

Effects of artificial defoliation on growth, reproduction and leaf chemistry of the mangrove *Kandelia candel*

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Abstract: The effects of defoliation on leaf and propagule production, and leaf chemistry of the mangrove *Kandelia candel* (L.) Druce were evaluated in a manipulative experiment in Hong Kong. Artificial defoliation of leaf lamina at 50% of the length of midrib resulted in significant reduction in leaf, twig and propagule production, and size of the latter. Through the negative effects on propagule number and size, severe herbivory may influence fitness of the mangrove, and, thus, community structure. In contrast, no apparent adverse effects on growth and production were observable at 25% defoliation. Defoliation also significantly affected leaf chemistry of the trees, particularly those suffering 50% defoliation. Concentrations of soluble tannins and carbohydrates in leaves were significantly lower at 50% defoliation compared with the control. Total nitrogen also decreased significantly with increased per cent defoliation. Plants surviving in stressful habitats, such as mangroves, are probably more affected by loss of leaf biomass than those surviving in favourable environments.

Key Words: artificial defoliation, herbivory, *Kandelia candel*, leaf chemistry, mangrove, propagule production

INTRODUCTION

Herbivory can alter plant fitness by exerting effects on growth and reproduction (Crawley 1989, Kulman 1971, Obeso 1993). Data that substantiate these findings mainly come from either artificial defoliation or herbivore exclusion experiments. Mostly, the effects are negative for the plant (Anderson & Lee 1995, Ang *et al.* 1994, Heichel & Turner 1984, Lowman & Heatwole 1987, Rockwood 1973, Stone & Bacon 1995) but, in some cases, they can recover from the damage without any change in growth and reproduction (Lim & Turner 1996, Lubbers & Lechowicz 1989). There may even be overcompensation for the lost biomass (Hjalten *et al.* 1994, McNaughton 1986). These findings suggest that the effects of herbivory on plant growth and reproduction are subtle and deserve further investigation. Changes in plant growth and reproduction following herbivore attack have significant implications for the competitive fitness of plants in natural communities. Studies on insect–plant interactions have suggested that alterations in plant competitive relationships through selective herbivory can accelerate changes in community structure and development (Crawley 1989,

Schowalter *et al.* 1981, 1986; Seastedt & Crossley 1984, Springett 1978, Weis & Berenbaum 1989).

Although several incidences of high levels of herbivory in mangroves have been reported in recent decades (Anderson & Lee 1995, Murphy 1990, Pikakarnchana 1981, Whitten & Damanik 1986), assessments of the effects of herbivory on growth and reproduction remain scarce. Anderson & Lee (1995) reported that regular, severe, defoliation of the mangrove *Avicennia marina* by the larvae of *Nephoterix syntaractis* (Lepidoptera: Pyralidae) in Hong Kong could significantly lower reproductive output. Ozaki *et al.* (1999) documented that attack by the scale insect *Aulacaspis marina* on *Rhizophora mucronata* saplings could result in mortality 82–159 d after infestation. However, these studies did not assess the effects of herbivory on mangrove growth (e.g. leaf production). Mangroves live in an environment that is stressful to higher plants. There is, therefore, a strong pressure to conserve resources, and the response of mangroves to severe herbivory damage would have significant implications for survival in this energy-demanding habitat.

Physical damage to leaves by insects has been shown to affect plant species adversely (Edwards & Wratten 1986, Edwards *et al.* 1986, Gibberd *et al.* 1985, Haukioja & Niemela 1979, Silkstone 1987, Wratten *et al.* 1984). There is increasing evidence that effects induced by

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herbivore attack can be attributed mainly to changes in leaf chemistry, including decreases in nutrient levels and increases in levels of secondary chemicals (Edwards & Wratten 1986, Feeny 1970, Schultz & Baldwin 1982, Tuomi *et al.* 1988, Webb 1980, Wold & Marquis 1987). Insect-induced changes in plant chemistry have received the particular attention of scientists not only because they are regarded as a process leading to co-evolution (Ehrlich & Raven 1964) but they may also be mechanisms by which insects affect ecosystem nutrient cycling (Choudhury 1988).

