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Studies of a Mangrove Basin, Tuff Crater, New Zealand: I. Mangrove Biomass and Production of Detritus

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The mangrove, *Avicennia marina* var. *resinifera* in a tidally-flooded explosion crater, Tuff Crater, near the southern latitudinal limit of mangroves in New Zealand adopts two distinct growth forms, taller tree-like mangroves up to 4 m tall along the banks of the tidal creek, and low stunted shrub mangroves less than 1 m tall on the mudflats. Twelve trees were felled and on the basis of a biomass/height relationship for the taller trees and a biomass/canopy width relationship for the lower, above-ground biomass (excluding pneumatophores) was estimated. Average above-ground biomass for the taller mangrove was estimated to be 104·1 t ha^{-1} and for the lower 6·8 t ha^{-1}. While the value for the taller mangroves is similar to figures reported for more complex tropical mangroves, the fact that 94% of the basin is covered by low generally sparse mangroves means that total biomass for the basin is estimated to be 153 t, an average of only 7·6 t ha^{-1}. Litter-fall beneath the taller mangroves is estimated as $7{\cdot}6 \pm 2{\cdot}5$ t ha^{-1} a^{-1} and beneath the lower mangroves $3{\cdot}3 \pm 0{\cdot}5$ t ha^{-1} a^{-1}. The value for the taller mangroves is similar to that reported from mangroves in many other parts of the world, but because of the extensive low sparse mangroves the total for the basin is estimated as 53·7 t a^{-1}, an average rate of 2·7 t ha^{-1} a^{-1}, a very low rate of litter-fall when compared with elsewhere. Decomposition of mangrove leaves occurs relatively rapidly with leaves losing half their dry weight in 10 weeks and then continuing to degrade but at a slower rate. Substrate sediment samples contain high organic matter content, and although some organic matter appears to be exported via the tidal creek, a proportion of the detrital production is evidently recycled *in situ*.

Introduction

Coastal wetlands, comprising both salt marshes and mangrove swamps, are considered to be areas of high primary productivity which support economically important detrital-based marine food webs. Considerably more work has been done on the structure and functioning of salt marsh ecosystems and their role as sources or sinks of organic matter (Nixon, 1980), than has been done on mangrove ecosystems. Nutrient cycling occurs, in mangrove swamps as in other terrestrial ecosystems, with the uptake of nutrients by the plant roots and incorporation during photosynthesis into the mangrove biomass. Biomass is lost by the fall of litter and this decomposes releasing nutrients which can be recycled. In terrestrial ecosystems this nutrient cycle may be essentially closed, but in mangrove swamps it is open with exchange of nutrients, detritus and sediment facilitated by tidal flushing (Lugo *et al.*, 1976). Significant export of mangrove detritus to the adjacent estuary has been demonstrated in Florida (Heald, 1969; Odum & Heald,

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1972), and in Queensland, Australia (Boto & Bunt, 1981). However the relative proportions of detritus which are degraded and recycled *in situ* and which are exported from the system are not well understood.

This paper examines the above-ground biomass and productivity of a monospecific stand of the New Zealand mangrove, *Avicennia marina* var. *resinifera,* in a basin formed within a volcanic crater in Shoal Bay, Waitemata Harbour, Auckland, close to the southern latitudinal limit of mangroves. The rate of breakdown and incorporation of mangrove tissues into the sediment is discussed. Subsequent papers examine methods of estimating tidal flux in the basin and report observations on the exchange of particulate matter from the mangroves.

Materials and methods

Area of study

The Tuff Crater basin is an old volcanic explosion crater, with a surface area of 21·6 ha, on the western margin of Shoal Bay, Waitemata Harbour, Auckland (36°48′S, 174°45′E). The crater walls are composed of unbedded tuffs which overlie white, plastic clays and silts and interbedded peats of the Whau Formation (Searle, 1959). The basin is connected to Shoal Bay by a breach in the crater walls to the east and inundation of the basin has been accompanied by infilling with marine sediments. The basin is almost entirely covered with the mangrove, *Avicennia marina* (Forsk.) Vierh. var. *resinifera* (Forst.) Bakh. (Figure 1). The construction of the Northern Motorway (1958–1959) has further isolated the basin from Shoal Bay and flooding of the mangrove occurs through a tidal creek which flows through a culvert beneath the motorway.

