marina*, than the discrete method. In contrast to the unproven belief that premature loss of leaves due to insect damage is a relatively rare event in mangroves, this study found it to be a relatively common occurrence, especially for leaves less than three months old. Up to 14-15% of *R. stylosa* leaves and 52-56% of *A. marina* leaves did not reach senescence, with most of these lost because of insect damage. Additionally, the inclusion of just a few such leaves in herbivory assessments makes a large difference to the overall result.

Of particular significance was the finding that for both species, loss of entire leaves due to consumption by insect or premature abscission of damaged leaves was similar to that actually consumed by folivorous insects. Thus, consideration of the roles of insect folivores needs to include their influence on leaf fall and processing as well as leaf consumption. Although leaf fall occurs year-round in mangroves, it is strongly seasonal. Premature abscission of leaves due to insect damage promoted aseasonal leaf fall which may be significant for detritivores such as crabs, especially in *A. marina* forests where insect-induced leaf fall was found to be more common.

One of the premises of the discrete technique is that older, or at least mature, leaves are sampled in order to collect leaves that have had a greater amount of time over which to accumulate herbivore damage. However, this study found that many damaged leaves are prematurely abscised and the leaves that live longest are those that, on average, have the lowest damage levels. Thus, even in studies where for logistical or other reasons, a discrete sampling methodology is required, sampling young or recently mature leaves, rather than middle-age or older leaves would capture a greater proportion of the total herbivory.

Mangrove leaves have often been suggested as being quite tough and this has been suggested to be a major deterrent for herbivores. However, this study, and others (eg, Choong *et al.* 1992) have shown that mangrove leaves are not especially tough. Indeed, *R. stylosa* leaves are not tougher than *A. marina* leaves, they are just thicker. Thickness may in itself be a deterrent for some herbivores but, in general, there is currently little data to support the popularly held notion that mangrove leaves are especially tough and resistant to herbivores.

Mangrove leaves were shown to change substantially in their physical and chemical composition as they aged. These attributes are likely to affect their palatability and resistance to herbivory, probably explaining why more than 60% of the herbivory occurred on young, developing leaves with high nutrient concentration but low physical toughness. Additionally, the change in leaf composition with age suggests that premature leaf abscission due to insects has a significant effect on the quality of the leaf fall as well as its quantity.

8.2 Implications for Herbivory Studies

Herbivory studies need to take into account leaf damage other than leaf area missing. In this study, leaf area missing only comprised approximately one-third of leaf area damage. Other damage types, particularly galls, which are common on *A. marina* and not readily assessed by measures of leaf area, may be particularly damaging, especially via promotion of premature leaf drop and diversion of energy into gall production. There are additional mechanisms by which herbivores may affect mangroves. Damage to apical buds and developing leaves was substantial, being potentially the most significant form of herbivore damage on *R. stylosa* and possibly other mangrove Rhizophoraceae as well. Damage to apical buds consisted of only minor consumption of leaf area, but frequently resulted in loss of leaves as well as developing lateral branches and inflorescences, and often resulted in branch death. Damaged apical buds produced less leaves than undamaged apical buds. In this sense, loss of leaf production because of the feeding activities of insect herbivores may be more significant than actual consumption of emerged leaves. In essence, is the damage that is not visible more relevant than the damage that is visible?

Even insects that do not feed upon leaves may cause significant leaf loss and impact upon plant growth. Leaf area losses on *R. stylosa* due to branch death caused by wood-boring cerambycid beetle larvae were as great as losses due to insect consumption of emerged leaves at the Saunders Beach site. Even the nest and web-building of ants and spiders affected branch growth and leaf production in some cases. Thus a true evaluation of insect leaf herbivory involves not only assessment of leaf area missing, but also inclusion of other mechanisms by which insect herbivores impact upon their hosts.

Although the long-term method provides a more realistic estimate of herbivory, it is very time consuming and not practical for many purposes. This study has demonstrated several means by which shorter studies should be conducted. For instance, if a discrete survey is to be undertaken, apart from acknowledging the limitations of that method, developing or recently mature leaves should be sampled in preference to older leaves. A comparative sample of younger and older leaves may give some indication as to the degree of loss of heavily damaged leaves as they age. Where time permits and a long-term study is desired, the herbivore damage accumulation graphs demonstrate that 60% of the herbivory occurs in the first 2 months and 80% within the first 5-6 months. Thus, long-term studies can be conducted for a few months and still provide most of the information desired. For *R. stylosa*, apart from leaves lost to branch death caused by wood-borers, very few leaves were abscised because of insect damage once the leaves had matured. So in this instance, and probably for other members of the Rhizophoraceae which have very similar leaf production and development patterns, it can be assumed that leaves that survive until maturation have a high probability of reaching senescence.

Herbivory levels or rates are usually considered to relate directly to the level of impact they are having on the tree species. Though it will be true in some cases, there is little basis for this assumption as a general principle. The impact of herbivory depends on rates of leaf growth and replacement, energy invested in anti-herbivore defences, timing of herbivory, parts of the plant damaged, and external environmental conditions. Most of these factors are subject to external and other influences.

Although *R. stylosa* suffered much less herbivory than *A. marina*, this may not mean that herbivory has a lesser effect on the growth and performance of *R. stylosa* than on *A. marina*. *Avicennia marina* has copious leaf production from all locations on the plant and invests relatively less in each leaf compared to *R. stylosa*, which has limited abilities for compensatory leaf production and invests relatively more into each leaf. In addition, because *A. marina* can coppice and easily replace lost leaves, it can recover from damage. This contrasts with *R. stylosa* which cannot coppice and has very limited leaf production abilities, especially if the apical meristem is damaged. Because loss of the apical meristem can cause leaf production on an entire shoot to cease, *R. stylosa* is highly susceptible to small amounts of damage suffered to important locations. In contrast, apical buds and meristems are readily replaced in *A. marina*. Apart from the ability to recover from insect damage, the impacts from herbivory also include the energy invested in preventing or reducing herbivory. Anti-herbivore defence mechanisms such as tannins and physically tough leaves are energetically expensive to produce. In saline mangrove environments, such energy is limited. It is likely that *A. marina* invests less into anti-herbivore defence than does *R. stylosa* and that because it can more readily recover from damage and leaf loss, has a strategy of tolerance. This contrasts with *R. stylosa* which invests more into preventing or reducing herbivore damage. Thus, the impact of insect herbivores on tree species may not be directly related to the amount of herbivory measured. The effects of insect herbivory on tree growth and performance should be tested experimentally (eg. Lowman and Heatwole 1987, Balciunas and Burrows 1993).