The aim of this study was to investigate the effects of different levels of herbivory loss on growth, reproductive output and leaf chemistry of the mangrove *Kandelia candel* by means of an artificial defoliation experiment. We hypothesized that severe defoliation would have greater effects on growth, leaf chemistry and reproduction than moderate defoliation in *K. candel*. Although this method is essentially different from natural herbivory as interactions through saliva and frass production by the herbivore are absent (Agrawal 1998, Baldwin 1990, Stowe *et al.* 2000), it is comparatively less time consuming and allows better control of treatment levels. The extent of damage can be controlled easily, and kept constant across replicates.

MATERIALS AND METHODS

Effects of artificial defoliation on *Kandelia candel*

The defoliation experiment was undertaken in the *Kandelia candel* mangal at Ting Kok, north-east Hong Kong (22°28'N, 114°13'E). Nine trees of similar size were selected (girth: 25–30 cm, height: 1.6–1.8 m) in order to minimize age and other variations among them. Three trees per group were randomly assigned to one of the following treatments: control and one of two levels of artificial defoliation, i.e. 25% (the leaf lamina removed for the distal 1/4 of the long leaf axis) and 50% (1/2 of the long axis of each leaf removed). Levels of herbivory on *K. candel* are usually low (< 10%; Lee 1991) and the artificial damage levels were targeted at simulating massive defoliation events. Defoliation has been recorded for a sympatric mangrove species *Avicennia marina* (Anderson & Lee 1995) by a moth *Nephoterix sintaractis*, making this mangrove species unsuitable for the present experiment (because of the variable background herbivory levels). Defoliation was started in early June, at the period of flowering, and was finished within a period of 3 wk.

Effects of defoliation treatment on the growth of *Kandelia candel* were assessed by comparing the production rates of leaves and twigs, and the percentage increase in trunk diameter (dbh) of the control and experimental trees. Assessment of the production rates of leaves and twigs

were conducted by using the same methods for assessment of the turnover factors of the leaf and twig as described in Lee (1991). Ten shoots per tree were tagged randomly in April 1994. Changes in these shoots 1 y after treatment were recorded. The production rates/turnover factors were expressed as the ratio of leaves/twigs after 1 y to the initial value, using trees as replicates. Comparisons of the production rates of the control and experimental trees before treatment were not possible due to time constraints with this experiment. Tong (1998) has, however, shown that the turnover factors for leaves and twigs of *K. candel* at Ting Kok were both equal to 2.6×. It was therefore assumed that the production rates of the leaves and twigs of the control and experimental trees before the treatment were also equal to 2.6×. Percentage increases in trunk diameter of the trees were determined by measuring them at different points around the trunk at breast height (1.3 m, dbh) to the nearest 0.1 cm, before and 1 y after treatment.

To measure the effect of defoliation on the reproductive output of *Kandelia candel*, propagule production of the control and experimental trees were compared. Propagules of *K. candel* are cylindrical, and detach from the mother tree when mature after a 'gestation period' of about 8 mo and growth to < 25 cm. All the propagules detached from the control and experimental trees in 1994 and 1995, i.e. before and after treatment, were collected by litter traps. The litter traps used in this experiment were the enclosure type in which the entire tree was surrounded. Each enclosure was constructed by placing four 4-cm × 4-cm wooden stakes in the substratum, forming a polygon around the tree. Plastic screenings of mesh size 1 mm² were wrapped around the stakes enclosing the tree and around its trunk below the lowest branches. This setting formed an envelope around the experimental tree and caught only those propagules from it. The propagules inside the traps were collected during biweekly visits over the experimental period. These were washed and oven dried at 80 °C for 2 d. The numbers and mean dry weights of the propagules collected from each tree in 1994 and 1995 were recorded.

The effects of artificial defoliation on leaf chemistry were monitored. Pre-treatment foliage sampling was undertaken at the beginning of June. Triplicate samples of ten young leaves were removed randomly from each tree. Leaf samples were then oven dried at 40 °C for 24 h and analysed for total soluble tannins, total soluble carbohydrates and total nitrogen using methods described in Allen (1989). After treatment, leaf samples were collected monthly from July 1994 to February 1995 in the same way as described above and then subjected to chemical analysis.

Statistical analyses

One-way ANOVAs were used to compare the production rates of leaves and twigs of the three treatment groups

after treatment. In cases where significant differences between treatment groups were detected, Student Newman–Keuls multiple tests (SNK) were used to identify them (at $\alpha = 0.05$). Increases in trunk diameter of the three treatment groups were compared by analysis of covariance (ANCOVA) with the initial dbh of the trees as the covariate.