Flooding of the basin is dominated by the semidiurnal tides; freshwater input is minimal There is an ephemeral stream draining into the northern end of the basin and some storm water runoff, but due to the steep crater walls the catchment area is small.

The average tidal range in the Waitemata Harbour is 2·69 m at springs and 1·99 m at neaps. The culvert does not allow the full volume of the highest tides to enter so that water levels at high tide remain lower in Tuff Crater than in Shoal Bay.

Methods

Above-ground mangrove biomass was calculated by felling 12 trees from similar habitats in the Whangateau and Manukau Harbours and determining the biomass of each. These trees were divided into trunk plus branch, and leaf plus inflorescence components and the fresh weight of both components was measured. Subsamples were then dried at 100 °C and dry weights were recorded.

The heights and densities of mangroves in Tuff Crater were mapped initially from black and white aerial photographs at a scale of 1 : 3075 taken on 25 January 1981. Ground control was used to confirm classes and the point-centred quarter method (Mueller-Dombois & Ellenberg, 1974) employed to measure tree density and determine total above-ground biomass.

Litter-fall was determined over the period from 4 November 1980 to 2 November 1982 using the methods described by Woodroffe (1982). In the taller mangrove 8 litter traps, approximately 45 cm × 45 cm and made of 2-mm Sarlon shade cloth, were deployed. In 1980–1981 the total sampling area was 1·60 m^2 and after replacement by new traps in 1981–1982 the sampling area was increased to 1·80 m^2. In the lower