The role of herbivorous insects in mangrove ecology is more significant than currently recognised and deserves greater attention. This thesis has described, and to some extent quantifies, key mechanisms by which insect herbivores influence mangrove trees and mangrove ecology and demonstrates that herbivory investigations can deliver substantial insights into the dynamics of mangrove ecosystems. The most fertile areas for further research into the role and importance of insect folivores in mangrove ecosystems are:

1) Further documentation of the herbivore faunas, especially determining the distinctiveness of the fauna and comparing the communities over large geographical scales.
2) Direct comparison of herbivory between mangroves and adjoining terrestrial habitats.
3) Examining the impact of insect herbivory on mangrove tree growth and performance.
4) Examining the impact of tip and apical bud damage on mangrove Rhizophoraceae, especially in relation to tree growth and form.
5) Examining the effects of altered seasonality and quality of leaf litter created by insect herbivores, on ground-dwelling detritivores such as crabs (ie, investigating a direct food chain link between terrestrial and marine food chains).

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APPENDIX A – NATURAL HISTORY AND MISCELLANEOUS OBSERVATIONS OF THE MANGROVE INSECT FOLIVORE FAUNA

Introduction

Central to the nature and importance of insect herbivory is the role and life habits of the herbivores present. Without understanding the basic habits of the fauna, we may overlook or underestimate their impact and role. Murphy (1990) has described the natural history of mangrove insect herbivores in Singapore. Most other articles on mangrove herbivores have made incidental observations of the habits of particular herbivores, but do not place them in the context of the herbivore community as a whole. During the course of this study, numerous observations have been made, again mostly incidental, that are worthy of note. Such observations and qualitative descriptions will greatly assist future workers studying herbivorous insects in mangroves. These observations are summarised in this appendix by functional groups.

Leaf-Binders

This category of insect herbivores consists entirely of several species of lepidopteran moth caterpillars that bind leaves together, and then graze the leaves from within this protective location (Figure A.1). They were among the most common and conspicuous insect herbivores on *A. marina* in this study, but were less common on *R. stylosa*. Only the surface of the leaf is grazed initially, but as the larvae grow older, the leaves are grazed through to the cuticle on the opposite side of the leaf (Figure A.2). The frass is retained within the feeding area between the leaves, and pupation also occurs there. The act of binding the leaves together is presumably for protection against predators and parasites. Most bound leaves encountered were vacant; either the caterpillar had completed its life-cycle or had been predated. Spiders, ants, cockroaches and other smaller insects were often found inside vacant bound-leaf enclosures. In some cases, a third leaf may be stuck to the enclosure and grazed. Typically, one leaf is grazed on the underside and one on the upper surface, although in a few instances, both leaves may be grazed on the same side and in the case of a

Figure A.1 Leaves of *A. marina* bound together by grazing caterpillars. Note dead leaf detached at petiole but still bound to other leaves.

Figure A.2 Examples of leaf-grazing damage on *A. marina* leaves. Note different depths of grazing damage and different colours, indicating the relative age of the damage third leaf being in the middle, it may be grazed on both sides. Generally, there was only one caterpillar in each bound enclosure. The same leaf may be bound into more than one enclosure, although this is rare. Leaves may be bound to other leaves on the same twig up to three nodes away, but are more commonly bound to closely-located leaves from adjacent twigs. Leaf-binders appear to be a major cause of premature leaf abscission. In many cases, one of the leaves becomes detached from its twig at the petiole but remains bound to the other leaf. A dead leaf stuck to other live leaves is a common sight on *A. marina* at certain times of the year (Figure A.1). As such leaves are easily observed from a distance, rapid assessments of the presence of these herbivores are readily made.

As with most forms of grazing damage on *A. marina*, the damage appears brown when fresh and then goes a white/grey colour with time, enabling some determination of the relative age of the damage. The life-cycle of any species involved has not been examined but is likely to be only a few weeks to months duration. Most larvae probably complete their entire life-cycle on the same leaf although larvae feeding on very young developing leaves may need to find new leaves to complete their life-cycle. In the laboratory, they can be induced to form new enclosures on new leaves.

Leaf-binders on *A. marina* fed on both the young developing leaves, and on mature leaves, and are thus readily found throughout the year. On young developing leaves, they may kill or deform the leaf as it grows. The distinctive dead leaf attached to a live leaf as described above, was only observed on older leaves. Leaf-binders are the most common group of herbivores noted in this study on *A. marina* and probably consume the most amount of leaf tissue. For older *A. marina* leaves, they may be the major source of herbivory and leaf death. Some of the leaf-binding caterpillars also bore into large galls (eg, the bulbous gall) to consume plant tissue there and to pupate there. Leaf-binding caterpillars on *A. marina* have been observed on leaves that are below recent high tide marks suggesting that the binding on the enclosure may be watertight. The frequency and duration of inundation has not been determined.

Leaf-binders are less common on *R. stylosa* and are mostly restricted to developing immature leaves. The most common leaf-binder found on *R. stylosa* is *Procalyptis parooptera*, a well known mangrove herbivore (Hutchings and Saenger 1987). On *R.*

stylosa, the butterfly, *H. apelles* can occasionally be found grazing between leaves previously bound by *P. parooptera*. The polyphage moth *Adoxophyes templana* (Lepdiptera: Tortricidae) also binds and grazes leaves of *R. stylosa,* though I have more commonly found it employing this habit on the river mangrove, *Aegiceras corniculatum* and occasionally, *Excoecaria agallocha*. This moth has also been reared from *M. dealbata* and *M. quinquenervia* in Townsville (Balciunas and Burrows 1995). All the leaf-binding moth caterpillars observed appear to be obligate leaf-binders. If removed from this protective enclosure, even in the laboratory, they react vigorously, and will attempt to either re-bind the leaves, find a similar protective location, or rapidly move elsewhere.

Avicennia Petiole-Grazing Weevil

On *A. marina*, grazing damage from the weevil *Alcidodes ?bubo* (Coleoptera: Curculionidae – Figure A.3), is very common, becoming almost ubiquitous at certain times and places. This weevil feeds upon the petiole of leaves and occasionally some damage may occur to the part of the leaf lamina adjacent to the petiole (Figure A.4). In no cases has feeding or feeding damage been observed on any other part of a leaf. In fact, laboratory observations suggest that they would die without feeding on other parts of leaves, even if they had already fed on the petiole of the same leaf. Feeding occurs on petioles of both young and mature leaves. In all cases where the weevils were observed feeding, they oriented toward the leaf with their rear toward the stem.

In the laboratory, leaves with damaged petioles quickly separated from the stem, but this was not observed to occur so readily in the field. Feeding damage on petioles in the laboratory appeared to be more extensive and cut deeper into the petioles, than did the feeding damage observed in the field. If deeper and more extensive grazing damage on young leaves was more common under field conditions, significant leaf mortality and tree defoliation may occur. When feeding on newly emerging leaves on a rapidly elongating branch, some feeding damage occurs on the soft, green branch itself, causing a necrotic effect on the branch. Similar damage by *Haplonyx* sp. weevils feeding on *M. quinquenervia* results in the death of the entire developing shoot (unpub. data).