The difference in the number and mean dry weight of propagules produced by the three groups before and after treatment were compared by two-way ANOVAs with time and treatment as the factors. Thereafter, SNK multiple tests were used to identify the differences, if any.

All percentage data on leaf chemical contents were arcsine transformed prior to analysis in order to conform to the assumptions of normality and homoscedasticity for the ANOVA. The chemical contents of the three groups of trees before treatment were compared statistically using one-way ANOVA. After defoliation, the chemical contents of the leaves of the control and experimental trees were compared by repeated-measure ANOVAs, with time (month) as the repeated measure. Sphericity was accounted for in all repeated-measure ANOVAs by modifying degrees of freedom using the Geisser–Greenhouse approximation (Stevens 1999). Significant differences between treatments were identified using Bonferroni t-tests as the *post hoc* procedures. Statistical analyses were performed using SPSS for Windows, SPSS Inc.

RESULTS

Leaf and propagule production

The production rates of leaves and twigs of the control trees recorded in 1995 were comparable with those recorded at the same site. This finding implies that there were no remarkable changes in the production rates of leaves and twigs of the control trees 1 y after the commencement of the experiment. Significant differences in the production rates of leaves and twigs among groups were evident 1 y after defoliation (Table 1). Trees subjected to 50% defoliation showed a significant reduction in the production rates of leaves and twigs as compared with the control (SNK multiple test: $p = 2, q = 6, P < 0.05, p = 3, q = 5.1, P < 0.05$, respectively) and the 25%

defoliated trees ($p = 3, q = 16, P < 0.05, p = 2, q = 4.5, P < 0.05$, respectively). The leaf production rate of the 25% defoliated trees was significantly higher than that of the control ($p = 2, q = 10, P < 0.05$) but no significant difference in twig production rate was detected among these two treatment groups ($p = 2, q = 0.59, P > 0.05$). No significant differences were recorded in the percentage increases in trunk diameters among the treatment groups.

Results of the two-way ANOVAs show that the number and mean dry weight of the propagules produced by *Kandelia candel* were influenced by the degree of defoliation (Table 2). The higher the level of defoliation experienced by the trees, the fewer the number of propagules they produced and the lower their mean dry weight (Figure 1). Significant differences in the number of propagules were detected between the control and the 50% defoliated trees (SNK multiple test: $p = 3, q = 7.11, P < 0.05$) and between the 25% and 50% defoliated trees (SNK multiple test: $p = 2, q = 4.86, P < 0.05$). Significant difference in the mean dry weight of the propagules was found between the control and the 50% defoliated trees only (SNK multiple test: $p = 3, q = 4.38, P < 0.05$). In addition to the defoliation treatment, time and the interaction effects of these two factors could significantly influence the number and average dry weight of the propagules produced.

The pretreatment levels, i.e. levels measured in June, of total nitrogen, total soluble carbohydrates and total soluble tannins did not differ between the three groups of trees (one-way ANOVA: $F = 0.065, P = 0.94, F = 0.447, P = 0.66, F = 0.321, P = 0.74$, respectively; Figure 2). Shortly after the defoliation treatment, i.e. in July, differ-

Table 2. Results of two-way ANOVAs on the effects of defoliation and time on the number and the mean dry weight of propagules produced by *Kandelia candel*.

Source of variance	df	F	P
Number of propagules			
Treatment	2	13.2	< 0.001
Time	1	68.3	< 0.0001
Treatment × Time	2	6.61	0.012
Mean dry weight of propagules			
Treatment	2	4.86	0.028
Time	1	9.01	0.011
Treatment × Time	2	4.17	0.030

Table 1. The leaf and twig production rates and the percentage increase in trunk diameter of *Kandelia candel* that were subjected to three different levels of defoliation treatments. Production rates were expressed as the number of times of increase in the number of leaf or twig per shoot per year. Values are mean ± 1 SD.