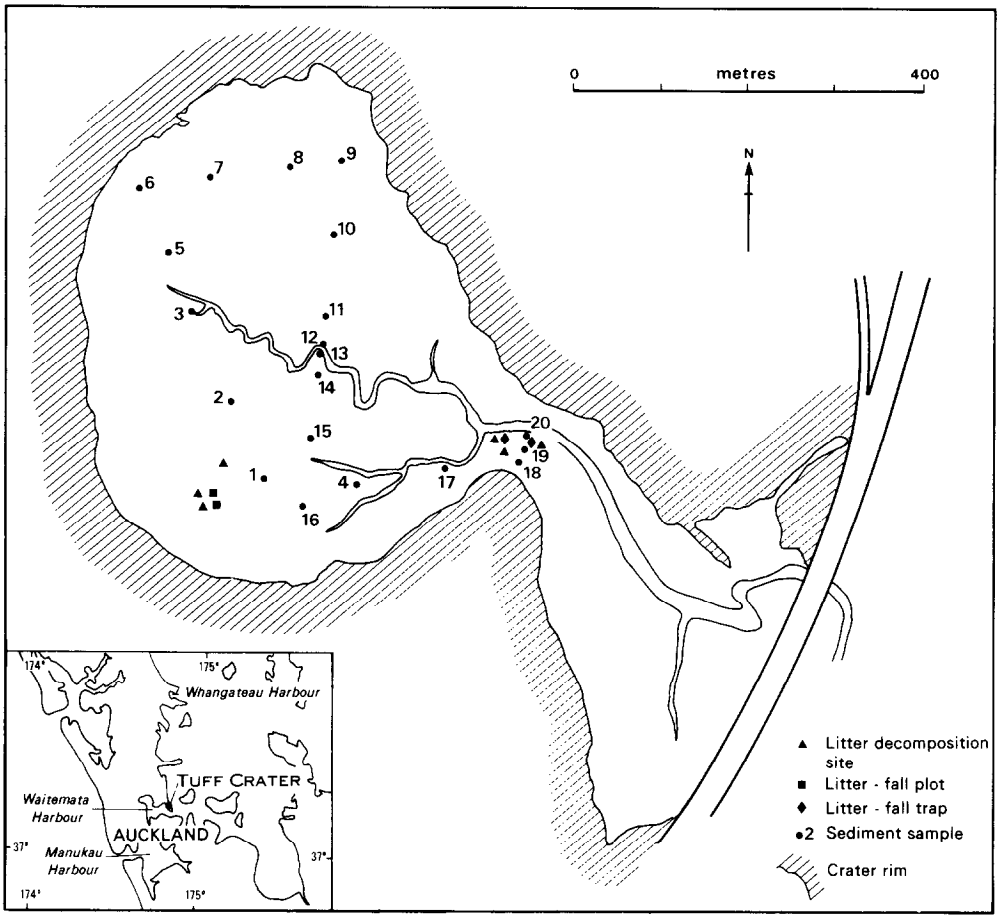

Figure 1. Location of Tuff Crater showing sites of litter-fall traps and plots, decomposition studies, and sediment samples.

mangrove 2 litter plots were fenced off, sampling a total area of 7·30 m^2 (Figure 1). Litter was collected from traps and picked from the substrate surface in the plots fortnightly, dried at 90 °C for 2 days and then the dry weight of the components was determined.

Shoot extension measurements were made on three shoots on each of 12 trees by measuring the length from the shoot apex to the sixth node back, marking that node, and remeasuring the length after one year.

The decomposition of litter was studied using litter decomposition bags (Goulter & Allaway, 1979; Woodroffe, 1982)—30 g (fresh weight) of leaves were placed in bags, 16 cm × 16 cm of 2-mm Sarlon shade cloth, with 13 bags placed at each site (Figure 1) and one bag collected fortnightly. Sediment accumulated in the bags and in order to determine leaf material remaining it was necessary to ash samples in a muffle furnace at 600 °C and ash free weights were used to calculate decomposition rate.

Surface sediment samples were collected and oven-dried at 105 °C. Combustible organic matter was determined by weight loss on ignition in a muffle furnace at 600 °C for 30 min. Total organic carbon was measured using a LECO carbon analyser. Total

Kjeldahl nitrogen and total phosphate were determined using an autoanalyzer on 0·5 g of dry sediment digested by a TKN digest containing a selenium catalyst.

Results

Mangrove biomass

Of the total basin area of Tuff Crater approximately 1·0 ha around the periphery is covered by salt marsh composed of *Leptocarpus similis* Edgar and *Juncus maritimus* Lam. var. *australiensis* Buchenau, and approximately 0·4 ha is tidal creek. The remaining 20·2 ha are covered by the mangrove *Avicennia marina* (Forsk.) Vierh. var. *resinifera* (Forst.) Bakh.

The mangroves have been mapped into 5 classes according to height and density (Figure 2). Mangroves of the creek banks are up to 4·0 m tall, are tree-like, and form a band 10–20 m wide. The physiognomic distinction between these and stunted recumbent shrub mangroves, less than 1·0 m tall, of the mudflats is pronounced.