Figure A.3 *Alcidodes ?bubo* petiole-grazing weevil on *A. marina*

Figure A.4 Grazing damage by petiole-feeding weevil on *A. marina* leaf

The weevil is quite distinctive, having prominent white markings on its dorsal surface (Figure A.3). It does not fly away when approached, but grips the petiole tightly. Its lack of movement and low profile against the petiole make it very difficult to locate in generalised searches, but its distinctive feeding damage is obvious.

The larvae of this weevil have not been encountered, though larvae of *Alcidodes* spp. are known to be bore stems and seeds (Zimmerman 1991), which have not been examined in this study. *Alcidodes bubo* is known to occur in Queensland, the Northern Territory and India (Zimmerman 1991). Although no individuals were seen, I have observed feeding damage I would attribute to this species on *A. marina* at Darwin. Neither this weevil, nor its feeding damage, were observed on any other mangrove species during this study; however, it does not appear to be host-specific to *Avicennia*. This species was, though on just a few occasions, also collected from *M. dealbata* and *M. quinquenervia* in north Queensland (Balciunas and Burrows 1995) and fed upon leaves of the latter in the laboratory (Burrows, unpub. data). Gardner (1934) recorded *A. bubo* from stems of the legume *Indigofera* (Fabaceae) in India. Due to the extremely high diversity of weevils and the often very minute details that differ between species, further taxonomic investigations may reveal these to be separate species.

The Copper Jewel Butterfly - *Hypochrysops apelles apelles*

The copper jewel butterfly, *Hypochrysops apelles apelles* (Lepidoptera: Lycaenidae), is a common butterfly species in north Queensland and is also found in New Guinea, west to Darwin and south to Port Macquarie (Braby 2000). Although not host-specific, its caterpillar was the most conspicuous insect herbivore found on *R. stylosa* in this study. It is known to feed on a variety of mangroves such as other *Rhizophora* species, *Ceriops tagal* and *Bruguieria* spp. (all Rhizophoraceae), *Lumnitzera racemosa* (Combretaceae) (Braby 2000) and *A. marina* (Manski 1960). Braby (2000) also lists 12 non-mangrove host species from 7 families, including species from common genera such as *Acacia*, *Eucalyptus*, *Planchonia*, *Terminalia* and *Alphitonia*. Various populations of *H. apelles* are known to have different habitat preferences and Sands (1999) considered there to be different biotypes of the species adapted to different habitats. For instance, only in the part of its range from Townsville to Cape York is this species known to occur in non-mangrove habitats (mostly coastal savanna woodlands), being confined to mangrove habitats in all other parts of its range (Hill 1992, Braby 2000). Apart from the larvae feeding on the leaves, adults feed on nectar from flowers of various mangrove species (Hill 1992).

Manski (1960) records *H. apelles* from *A. marina* at Maryborough and the Hervey Bay area in southern Queensland, but despite considerable effort, I have not observed any occurrences of this otherwise common herbivore on *A. marina* around Townsville and other locations in north Queensland visited opportunistically. Manski (1960) provides no indication of the extent and frequencies of its occurrence on *A. marina*, but I am inclined to judge it as minimal or incidental. Two other *Hypochrysops* butterflies have been recorded feeding on *A. marina.* The mangrove jewel butterfly, *H. epicurus* is a mangrove specialist, occurring from Rockhampton to Newcastle that has only been recorded from *A. marina* (Smales and Ledward 1942, Braby 2000). The narcissus jewel butterfly, *H. narcissus*, occurs from Cape York to just north of Townsville (Braby 2000) and has been reared from *A. marina* at Mossman and Innisfail (Muller 1998). It has also been recorded feeding on the mangroves *L. racemosa* at Cooktown and *R. stylosa* and *B. exaristata* at Mossman (Muller 1998) and *C. tagal* and *Aegiceras corniculatum* at Port Douglas (Valentine and Johnson 1988), as well as a variety of non-mangrove coastal plants listed in Braby (2000).

There are 57 *Hypochrysops* species, and all but one are confined to the Australasian region (Sands 1999). Sands (1999) describes the biology of the group including, *H. apelles apelles*. The eggs are laid on young leaves, often near feeding scars of previous larvae. The larvae of *H. apelles* have a distinctive bright-green colour with pink and black markings and are usually attended by several ants of the genus *Crematogaster* (Figure A.5). These probably provide protection against predators. The larvae only feed on young, developing leaves, thus are most common in the summer and autumn months when such leaves are more abundant. They usually feed individually with only one larva per leaf, though larvae would have to feed on several leaves to complete their life-cycle. They feed at night, and during the day, rest underneath leaves or in rolled-up leaf margins. Their grazing damage is distinctive (Figure A.6), being brown initially, then becoming grey/white with age. Damage

Figure A.5 *Hypochrysops apelles* larvae attended by *Crematogaster* ants

Figure A.6 Extensive grazing damage by *H. apelles* on young *R. stylosa* leaves from older larvae will appear transparent when fresh because the grazing has been taken right through to the cuticle on the other side of the leaf (Figure A.7). The obvious and distinctive nature of their feeding damage makes field searching more efficient. The feeding scars are broad, becoming more so as the larvae get larger. Damage to individual leaves is often extensive and can be up to 90% of the leaf area. Because of its extensive feeding on young leaves, it appears to contribute to their deformation and premature abscission. Badly damaged leaves, especially if the damage occurs whilst the leaves are still unfurling, often become rolled at the edges and necrosis may develop between feeding scars.

Lycaenid butterflies are also common in mangroves outside of Australia. Similar to the role of *H. apelles* on young expanding leaves on *R. stylosa* in this study, Rau and Murphy (1990) also found that a lycaenid butterfly, *Hypolycaena erylus*, is one of the most important pests of young expanding *R. apiculata* leaves at Ranong, Thailand. Like *H. apelles*, this butterfly is also known to have other mangrove and non-mangrove hosts (Rau and Murphy 1990, Veenakumari *et al.* 1997).

Tip-Feeding Caterpillars

These are represented by caterpillars that bore through the tips of *R. stylosa*, resulting in the damage or death of the apical bud and any new leaves being produced there. The effects of this damage have been discussed extensively in Chapter 6.

Only apical buds in the process of developing new leaves are attacked. Several moth species are involved and unidentified Curculionidae weevil larvae have also been recorded causing the same damage. In its early stages, this damage is recognised by a small hole bored through the protective stipules to the centre of the tip. The larvae continue feeding from within the stipules and developing leaves that are wound around the apical bud. Their feeding activities often damage or kill the apical buds as well. Usually both developing leaves are damaged. If they do successfully emerge, they may each have damage that mirrors the other. Often, however, the leaves do not emerge successfully and they become detached at their base. Because they did not unfurl, the dead leaves may stay wrapped around the apical bud for considerable periods of time (up to several months) until they are physically dislodged. The leaves go a dark brown/black colour and the presence of such leaves is a common sight and diagnostic of such damage. The striking visual appearance of the developing leaves wrapped around their apical bud but detached at their base, is the most effective way of searching for the insects that cause this damage. Feeding damage on the developing leaves themselves is often minimal during this process. Various other animals such as spiders and cockroaches are often found inhabiting the abandoned dead leaves. Not only does this type of damage result in the damage or loss of the developing leaves, but developing inflorescences and lateral branches are also killed during this process. Damaged apical buds have reduced leaf production and apical buds that are killed will no longer produce leaves at all, leading to the death of that shoot (see Chapter 6 for further details).