Treatment	Parameters		
	Production rate of leaf	Production rate of twig	Increase in trunk diameter (%)
Control	2.4 ± 0.1	2.6 ± 0.2	3.1 ± 1.5
25% defoliation	3.4 ± 0.2	2.5 ± 0.1	3.3 ± 0.7
50% defoliation	1.8 ± 0.2	1.8 ± 0.2	2.9 ± 1.0
F	65.3	7.78	0.026
P	< 0.0001	0.022	0.97

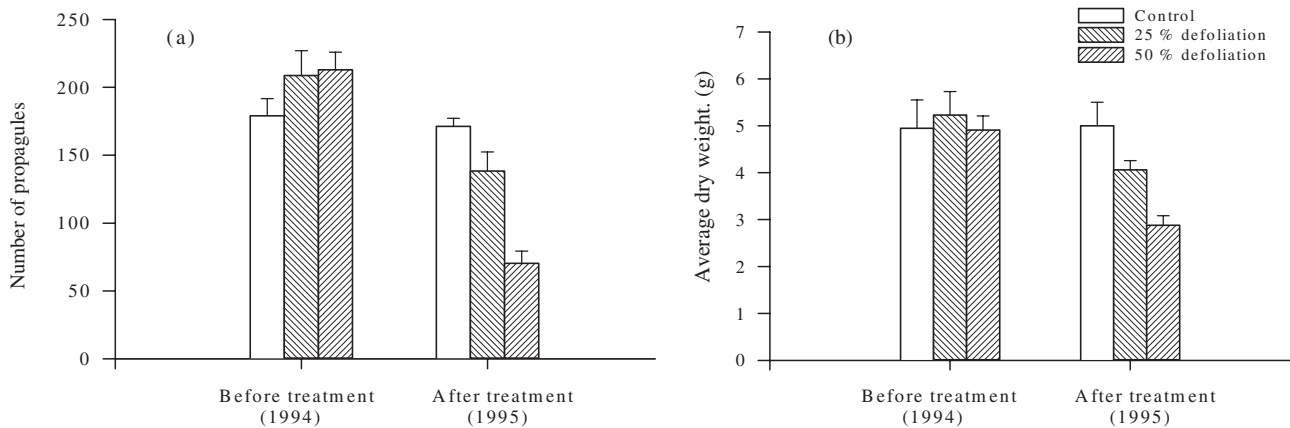


Figure 1. (a) Number and (b) average dry weight (g) of propagules collected from the control and defoliated trees before and after treatment. Values are mean + 1 SD.

ences in contents of total nitrogen, total soluble carbohydrates and total soluble tannins among the three treatment groups became obvious. Repeated-measure ANOVAs show that defoliation treatments had significant effects on the leaf chemical contents, as measured during the study period (nitrogen: $F = 32.2$, $P = 0.001$, carbohydrates: $F = 7.19$, $P = 0.026$, tannin: $F = 15.5$, $P = 0.004$, Table 3). Defoliation treatments (25% or 50%) caused reductions in the concentrations of all the measured leaf chemical parameters when compared with that of the control (Table 3). The higher the level of defoliation the trees experienced, the greater the decrease in concentrations of their leaf chemical contents. Differences in concentration of total soluble carbohydrates and total soluble tannins were, however, significant only between the control and the 50% defoliated trees (Bonferroni t-test: $t = 3.62$, $P < 0.05$, $t = 5.45$, $P < 0.05$, respectively) but not between the control and the 25% defoliated trees ($t = 0.82$, $P > 0.05$, $t = 2.70$, $P > 0.05$, respectively) or the 25% and 50% defoliated trees ($t = 2.79$, $P > 0.05$, $t = 02.75$, $P > 0.05$, respectively). Foliage concentration of total nitrogen differed significantly between the control and the 25% defoliated trees and between the control and the 50% defoliated trees (Bonferroni t-test: $t = 7.89$, $P < 0.05$, $t = 5.22$, $P < 0.05$, respectively) but not between the two groups of defoliated trees ($t = 2.67$, $P > 0.05$).

Significant effects of time on the total soluble carbohydrates and total soluble tannins of the treatment groups were shown even after the results had been adjusted by the Geisser–Greenhouse approximation ($F = 13.1$, Adj. $P = 0.0001$, $F = 28.0$, Adj. $P = 0.0001$, respectively) (Table 4b and c). There were, however, no clear patterns of change with time in these two parameters of the three treatment groups, as shown in Figures 2b and 2c. The interaction of treatment and time was significant for total soluble tannins ($F = 5.28$, Adj. $P = 0.002$) but not for total soluble carbohydrates ($F = 2.66$, Adj. $P = 0.052$). The effects of time and its interaction with treatment for total

nitrogen were also not significant ($F = 2.50$, Adj. $P = 0.123$, $F = 1.70$, Adj. $P = 0.213$, respectively, Table 4a).