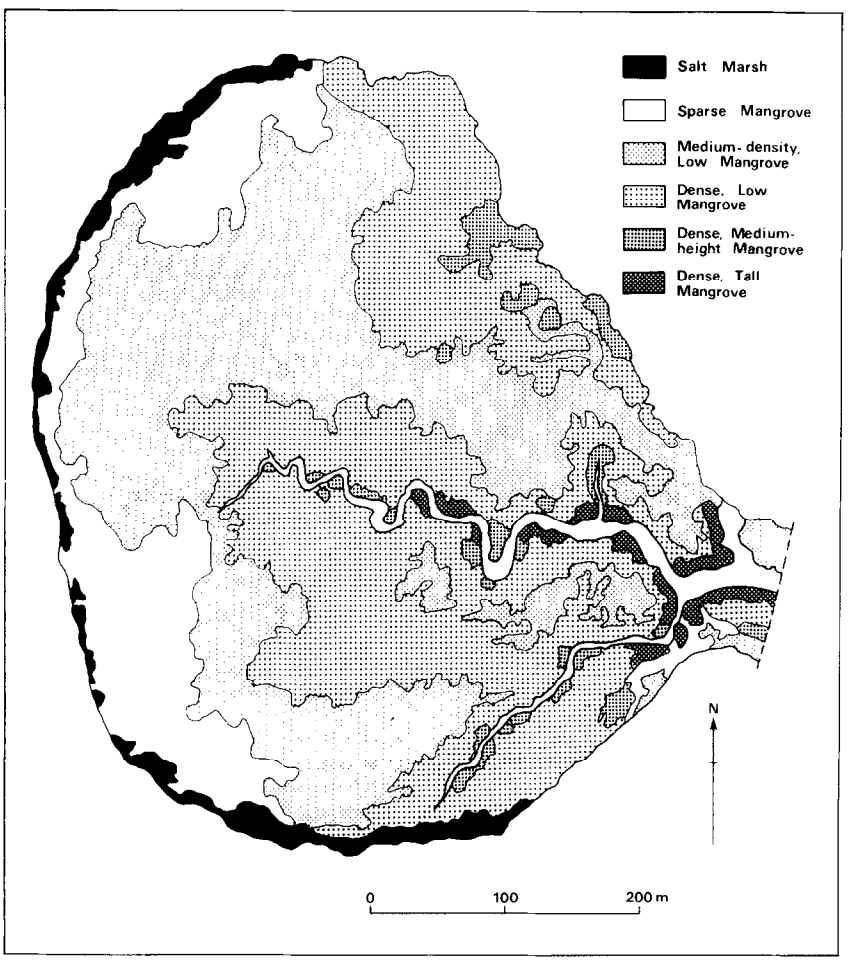

Figure 2. The distribution of mangrove height and density classes in Tuff Crater, interpreted from aerial photographs.

TABLE 1. Characteristics of individual trees in biomass calculations

Tree	Height, H (cm)	Trunk diameter D_5, 5 cm above ground (cm)	Canopy width, C (cm)	Trunk and branch biomass, T (g dry wt)	Leaf and inflorescence biomass, L (g dry wt)	Total above-ground biomass, B (g dry wt)	Leaf biomass as percentage of total biomass	Site [a]
1	115	3·22	80	406	303	709	43	W
2	110	3·06	80	380	280	660	42	W
3	215	8·18	215	11586	2863	14449	20	W
4	160	7·00	220	6857	3354	10211	33	M
5	110	2·20	67	150	151	301	50	M
6	100	2·80	70	241	192	433	44	M
7	248	9·65	220	5009	4251	9260	46	M
8	75	1·87	35	59	45	104	44	W
9	76	1·66	32	39	27	66	42	W
10	40	4·00	127	633	702	1335	53	W
11	65	3·00	75	176	241	417	58	W
12	40	3·00	60	96	107	203	53	W

W = Whangateau Harbour, M = Manukau Harbour.

There is a sharp break in the size of the mangroves behind the creek bank, and as the stunted shrub mangroves are gnarled but mature with stem diameters up to 10 cm, they were considered to be a distinct population from the creek bank stands when biomass was calculated. The 12 trees sampled for biomass were felled from areas where mangroves were being cleared in the Whangateau Harbour approximately 50 km north of Tuff Crater and the Manukau Harbour a similar distance south. Trees were not taken from Tuff Crater so that the system under study would undergo minimal disturbance. Trees 1 to 9 inclusive, ranging from 75 to 248 cm tall, came from open embayments and exhibited growth forms similar to those fringing the tidal creeks in Tuff Crater. Trees 10–12 inclusive were from more landward swamps and were stunted shrubs with well-developed recumbent stems. The dry weight of components of the trees are recorded in Table 1. Best fit linear correlations can be fitted to the cube root of biomass against measures of tree size as has been done by Golley *et al.* (1975). In this way for all 12 trees total above-ground biomass was found to be correlated to stem diameter 5 cm above the ground:

$$B^{-1/3} = 0{\cdot}264 + 2{\cdot}597\, D_5, \qquad R^2 = 0{\cdot}92, \tag{1}$$

Where B is total above-ground biomass (g) and D_5 is stem diameter 5 cm above the ground (cm).