Galls

Galls are abnormal swellings of plant material and may form on leaves, petioles, twigs, flowers and fruit. They are usually formed by the plant in response to the presence and/or feeding of particular galling insect species. Leaf galls form as the leaf develops, thus they cannot form on already mature leaves and their seasonality matches that of new leaf production. Some galls are merely swellings or deformations of the plant tissue, whilst others are complex, chambered structures (Gagne 1989). These latter gall types have significant layers of so-called nutrititive tissue upon which the developing larvae, and often invading inquilines, feed (Figure A.8). Because of their small size, gall-forming species generally have difficult taxonomy, and have thus been largely ignored in many studies. Fortunately, each species forms galls that often have a distinctive shape and site of occurrence, thus in many instances, gall morphology can be substituted for individual species with confidence.

Galls can be particularly detrimental to plants. A good example is the hymenopteran gall-former *Trichilogaster acaciaelongifoliae*, introduced to South Africa as a biological control agent for *Acacia longifolia*. Even though only 50% of branches were galled, this reduced reproductive potential by 89% and vegetative growth by

Figure A.7 Grazing damage by *H. apelles* larvae passes through *R. stylosa* leaf lamina to cuticle on other side of the leaf

Figure A.8 ‘Bulbous’ gall dissected to show layers of internal tissue

53% (Dennill 1988). The galls constituted up to 21% and 40% of the above-ground dry and wet biomass of the trees, resulting in breakage and mortality of large branches (Dennill 1988). This excessive biomass diversion to gall production is obviously a significant stress upon the tree and consumed up to 23% more energy than reproduction by the host plant (Dennill 1988).

There is a large variety of insect taxa that include gall-forming members. Only eight gall-formers have been described for mangroves (all on *Avicennia* spp.), seven of which are formed by flies of the midge family Cecidomyiidae (Diptera) which are known for their gall-making abilities across the world (Gagne 1989). The eighth gall type is formed by a mite on *A. marina* var. *australasica* in New Zealand where it is reported to be a common and conspicuous feature of those trees, often causing significant leaf distortion (Baylis 1940, Lamb 1953, Chapman 1976). Of these seven cecidomyiid species, one is from Florida, Central and South America (Gagne and Etienne 1996, Goncalves-Alvim *et al.* 2001), one is from Java (Felt 1921, Gagne and Law 1998) and five from Queensland (Gagne and Law 1998). The species from Java and Queensland are in the genus *Actilasioptera*, and are the only members of that genus (Gagne and Law 1998). *Actilasioptera* is radically different from other members of the Lasiopterini tribe and its closest relatives are not apparent (Gagne and Law 1998). The galls formed by the 230 members of the Lasiopterini tribe are normally simple swellings in plant tissue, but three of the five species described by Gagne and Law (1998) from *A. marina* in Queensland form complex gall structures.

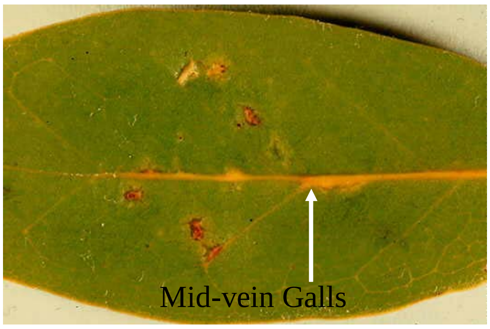
Galls formed by other insects are also present on *A. marina* (pers. obs.) although they have a simple structure (eg, leaf deformation), compared to the more complex and chambered cecidomyiid galls that may comprise considerable biomass. Galls were not observed on any of Rhizophoraceae species during the current study. Despite galls commonly being reported from *Avicennia* species across the world, reports of their occurrence on mangrove Rhizophoraceae are very rare (see Chapter 3). Several authors have noted the presence of galls on mangrove trees but without further study. Wium-Andersen and Christensen (1978) note the presence of two species of undetermined gall-forming species on *A. marina* in Thailand that caused a drop in leaf production. Rau and Murphy (1990) noted but did not describe, at least six different gall types on *A. officinalis* (five formed by Cecidomyiidae and one by Eriophyidae mites) in south east Asia. Murphy (1990 p.125) considered these galls were a "conspicuous feature of the genus" (*Avicennia*) and Rau and Murphy (1990) considered this to be the most important difference between the insect fauna of *A. officinalis* and the members of the Rhizophoraceae. They suggested that the persistence of post-axial meristematic tissue makes *A. officinalis* susceptible to galling in contrast to the extreme localisation of such tissues in the Rhizophoraceae.

Of the five species described by Gagne and Law (1998) from Brisbane, I have only found two in Townsville, with the remaining Townsville species being different. The species known from Java has not yet been recorded from Australia. There is also an additional undescribed *Actilasioptera* species known only from adults in Papua New Guinea (Gagne and Law 1998). Given the diversity and lack of significant range overlap of *Actilasioptera* species along the Queensland coast, there may be many more species in other parts of Australia and south east Asia. The apparent lack of range overlap between gall-forming species on *A. marina* within Australia, and the high level of host fidelity most gall-formers have, suggests that the cecidomyiid gall-formers noted on *A. officinalis* by Rau and Murphy (1990) are likely to be different species. Although they have been little studied, it appears from the above accounts, that galls are conspicuous features of *Avicennia* species over most of the world.

Many other insect herbivores feed on the nutrititious gall tissue. The bulbous galls, the largest of the galls recorded in this study, were regularly infested with numerous moth caterpillars boring into the galls. Most of these caterpillars normally feed on leaves. Their feeding activities may have caused mortality for the gall-formers themselves. One of the more common moth species found feeding on the galls was, however, not found on any other plant part. Numerous hymenopteran parasites have been reared from the above galls. These may be parasitic on the gall-formers or other inquilines, especially the caterpillars. Several species may emerge from the one gall and some may be parasites of other parasites (hyperparasites). These were beyond the scope of this study. The galls found on *A. marina* during this study are briefly described below and pictured in Figure A.9.