DISCUSSION

Results of the present study demonstrated that defoliation could impact the growth of *Kandelia candel* differentially in accordance with the level of leaf area lost (Table 1). The treatment plants with 25% total leaf area removal did not differ significantly in the production of new twigs and growth in trunk diameter as compared with the control. The defoliation treatment, however, did significantly increase the production rate of new leaves by 41.7%. Increase in leaf initiation is probably a compensatory response by *K. candel* to moderate levels of insect herbivory (< 25%) so as to alleviate the potential deleterious effects of tissue loss. By comparing the degree of damage of leaves in litter traps and on the canopy, Lee (1990) concluded that herbivory probably reduced leaf longevity of *K. candel*, a result that was supported by an artificial damage experiment (Lee 1991). Compensatory plant growth in response to herbivory has already been reported for a large variety of plants of different taxonomic origins and habits (Doak 1992, Escarre *et al.* 1996, Harrison & Maron 1995, Lim & Turner 1996, Marquis 1984, Oba 1994, Schierenbeck *et al.* 1994). In this study, the mechanisms involved in the compensatory response of *K. candel* are not known, although resource allocation is certainly altered as a result of defoliation. A plant's temporal variation in allocation can have important consequences for either the ultimate gain or loss of its resources and subsequently define its ecological role and distribution (Bazzaz *et al.* 1987). The adaptive response to reallocate more resources for leaf production can be beneficial to the mangroves in at least three ways. First, an increase in leaf production can speed up the replacement of lost tissues and ensure future photosynthetic production. Second, as leaves of *K. candel* are important in the process of salt

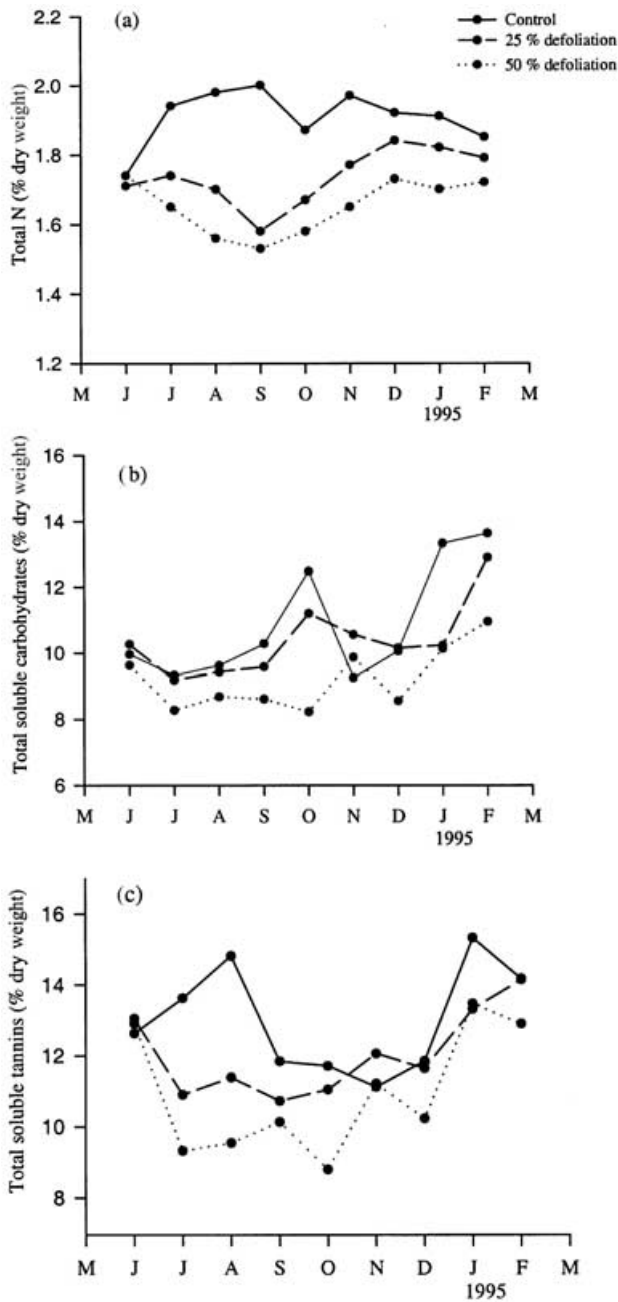


Figure 2. Variations in the mean concentration of (a) total nitrogen; (b) total soluble carbohydrates; (c) total soluble tannins in the leaves of *Kandelia candel* collected from defoliated and control trees. Error bars have been omitted for clarity.