A stronger correlation exists between total above-ground biomass and canopy diameter:

$$B^{-1/3} = 0{\cdot}489 + 0{\cdot}100\, C, \qquad R^2 = 0{\cdot}97, \tag{2}$$

where C is the average canopy width (cm) (calculated as the average of the greatest canopy width and the width of the canopy at right angles to the greatest width).

However, as the classes of creek bank mangroves are differentiated principally on the basis of height it is preferable to choose height as the independent variable against which to relate the biomass of the tree growth form. This is convenient as height is more easily

measurable in the field, or from aerial photographs, than is stem diameter or canopy width. A correlation between total above-ground biomass and height for trees 1–9 inclusive was found:

$$B^{-1/3} = -4{\cdot}215 + 0{\cdot}121\,H, \quad R^2 = 0{\cdot}84, \tag{3}$$

where H is tree height (cm).

Although this was not as strong a relationship as with stem diameter or canopy width, it has the advantage of being easily measurable. At a survey site within the tall mangrove 40 trees were randomly selected using the point-centred quarter method and were found to have a mean height ($\pm$standard deviation) of $2{\cdot}75 \pm 0{\cdot}75$ m. The biomass of each of these trees was calculated on the basis of tree height using equation 3 and a mean value of $31{\cdot}09 \pm 27{\cdot}69$ kg (excluding pneumatophores) was determined. With a tree density of 3350 trees ha^{-1}, the average total above-ground biomass for the taller class of mangroves is 104·13 t ha^{-1} (Table 2).

As the stunted *Avicennia* of the mudflats show little variation in height but considerable variation in canopy size it is inappropriate to calculate above-ground biomass by the method used for the taller mangroves. Instead, trees 8–12, all less than 1 m tall and with canopy widths varying from 32 to 127 cm, were found to show a correlation between biomass and canopy width:

$$B^{-1/3} = 1{\cdot}909 + 0{\cdot}072\,C, \qquad R^2 = 0{\cdot}99. \tag{4}$$

A sample of 40 trees was measured in the low dense mangrove. These varied little in height, mean ($\pm$standard deviation) of $0{\cdot}44 \pm 0{\cdot}07$ m, and had a mean canopy width of $0{\cdot}60 \pm 0{\cdot}42$ m. Using equation 4 for each tree the mean above-ground biomass of these trees was calculated to be $0{\cdot}42 \pm 0{\cdot}62$ kg. On the basis of a density of 16 000 trees ha^{-1} measured in the low dense mangrove, total above-ground biomass was estimated to be 6·79 t ha^{-1}. The percentage ground cover in each of the density classes was measured from aerial photographs and total above-ground biomass scaled accordingly for the low sparse and the low medium density classes of mangrove (Table 2).

The medium-height dense mangrove is the most impenetrable and the hardest in which to measure height or density accurately. Total above-ground biomass of this class was estimated using an average height of 1·75 m and equation 3, and a density of 5000 trees ha^{-1}. The value of 23·67 t ha^{-1} may be an underestimate for the biomass in this class in Tuff Crater but as can be seen in Table 2 the class makes a relatively minor contribution to the total standing crop of the basin (Figure 1).

The total above-ground mangrove biomass in Tuff Crater is estimated to be 153·1 t (Table 2). This estimate has large margins of error for a number of reasons.