Figure A.9 Examples of Galls From *A. marina* Around Townsville

Figure A.9 cont'd



Raised-Pit Galls

Figure A.9 cont'd

Stem Galls

“Bulbous galls” were the largest of the leaf galls on *A. marina* in the current study and were quite common. The causative agent was described by Gagne and Law (1998) as *Actilasioptera tumidifolium*. In addition to material from the Brisbane area, the type series includes specimens I supplied from Saunders Beach. Only one gall occurs on each leaf, though both leaves in a pair are usually affected. Affected leaves are commonly, though not always, reduced in size compared to average-sized leaves, and in these cases, the gall may engulf the entire area of the leaf. Large bulbous galls have a similar dry weight to recently mature ungalled leaves (unpub. data). They thus may comprise a significant diversion of energy away from leaf production. Bulbous galls always occur near the base of the leaf, although this may not be so obvious in cases where it occupies large areas of the leaf. The gall is similar in colour and texture to the leaf, including being green on the upper surface and grey on the lower surface (Figure A.9). The volume of the galls is approximately evenly divided between the upper and lower leaf surfaces. The galls are complex and contain several to many chambers, each containing a single larva. These galls (and sometimes the other large galls) are often fed upon by moth caterpillars that bore within them. Bulbous galls are rarely found on mature or senescent leaves, suggesting that infected leaves are very likely to be abscised at an earlier stage of leaf development.

“Edge galls” occur only along the edges of leaves and are very common. These galls appear to be identical to those described from *A. marina* in Brisbane formed by *A. subfolium* (Gagne and Law 1998) in recognition that the majority of the gall biomass is found on the lower leaf surface. These galls may be up to 7cm long (Gagne and Law 1998, unpub. data) and up to 5.8 mm thick (unpub. data). Gall width is usually fairly uniform, between 4-6mm (unpub. data). Though galls were most commonly found individually on leaves in the current study, many separate galls may be found on each leaf, and these may occupy up to 75% of the overall leaf margin. In addition to the common yellow colour on the upper surface, the galls often appear red in various places, especially along the lateral mid-line. The lowerside is grey in colour.

“Spike galls” are very common galls. Each gall is an individual spike on the upper leaf surface up to 3 mm high. Typically there are numerous spikes on each leaf. These galls were not recorded by Law (1995) or Gagne and Law (1998) from *A. marina* in south-east Queensland.

“Yellow-lump galls” are large, multi-chambered galls that always occur near the centre-base of the leaf. They were moderately common in this study. The gall biomass is approximately evenly distributed between the lower and upper leaf surfaces. On the upper leaf surface, the galls appear a strong yellow colour, but are grey on the underside, which matches the leaf colour there. The edge of the galls merge with the surrounding leaf, in contrast to the bulbous gall, which has distinct, sharply demarcated edges. Gall midges emerge from the underside of the gall.

“Cabbage galls” are relatively uncommon galls that always occur near at the leaf base, near the petiole. “Marble galls” are green galls with a well-rounded shape that occur on the leaf lamina, usually centred on the mid-vein. They are smaller and more spherical than the bulbous gall, which they otherwise resemble. “Acne galls” occur as a cluster of galls. On the upper surface, the galls may be yellow in colour or often they are red, but on the bottom, they retain similar colour to the underside of the leaf.

“Pimple galls” were the most common galls found on *A. marina* in this study. They are small, individual galls (1-2mm diameter), that always appear bright yellow in colour. They are usually found in large numbers with up to 275 individual galls having been recorded from one leaf. The galls are only apparent on the upper leaf surface and there is very little evidence of their presence on the leaf underside.

“Mid-vein galls” are the smallest and least visible of the galls. They are a small (1-2mm) long gall in the mid-vein of leaves. Each gall houses only one larva. Because of its size it is rarely observed in general searches, but may be found to be more common if specifically searched for.

“Raised-pit galls” are moderately common galls but the causative agent is unknown. Several galls may occur on each leaf and they appear as a raised mound on the upper leaf surface. The mound is hollow with the underside conforming to the shape of the upper surface.

“Stem galls” are not actually leaf galls but are mentioned here for completeness. They may very well affect leaf production and stem growth although this has not been tested. Stem galls were common in this study and are easily spotted by the swollen stem. When larvae have emerged from the gall, they leave numerous distinctive holes in its side (Figure A.9).

Leaf-Mines

Leaf-mines are formed by larvae that tunnel beneath the leaf surface and feed on leaf tissue from that location. They may be just beneath the cuticle or deeper in the leaf tissue. Each species forms a distinctively-shaped leaf mine. The leaf-mining habit is displayed by species from a wide variety of orders, most commonly being caterpillars, fly larvae or beetle larvae. There are several species of leaf-miners on both *R. stylosa* and *A. marina*. They are less common on *R. stylosa* compared to *A. marina* where they occur on a very high proportion of leaves. The mines found in this study were either a round-shape or linear-shape. Linear shape mines reflect the path taken by the larvae as they move and feed, with the mine becoming wider as the larva grows. Frass is retained within the mines and the larvae pupate at the end of the mine, often in an enlarged circular section. Emergence is marked by a small hole at that location. Generally, the causative agents for leaf-mines are very small and difficult to rear to adult for identification, which is why little is known about them. Because the leaf lives for much longer than the leaf-miner, most mines encountered in the field are empty with the miner either emerged, predated or parasitised. Unlike for heavily galled leaves which were only present on immature leaves, many mature leaves had significant leaf mine development and though it may occur, I saw no obvious evidence for significant premature leaf-fall caused by any of the mangrove leaf-mines.

A. marina leaf mines

Three leaf-mines have been identified from *A. marina* at the two sites sampled in this study. More have been observed at other locations around Brisbane (Law 1995, unpub. data). The leaf mines recorded from *A. marina* in this study are pictured in Figure A.10.