Table 3. Chemical concentrations in the leaves of *Kandelia candel* from the control and experimental trees after defoliation. Values are means of the data taken from July 1994 to February 1995 (± 1 SE).

Chemical concentration (%)	Treatment		
	Control	25% defoliation	50% defoliation
Tannins	13.1 \pm 0.6	11.9 \pm 0.4	10.7 \pm 0.6
Carbohydrates	11.0 \pm 0.7	10.4 \pm 0.4	9.2 \pm 0.4
Nitrogen	1.93 \pm 0.02	1.74 \pm 0.03	1.64 \pm 0.03

Table 4. Results of repeated-measure analysis of variance on the percentage of (a) total nitrogen, (b) total soluble carbohydrates and (c) total soluble tannins in leaves of *Kandelia candel* from experimental and control trees.

(a) Total nitrogen

Source of variance	df	Between subjects		Adj. P (G-G)
		F	P	
Treatment	2	32.2	0.001	
Error	6			
Source of variance	df	Within subject		Adj. P (G-G)
		F	P	
Time	7	2.50	0.031	0.123
Treatment \times Time	14	1.70	0.092	0.213
Error	42			

Greenhouse-Geisser $\epsilon = 0.289$

(b) Total soluble carbohydrates

Source of variance	df	Between subjects		Adj. P (G-G)
		F	P	
Treatment	2	7.19	0.026	
Error	6			
Source of variance	df	Within subject		Adj. P (G-G)
		F	P	
Time	7	13.1	0.0001	0.0001
Treatment \times Time	14	2.66	0.007	0.0520
Error	42			

Greenhouse-Geisser $\epsilon = 0.420$

(c) Total soluble tannins

Source of variance	df	Between subjects		Adj. P (G-G)
		F	P	
Treatment	2	15.5	0.004	
Error	6			
Source of variance	df	Within subject		Adj. P (G-G)
		F	P	
Time	7	28.0	0.0001	0.0001
Treatment \times Time	14	5.28	0.0001	0.002
Error	42			

Greenhouse-Geisser $\epsilon = 0.477$

excretion, the rapid replacement of lost tissues is essential to ensure the adaptability of the mangroves to the saline habitat. Increases in leaf production may also lead to over-compensation and possibly increase the fitness of the affected plants.

The ability of plants to regrow has also been suggested

as an alternative defence strategy in the struggle against herbivores (van der Meijden *et al.* 1988). A plant's susceptibility and response to herbivory, however, is plastic and varies according to the biotic and abiotic conditions it experiences (Ang *et al.* 1994, Foggo 1996, Lim & Turner 1996, Maschinski & Whitham 1989, McKillup & McKillup 1997, Trlica & Rittenhouse 1993). In this study, the treatment plants subjected to 50% defoliation did not show any additional compensatory response to replace the lost tissues. Instead, leaf and twig production rates were significantly reduced by 25% and 30% respectively, as compared with the control (Table 1). The increment in trunk diameter of the 50% defoliated plants was lower in magnitude than that of the other treatment groups, although statistical analysis did not indicate a significant treatment effect. These findings suggest that the growth of *Kandelia candel* in Hong Kong can be hampered by a high level of herbivory, even a single attack. The fact that mangroves survive in habitats generally stressful to higher plants means that severe defoliation may have strong fitness implications for the trees. In cases of severe and repeated defoliation, as reported from other mangroves, e.g. *Avicennia alba* in Thailand (Pikakarnchana 1981), *Excoecaria agallocha* in Indonesia (Whitten & Damanik 1986), *Avicennia marina* in Hong Kong (Anderson & Lee 1995), there may well be loss of tree vigour and the mangroves may become more susceptible to other stresses such as increases in salinity and flooding (Grace & Ford 1996).