Firstly the trees used for the initial biomass calibrations came from a different site and were sampled at different times of the year which may mean they are not representative of mangroves in Tuff Crater. Secondly the correlations with tree height and canopy width are not perfect. Thirdly because of the variability of trees within a stand there is a very large standard deviation around the mean value for tree biomass.

Litter production

Preliminary litter-fall rates for the period 4 November 1980–3 November 1981 have been reported by Woodroffe (1982) as $8{\cdot}10 \pm 2{\cdot}74$ t ha^{-1} a^{-1} beneath the tall mangroves and 3·65 t ha^{-1} a^{-1} beneath the low mangroves. Litter-fall rates for the period 3 November 1981–2 November 1982 were $7{\cdot}12 \pm 2{\cdot}40$ t ha^{-1} a^{-1} beneath the tall

TABLE 2. Calculation of total above-ground mangrove biomass, Tuff Crater

Height and density class	General height (m)	Height (mean ± S.D.), $N=40$ (m)	Percent cover (%)	Tree density by point centred quarter, $N=40$ (trees ha^{-1})	Canopy width (mean ± S.D.) $N=40$ (m)	Tree biomass (mean ± S.D.), $N=40$ (kg)	Total above-ground biomass (t ha^{-1})	Total area (ha)	Total biomass (t)
Low sparse	<1	–	26	—	—	—	1·96[a]	3·18	6·24
Low medium density	<1	—	52	—	—	—	3·92[a]	8·20	32·18
Low dense	<1	0·44 ± 0·07	90	16 000	0·60 ± 0·42	0·42 ± 0·62	6·79	7·61	51·69
Medium height dense	1–2·5	—	100	—	—	—	23·67[b]	0·77	18·22
Tall dense	2·5–4	2·75 ± 0·75	100	3350	–	31·09 ± 27·69	104·13	0·43	44·78
Total								20·19	153·11

[a]Scaled according to percentage cover against low dense class
[b]calculated on a mean height of 1·75 m and a density of 5000 trees ha^{-1}