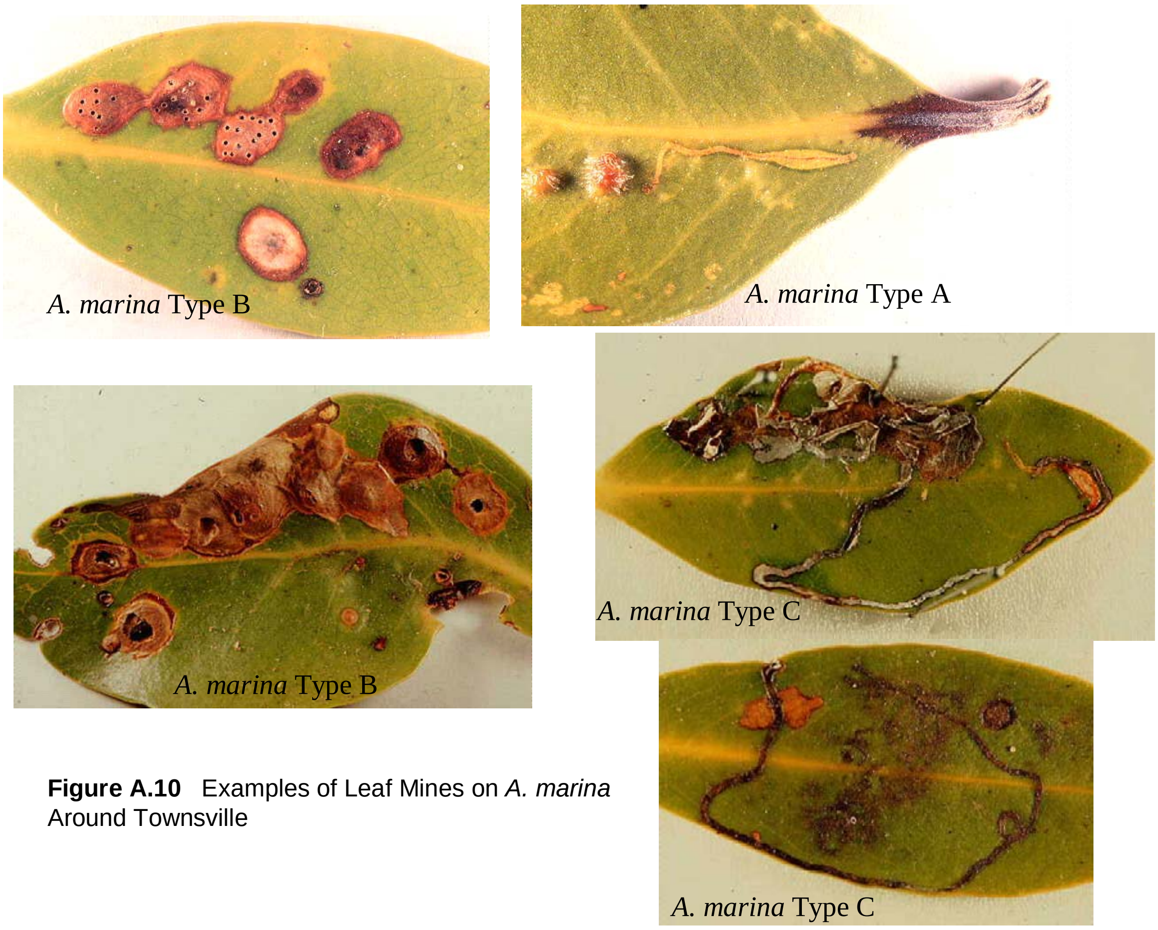


Figure A.10 Examples of Leaf Mines on *A. marina* Around Townsville

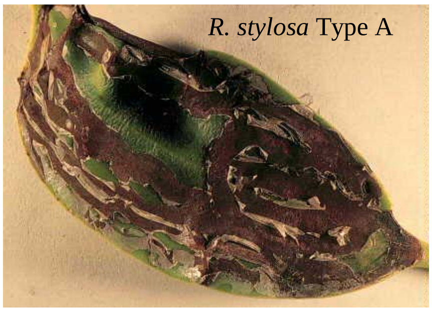
Type A – "Linear trail leaf mine". This leaf mine, caused by an unidentified moth caterpillar, was very common. The mine consists of a short trail abruptly opening to a wider trail area, in contrast to other patterns where the trail gradually widens. They are usually 10-15 mm long but only 1-2mm wide. Most commonly, there is only one mine per leaf but up to 10 individual mines have been found on a leaf. The pupation site is rarely wider than the previous parts of the trail, in fact is actually narrower than the part of the trail immediately preceeding it. The mine is distinguished from the leaf by its yellow colour, often with a distinct red centre-line.

Type B – "Circular leaf mine" – These are common leaf mines though the causative agent has not been determined as mines are usually unoccupied when encountered. On the surface, the mine appears as a hard brown circle, often with numerous (up to 14) small holes representing emergence holes, probably of parasites. No such holes are present underneath the mine.

Type C – "Worm-trail leaf mine" – a rare leaf mine that follows a long, winding path around a leaf and never widens substantially. The causative agent is unknown but probably a caterpillar. The mine appears brown and is not transparent suggesting that the mine is deeper than just beneath the cuticle.

R. stylosa leaf mines

At least seven types of leaf mines have been recorded for *R. stylosa* from the two sites studied. These are pictured in Figure A.11. None are common and several have only been collected once. The type A mine was more commonly encountered than the remaining six types combined. Due to their close association with the host plant, leaf-miners tend to be host-specific. Thus, although rare, these mines are not expected to be caused by vagrants.



R. stylosa Type A

R. stylosa Type B

R. stylosa Type C

R. stylosa Type D

Figure A.11 Examples of Leaf Mines on R. *stylosa* Around Townsville

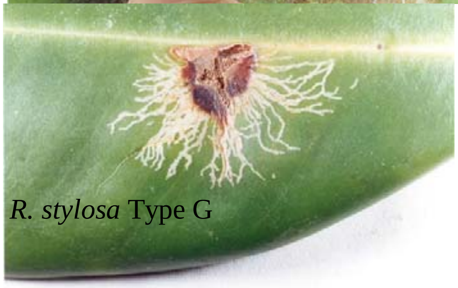
R. stylosa Type E

R. stylosa Type E

R. stylosa Type E

R. stylosa Type F

R. stylosa Type G



R. stylosa Type G

Figure A.11 cont'd

Type A – this is the most common leaf mine found on *R. stylosa*. The mine is up to 3mm wide and can occupy 80% or more of the surface area of a leaf. Unlike most linear leaf mines, the mine becomes quite wide from a very early stage and there is no obvious gradual widening of the mine trail as the insect grows (an effect seen clearly in Type B). The mine usually runs up and down the length of the leaf several times, rarely traversing across the leaf. The mine is just underneath the cuticle resulting in a transparent appearance although underneath the cuticle, the mine is a deep brown colour. In Figure A.11, the cuticle has been torn away but is normally intact whilst the mine is active. The causative agent is unknown but is presumed to be a Lepidoptera caterpillar.

Type B – This mine has only been recorded once. It resembles Type A but the mine occurs deeper beneath the leaf tissue, not just the cuticle. Whilst it too has a distinctive brown colour, there is no transparent cuticle above the mine. As can be clearly seen in Figure A.11, this mine also gradually widens as the causative agent (which is unknown) grows.

Type C "Paper-tissue leaf mine" – This mine is not a linear mine but rather a contiguous area. The upper leaf lamina is separated from the lower surface, becomes brown and has a texture resembling a paper bag. This mine has only been collected once and the causative agent is unknown. Figure A.11 shows three insect emergence holes which may belong to the causative agent but more likely are the result of parasites emerging.

Type D – This leaf mine has only been collected once. It is similar to Type B but does not follow the same linear pattern and the leaf lamina within the mine remains green. The mine is caused by a lepidopteran caterpillar but this was not successfully reared to adult for identification.

Type E – This leaf mine has been seen on a few occasions but the causative agent remains undetected. The mine is very small and appears more like a tattoo marking on the leaf than a well-defined mine. The three images shown in Figure A.11 may represent separate types of mines but in the absence of more detailed information, have been treated as one type here.

Type F – This leaf mine has only been collected once. As depicted in Figure A.11, the mine is a single strip of 5mm width beneath the transparent cuticle. The markings on the leaf lamina underneath the cuticle are very unusual, and are also visible on the leaf underside. The causative agent is unknown.