The reproductive output of *Kandelia candel* was apparently impaired 1 y after defoliation (Figure 1, Table 2). The number of propagules produced by the defoliated trees decreased as the percentage of leaf area lost increased, indicating that reproductive output of *K. candel* may be dependent on leaf area. At a high level of defoliation, i.e. 50%, the mean number of propagules produced by the defoliated trees was significantly different from that of the controls, by ~60%. Reduction in seed production after defoliation strongly suggests that there is a limitation in the availability of carbohydrates (Crawley 1983). Viviparous trees, such as *K. candel*, are expected to invest a large proportion of their photosynthate in seed production because of the long gestation period (*c.* 8 mo in *K. candel*) and large propagule size. Mature propagules of *K. candel* have the same energy content (18.3 kJ g⁻¹ dry weight; S. Y. Lee, unpubl. data) as other components of the mangrove litter but contribute to about 40% of total litter fall of the species (Lee 1989). After defoliation, competition for growth and reproduction resources may occur. To ensure survival and fitness and to regain a competitive status, the best strategy for recovery from defoliation is always to produce as nearly normal a photosynthetic machinery as possible (Hodkinson & Hughes 1982). Resources allocated to reproduction will, therefore, be diminished. In a similar study, Anderson & Lee (1995)

showed that leaf regeneration of *Avicennia marina* after being attacked by the larvae of *Nephoterix syntaractis* (Lepidoptera: Pyralidae) was rapid, being achieved within 3 mo of defoliation, but reproduction was seriously impaired. They showed that reproduction only occurs in years in which defoliation is absent or less severe.

In addition to the suppression of propagule production, the mean size of the propagules on those plants that had experienced a high level of defoliation, i.e. 50%, was significantly reduced (Figure 1b). Studies on the impact of insect herbivory on seed production are many but the effects on their mass are often neglected. Among the few studies which report upon this, it has been shown that a plant's seed mass can be increased, e.g. *Erythroxylum havanense* (Dominguez & Dirzo 1994), *Raphanus sativus* (Agrawal 1998); decreased, e.g. *Acacia farnesiana* (Rockwood 1973), *Vicia hirsuta* (Brown *et al.* 1987) or remain unaffected, e.g. *Vicia sativa* (Brown *et al.* 1987) as a consequence of defoliation, indicating that effect varies with species. Although smaller propagules will still germinate, seedling establishment may be impaired, particularly in viviparous species, such as many mangroves. Lin & Sternberg (1995) argued that seedlings of *Rhizophora mangle* from large propagules may have a greater chance of success in early establishment than those from smaller ones because of the former's better capability to grow and fix carbon dioxide. In addition to direct seed predation (Robertson 1991, Robertson *et al.* 1990, Smith *et al.* 1989), the present findings collectively suggest that species-specific insect herbivory, especially under a severe attack, may influence the community structure and development of mangroves through detrimental effects on the quantity and quality of propagule production.

The data in the present study provide evidence that herbivory damage on the mangrove *Kandelia candel* can lead to changes in leaf chemistry including the levels of nutrients and secondary chemicals. As changes in leaf chemistry after wounding have been shown to have adverse effect on insect performance in many plant species, there is a tacit assumption in plant-herbivore studies that deterioration in leaf quality upon herbivore attack may actually represent an active defence by plants against insect herbivores (Edwards & Wratten 1986, Edwards *et al.* 1986, Rhoades 1979). Although nutrient concentrations in the regenerated foliage of *Kandelia candel* were shown to decrease after defoliation, the concentration of total soluble tannins, which is commonly regarded as an insect-deterrent, also decreased. As such, it seems that the idea of short-term active plant defensive responses induced by herbivory does not apply to *K. candel*. In fact, the lack of a plant response in the production of secondary chemicals to herbivore attack has also been recorded in other studies (Hjalten *et al.* 1994, Perebolotsky 1994), indicating that such a notion is still equivocal. Although the concentrations of tannin were lower in the foliage after defoliation,