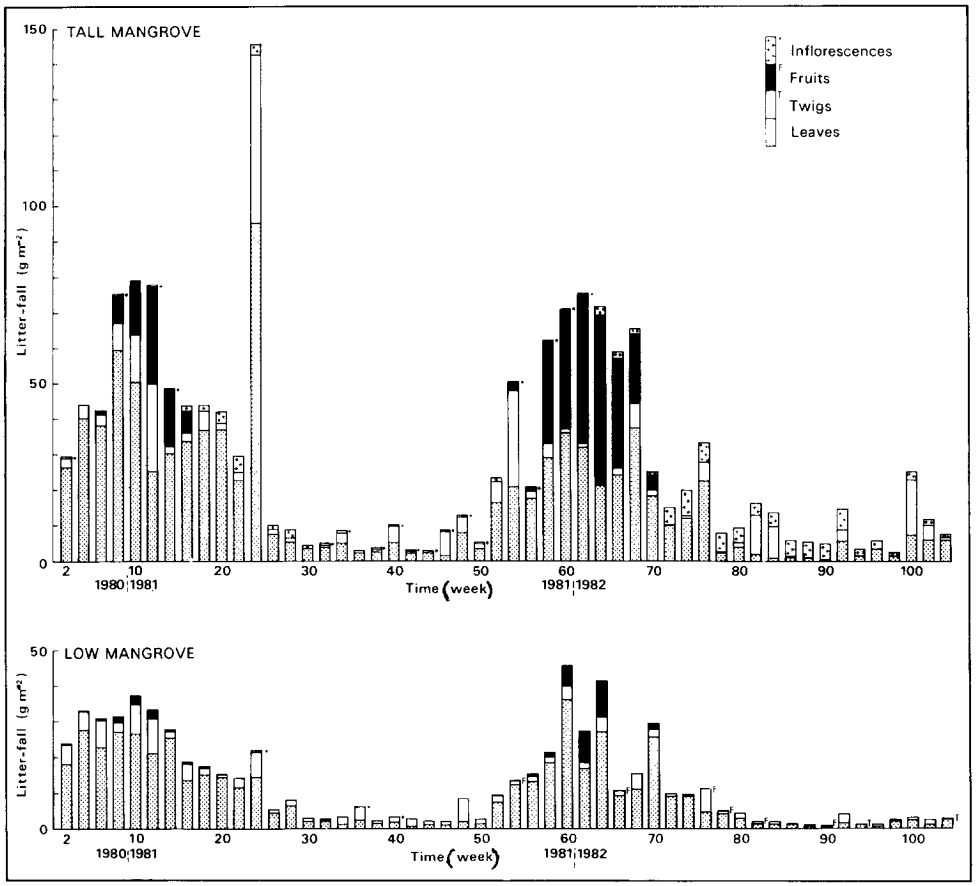

Figure 3. Litter-fall by components beneath taller mangrove and lower mangrove in Tuff Crater (4 November 1980–2 November 1982).

mangroves and 2·90 t ha^{-1} a^{-1} beneath the low mangroves. Values for the second year are slightly lower than for the first and annual means for the two years are $7{\cdot}61 \pm 2{\cdot}54$ t ha^{-1} a^{-1} for the tall mangroves and $3{\cdot}28 \pm 0{\cdot}48$ t ha^{-1} a^{-1} for the low mangroves.

The distribution of litter-fall by component is shown in Figure 3. In the tall mangroves, leaves accounted for 69·4% of the total in 1980–1981 and 45·5% in 1981–1982; twigs for 18·3% in 1980–1981 and 14·8% in 1981–1982 while inflorescences rose from 3·1% to 10·0% and fruits from 9·2% to 29·7% from 1980–1981 to 1981–1982. In the low mangroves leaves accounted for 74·4% in 1980–1981 to 76·0% in 1981–1982, twigs for 23·0% and 13·9% respectively and fruits rose from 2·5% to 10·1%. The method of collection from plots in the low mangroves made recovery of inflorescences unrepresentative.

Despite the similarity of the total litter production in 1980–1981 and 1981–1982 the relative proportions of the components changed and it appears that the mangroves apportioned a larger fraction of their total energy budget into reproductive tissues in 1981–1982. The fall of litter was markedly seasonal with peak fall in summer between December and April coinciding with the period of fruit production.

TABLE 3. Mean annual litter-fall rate by component beneath tall and beneath low mangrove, Tuff Crater, 1980–1982, and total annual litter-fall for entire basin

	Litter-Fall ($g\ m^{-2}\ a^{-1}$)									
	Leaves		Twigs		Fruits		Inflorescences		Total	
	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
Tall mangrove										
4 Nov 1980–3 Nov 1981	561	169	147	120	75	42	25	17	809	274
3 Nov 1981–2 Nov 1982	323	112	104	80	213	173	71	11	712	240
1980–1981 and 1981–1982	442	185	126	101	144	141	48	28	761	254
Low mangrove										
4 Nov 1980–3 Nov 1981	272	—	84	—	9	—	—	—	365	—
3 Nov 1981–2 Nov 1982	220	—	41	—	29	—	—	—	290	—
1980–1981 and 1981–1982	246	32	62	27	19	18	—	—	328	48

	Litter-fall (t)				
	Leaves	Twigs	Fruits	Inflorescences	Total
Low sparse (3·18 ha)	5·4	1·4	0·4	—	7·2
Low medium density (8·20 ha)	10·8	2·8	0·8	—	14·4
Low dense (7·61)	18·7	4·7	1·4	—	24·8
Medium height dense (0·77 ha)[a]	2·6	0·7	0·6	0·1	4·0
Tall dense (0·43 ha)	1·9	0·6	0·6	0·2	3·3
Total	39·4	10·2	3·8	0·3	53·7

[a]Calculated as mean of tall and low mangrove.