Type G – This leaf mine has been collected twice. Numerous small trails radiate from a central point. Figure A.11 shows both the upper and lower leaf surface. The causative agent is unknown but the number of trails suggests that many individuals may be present.

Beetles

Beetles (Coleoptera) are the most diverse animal group in the world but the low diversity of folivorous beetles in mangroves is notable (see Chapter 3). Only six species (petiole-feeding weevil, tip-boring weevil, two chrysomelids and two *Apion* weevils) were located in this study and only the first four of those were confirmed as feeding upon mangrove leaves. Field examination of other mangrove species also found a general lack of leaf-feeding beetles. Apart from the petiole-feeding weevil, beetles appear to be relatively unimportant herbivores of mangrove leaves, though their role as wood-borers appears to be significant (see below).

Two species of Chrysomelidae beetles were found to feed on both *A. marina* and *R. stylosa*, though as they belong to difficult species complexes (eg, *Monolepta*), further taxonomic work may alter this count. Both graze small holes in leaf tissue, most commonly along the leaf margins. Often, the leaf is eaten right through (Figure A.12). Generally, this damage only amounted to only 1-2% of leaf area in the current study. All folivorous beetle species located during the current study were found as adults, and no larvae were collected. The larvae of these species may have been borers of other parts of the plant such as flowers, propagules or even the roots.

At least two species of *Apion* sp. weevils (Family Apionidae) were abundant in mangroves on both *A. marina* and *R. stylosa*. However, they were never observed to feed, even when held in the laboratory. They were present at all times of the year. *Apion* larvae commonly have short larval periods (one to a few weeks) and burrow within flowers, fruit or other plant structures (Bernays and Chapman 1994). The adults are usually folivorous. The taxonomy of the group is complicated and it may be that the weevils found on both mangrove plants are different species. Despite the abundance of *Apion* in this study, I have found no mention of them anywhere else in the mangrove entomology literature apart from Hockey and de Baar (1988) who collected numerous *Apion* sp. (not necessarily the same species) from branches of *Bruguiera* sp. at Port Alma, near Rockhampton but were also unable to determine their feeding habits.

Possibly of greatest interest are wood-boring beetles of the family Cerambycidae. As these are wood-borers and not folivores, they were not part of the current study. They feed by tunnelling within twigs and branches, destroying the plant cambium tissue resulting in the death of all leaves and twigs proximal to the site of feeding. In the current study, ~5% of marked *R. stylosa* leaves at Saunders Beach died this way, the only notable mortality factor for mature leaves at this site. Other studies in central America indicate even greater levels of leaf loss from wood-boring beetles (Feller and Mathis 1997, Feller and McKee 1999, Feller 2002). Damage resulting from wood-borers was noted at Gordon Creek but was less common and did not affect any of the tagged leaves. These are very difficult to rear and may have long life-cycles, making them difficult to study. This, along with their cryptic wood-boring habit, means they are not often studied or observed. No adults were ever observed, but these typically feed on wood (not examined in this study) and the larvae have long life-cycles. Although these beetles are among the most serious pests in forestry, their distribution and occurrence is often patchy.

Figure A.12 Typical Chrysomelidae beetle feeding damage around leaf margins on *R. stylosa* leaves

Figure A.13 Leaf yellowing typical of diaspid scale insect feeding damage on *R. stylosa* leaves

Sap-feeders

Sap-feeding insects belong to the Order Hemiptera and are most commonly represented by scale insects, leafhoppers and sap-feeding bugs. These insects are among the most commonly encountered in most plant systems, including mangroves. In general, they appear to have little effect on the host plant unless in very large numbers. Rau and Murphy (1990) noted that heavy infestations of a diaspid scale insect caused premature abscission of leaves on *R. apiculata* at Ranong, Thailand and Ozaki *et al.* (1999, 2000) noted the large populations of scale insects caused premature leaf drop and death of planted *R. mucronata* saplings in Bali. I have yet to note large infestations of any sap-feeding insects on mangroves in north Queensland. Feeding damage is generally not noticeable although on *R. stylosa* leaves, minor necrotic yellowing of the leaf tissue occurs around the feeding site of diaspid scale insects (Figure A.13). In the current study, the most common sap-feeding insects were diaspid scale insects on *A. marina* and members of the planthopper family Flatidae on both species. Aphids are among the most well-known sap-feeding insects, yet none are known from mangroves anywhere in the world.

Other Insects

Grasshoppers are common herbivores and may consume large amounts of leaf area. These were common in mangroves in the current study, although no single species was particularly abundant. There were usually encountered as nymphs rather than adults. They are generally polyphagous and may also feed on other plant parts (eg, flower petals) in addition to leaves (unpub. data). They appeared to be more common and diverse at Saunders Beach, which may reflect the greater diversity of woodland in close proximity to that site.

Figure A.14 Spiders web in *R. stylosa*. Like insects, spiders probably also play an important role in mangrove canopy food webs.

Although not herbivorous, green tree ants (*Oecophylla smaragdina*) are a very abundant and conspicuous feature of the mangrove arboreal insect fauna. They build their nests by webbing together numerous leaves. This activity occasionally results in the death or loss of leaves, though it is to be expected that the available photosynthetic leaf area is reduced. Potentially the most significant effect of ants is their role as predators of insect herbivores. The role of predatory ants in regulating herbivory has been the topic of several studies. In mangroves, Ozaki *et al.* (2000) found that scale insects built up large populations that caused the death of *R. mucronata* saplings planted as part of a restoration program. In the adjoining natural mangrove forests, they found that predation by ants substantially suppressed the scale insect populations. As ants may be the most abundant arthropods in mangrove forests (Simberloff and Wilson 1969), they may have significant effects on herbivore populations and patterns of herbivory.

Spiders are also an abundant and conspicuous feature of the mangrove arboreal fauna. Like green tree ants, their webs encase numerous leaves, though apparently without loss or damage to them (Figure A.14, pers. obs). They may also have an important role in regulating herbivory through predation. No spiders are known to be obligate mangrove-dwellers, but this most likely reflects the relative lack of research on them in mangroves. The role of spiders in regulating herbivores is less studied than that of ants but may also be similarly significant.

APPENDIX B THREE-WAY ANOVA'S FROM CHAPTER SEVEN

Detailed Results From ANOVA's Summarised in Tables 7.1 and 7.2

From Table 7.1 are tables summarising three-way ANOVA's for a) Leaf Area, b) Leaf Dry Weight, c) Leaf Mass per Unit Area, d) Leaf Thickness and e) % water content.

From Table 7.2 are tables summarising three-way ANOVA's for f) chlorophyll concentration, g) chlorophyll content per leaf, h) nitrogen concentration, i) nitrogen content per leaf, j) phosphorus concentration and k) phosphorus content per leaf.

For all ANOVA's, there are two species (*A. marina* and *R. stylosa*), two sites (Gordon Creek and Saunders Beach) and five developmental stages (see 7.2.1). All ANOVA's were performed using SPSS 10.0.