it is anticipated that the defoliated plants would be less attractive to subsequent attack by insect herbivores for two reasons. First, the insect herbivores may avoid feeding on the regenerated leaves of the treatment plants as the decrease in nutrients, especially nitrogen, may delay the herbivores' development and lead to increased mortality (Mattson 1980, Slansky 1993, Wratten *et al.* 1988). Low plant nutritive quality may probably have evolved in part as a defence against herbivores (Moran & Hamilton 1980). Second, Tong (1998) has shown that there were differences in the contents of sodium, chloride, ash and crude fibre of *K. candel* leaves between two mangrove forests with different growth conditions. Such differences suggest that these chemicals may have potential deterrent effects on insect herbivores. Therefore, even though the foliage concentration of tannins was decreased after treatment, the defensive ability of the defoliated plants may not be weakened. The combined effect of poor nutrient level and the presence of deterrents may render regenerated leaves less palatable to insect herbivores. The changes in *K. candel* leaf chemistry after herbivory may protect the plant from chronic attack and hence allow regrowth.

Alternatively, the observed changes in leaf chemistry following defoliation could simply be a response dictated by the need to adjust the nutrient and energy allocation pattern of the trees to cope with the damage. It is also possible that the trees responded in producing defensive compounds that were not examined in this study. Chemical responses to herbivory in mangroves are poorly known. Feller (1995) recorded no effect of nutrient (C:N) ratio or concentrations of phenolics on the degree of herbivory on dwarf *Rhizophora mangle* trees, a result in contradiction with the earlier finding of Onuf *et al.* (1977). Farnsworth & Ellison (1993), however, documented a significant effect of prior damage on subsequent herbivory level in *R. mangle* and *Avicennia germinans* in Belize, suggesting that the response of mangroves to herbivory is probably complex. More data on herbivory on mangroves in different nutrient and growth conditions are needed before an assessment of the general response pattern can be established.

Foliage concentrations of nitrogen and carbohydrates in *Kandelia candel* were shown to decrease after defoliation. As the defoliation level increased, both foliage concentrations of nitrogen and carbohydrates were significantly diminished. Such significant decreases in foliage nutrients in response to defoliation treatment suggest that the same process by insect herbivores is likely to have negative impact on the nutrient budget of *K. candel*. The effects of defoliation on the nutrient budget of plants have been investigated in other studies. For example, May & Killingbeck (1995) reported that defoliation of *Quercus ilicifolia* by gypsy moth larvae (*Lymantria dispar*) caused a pronounced increase in the re-absorption of zinc and

copper from senesced leaves and suggested that such changes represent a response to nutrient deficiencies induced by defoliation. Carbohydrate content in *Pinus sylvestris* foliage of different ages (Ericsson *et al.* 1980) and starch contents in all vegetative parts of the conifers *Abies concolor* and *Pseudotsuga menziesii* (Webb 1980) were shown to be reduced as a result of defoliation, which clearly reflects a shortage of these nutrients on a whole-tree basis. Such herbivory-induced effects are understandable because removal of biomass by herbivores always means a loss of nutrients from the plant. Effects of defoliation on plant nutrient budgets are more severe in evergreens than deciduous species. This is because the former, such as *K. candel* (Lin & Lin 1990), usually store a much larger proportion of the total plant nutrient capital in their leaves than the latter group (Chapin 1980, Chapin *et al.* 1980, Mooney 1972), which leads to a rapid depletion in nutrient resources when herbivores consume the leaves. Rapid replenishment of nutrients by an increased nutrient uptake is unlikely as the mangrove ecosystem is usually nutrient limited, particularly with respect to nitrogen (Alongi *et al.* 1992, Clough *et al.* 1983, Onuf *et al.* 1977) and loss of photosynthetic tissues will diminish the production of photosynthate. Therefore, the nutrient loss upon herbivory, followed by a demand for additional nutrients for production of secondary leaves and repair, may adversely affect the mangrove nutrient budget and cause the plant to spend a long time recharging its nutrient resources. This herbivory-induced effect may limit the availability of nutrients to the various physiological processes of the plant.

In conclusion, as there are no apparent adverse impacts on the growth and reproductive output of the mangrove *Kandelia candel* with 25% defoliation, insect herbivory at nominal and medium levels is unlikely to affect the overall fitness of the plant. At either severe (> 50%) or repeated levels of defoliation, however, the overall fitness of the mangrove may be impaired through deleterious effects on growth and reproduction. Leaf quality in *K. candel* is generally depleted in response to herbivory and such changes become intensified as the level increases. These herbivore-induced effects may have significant implications for community dynamics.

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