A) Leaf Area

Source of Variation	**Sum of Squares**	**df**	**Mean Squares**	**F**	**P**
Species	42540.27	1	42540.27	3320.97	0
Site	677.08	1	677.08	52.85	7.33E-13
Leaf Stage	41956.3	4	10489.07	818.84	0
Species x Site	38.49	1	38.49	3.00	0.0833
Species x Stage	4634.72	4	1158.68	90.45	0
Site x Stage	360.68	4	90.17	7.039	1.38E-05
Species x Site x Stage	293.64	4	73.41	5.73	0.000147
Error	12553.4	980	12.80		
Total	380655.8	1000			

B) Leaf Dry Weight

Source of Variation	**Sum of Squares**	**df**	**Mean Squares**	**F**	**P**
Species	56.77	1	56.77	2908.40	0
Site	0.78	1	0.780	39.97	3.92E-10
Leaf Stage	52.67	4	13.17	674.52	0
Species x Site	0.016	1	0.016	0.822	0.365
Species x Stage	12.51	4	3.129	160.30	0
Site x Stage	0.55	4	0.139	7.14	1.14E-05
Species x Site x Stage	0.27	4	0.069	3.55	0.0068
Error	19.13	980	0.019		
Total	354.37	1000			

C) Leaf Mass per Unit Area

Source of Variation	Sum of Squares	df	Mean Squares	F	P
Species	13260.38	1	13260.38	695.50	0
Site	188.48	1	188.48	9.88	0.0017
Leaf Stage	15235.85	4	3808.96	199.77	0
Species x Site	157.58	1	157.58	8.26	0.0041
Species x Stage	1359.21	4	339.80	17.82	3.9E-14
Site x Stage	74.88	4	18.72	0.98	0.416
Species x Site x Stage	437.80	4	109.45	5.74	0.00014
Error	18684.52	980	19.06		
Total	677848.3	1000			

D) Leaf Thickness

Source of Variation	Sum of Squares	df	Mean Squares	F	P
Species	0.803	1	0.803	71.34	1.11E-16
Site	0.154	1	0.154	13.73	0.0002
Leaf Stage	1.819	4	0.454	40.40	0
Species x Site	0.0034	1	0.0034	0.303	0.581
Species x Stage	0.155	4	0.038	3.440	0.008
Site x Stage	0.036	4	0.009	0.800	0.525
Species x Site x Stage	0.022	4	0.006	0.501	0.734
Error	11.030	980	0.011		
Total	50.74	1000			

E) Leaf % Water Content (data arcsin transformed)

Source of Variation	Sum of Squares	df	Mean Squares	F	P
Species	862.61	1	862.61	315.38	0
Site	22.07	1	22.07	8.07	0.005
Leaf Stage	687.55	4	171.89	62.85	0
Species x Site	5.86	1	5.87	2.15	0.144
Species x Stage	917.00	4	229.25	83.82	0
Site x Stage	27.89	4	6.97	2.55	0.041
Species x Site x Stage	13.57	4	3.39	1.24	0.295
Error	508.73	186	2.74		
Total	553841.6	207			

F) Leaf Chlorophyll Concentration (data arcsin transformed)

Source of Variation	Sum of Squares	df	Mean Squares	F	P
Species	21.28	1	21.28	9.81	0.0020
Site	0.246	1	0.246	0.113	0.736
Leaf Stage	944.34	4	236.09	108.90	0
Species x Site	26.95	1	26.95	12.43	0.0005
Species x Stage	35.32	4	8.83	4.07	0.0034
Site x Stage	6.25	4	1.56	0.72	0.579
Species x Site x Stage	19.39	4	4.85	2.24	0.067
Error	390.21	180	2.168		
Total	5625.36	200			

G) Chlorophyll Content per Leaf

Source of Variation	Sum of Squares	df	Mean Squares	F	P
Species	26060.11	1	26060.11	258.57	0
Site	240.94	1	240.93	2.39	0.124
Leaf Stage	54626.03	4	13656.51	135.50	0
Species x Site	628.14	1	628.14	6.23	0.013
Species x Stage	17586.95	4	4396.74	43.62	0
Site x Stage	547.50	4	136.87	1.36	0.250
Species x Site x Stage	1047.13	4	261.78	2.59	0.038
Error	18141.39	180	100.78		
Total	205945.8	200			

H) Leaf Nitrogen Concentration (data arcsin transformed)

Source of Variation	Sum of Squares	df	Mean Squares	F	P
Species	127.28	1	127.28	1007.08	0
Site	0.519	1	0.519	4.11	0.044
Leaf Stage	263.46	4	65.87	521.15	0
Species x Site	3.36	1	3.356	26.56	6.49E-07
Species x Stage	8.16	4	2.040	16.14	2.29E-11
Site x Stage	1.879	4	0.469	3.718	0.006
Species x Site x Stage	0.568	4	0.142	1.124	0.346
Error	23.51	186	0.126		
Total	8334.39	207			

I) Nitrogen Content per Leaf

Source of Variation	**Sum of Squares**	**df**	**Mean Squares**	**F**	**P**
Species	0.12	1	0.1245	316.84	0
Site	0.031	1	0.0315	80.16	4.44E-16
Leaf Stage	0.381	4	0.0954	242.80	0
Species x Site	0.017	1	0.0171	43.55	4.47E-10
Species x Stage	0.029	4	0.0074	18.97	4.96E-13
Site x Stage	0.0027	4	0.0007	1.76	0.139
Species x Site x Stage	0.0035	4	0.00087	2.21	0.069
Error	0.0707	180	0.00039		
Total	2.932	200			

J) Leaf Phosphorus Concentration (data arcsin transformed)

Source of Variation	**Sum of Squares**	**df**	**Mean Squares**	**F**	**P**
Species	8.62	1	8.620	282.99	0
Site	3.16	1	3.160	103.75	0
Leaf Stage	35.05	4	8.762	287.68	0
Species x Site	1.85	1	1.854	60.89	4.22E-13
Species x Stage	1.57	4	0.392	12.90	2.73E-09
Site x Stage	0.03	4	0.008	0.26	0.900
Species x Site x Stage	0.18	4	0.046	1.52	0.198
Error	5.66	186	0.030		
Total	701.41	207			

K) Phosphorus Content per Leaf

Source of Variation	**Sum of Squares**	**df**	**Mean Squares**	**F**	**P**
Species	3.36	1	3.356	605.95	0
Site	1.65	1	1.6543	298.65	0
Leaf Stage	2.17	4	0.5426	97.96	0
Species x Site	0.765	1	0.7650	138.11	0
Species x Stage	0.220	4	0.0549	9.92	2.8E-07
Site x Stage	0.140	4	0.0352	6.36	8.28E-05
Species x Site x Stage	0.088	4	0.0220	3.97	0.004
Error	0.997	180	0.005		
Total	33.51	200			