Shoot extension

Measurement of shoot extension was undertaken on the stunted mangroves of the mudflat in order to determine whether the stunting of these mangroves had occurred because of shoot dieback. Of the 36 shoots tagged, 33 were located and remeasured after 12 months and shoot extension varied from −3·0 cm where a tip had been broken to +7·5 cm of growth. The average extension was $2{\cdot}42 \pm 2{\cdot}77$ cm. Seven of the 33 shoots appeared to be dead at the tip though the cause of this dieback could not be determined.

The breakdown of mangrove detritus

The decomposition rates of mangrove leaves have been examined on the sediment surface at creek and mudflat sites in summer and winter in this paper and in a previous one (Woodroffe, 1982). The rates of decomposition are summarised in Table 4. Litter decomposition in bags exhibited local variability but the overall trend of leaf degradation was fairly constant with 50% weight loss in 10 weeks and thereafter a slower rate of breakdown. Site-specific and season-specific differences are not discernible. The rates of breakdown of the leaves were similar to the rates found by Albright (1976) for leaf degradation both on the sediment surface and in the sediment. Degradation of roots and pneumatophores was shown by Albright (1976) to be much slower (Table 4).

Table 5 records the nutrient status of a number of sediment samples from Tuff Crater. The combustible organic matter in the soil, determined by weight loss on ignition varied

TABLE 4. Summary of rates of decomposition (as percentages) from Tuff Crater (Woodroffe, 1982) and Whangateau Harbour (Albright, 1976)

		Week												
		2	4	6	8	10	12	14	16	18	20	22	24	26
Percentage of ash free weight remaining (after Woodroffe, 1982)														
Mud flat : winter	($N=2$)	84	72	47	52	49	49	36	40	22	27	35	14	10
Mud flat : summer	($N=1$)	96	81	74	43	52	24	28	35	39	10	7	18	13
Creek : winter	($N=3$)	72	60	51	58	46	45	30	38	31	26	24	22	27
Creek : summer	($N=1$)	87	68	49	51	45	47	58	31	35	44	31	26	34
Average		81	68	53	53	48	43	35	37	30	27	26	20	21

	Week				
	4	8	12	16	22
Percentage of dry weight remaining (after Albright, 1976)					
Leaves at sediment–water interface	67	58	38	16	6
Roots at sediment–water interface	88	77	64	57	48
Pneumatophores at sediment–water interface	97	85	81	80	54
Roots in sediment	94	79	75	72	70
Pneumatophores in sediment	87	85	76	74	71

from 6–25%. The pattern of total nitrogen and total organic carbon is similar to that for loss on ignition with the highest nitrogen concentrations of 5197 mg kg^{-1} and organic carbon concentrations of 7·42% being found in the northern part of the basin. Total phosphorus shows a similar pattern. The C/N ratio varies from 6·44 to 17·35.

Although the concentration of organic matter in the substrate is relatively high, not all of this organic matter will have been derived from mangrove detritus or the products of decomposition. Major visible roots of mangroves were excluded from sediment samples but fine rootlets, micro-organisms and infauna may have been included.

Discussion

The mangroves in Tuff Crater are of two distinct growth forms; the taller tree-like *Avicennia* of the creek banks and the stunted *Avicennia* shrubs of the mudflat. This physiognomic distinction has been described from mangroves from elsewhere in New Zealand (Chapman & Ronaldson, 1958; Kuchler, 1972), and is also a characteristic of *Avicennia* at Cullendulla Creek, N.S.W., Australia (Ball, 1981). The above-ground biomass estimates for these two types are substantially different, being 104·1 t ha^{-1} for the tall mangroves and 6·8 t ha^{-1} for the lower. These estimates have large margins of error, but they are comparable with values reported for above-ground mangrove biomass

TABLE 5. Soil nutrient status, Tuff Crater

Sample	Combustible organic matter (% wt loss on ignition)	Total Kjeldahl nitrogen mg kg^{-1}	Total phosphorous mg kg^{-1}	Organic carbon (%)	C/N ratio
1	8·5	1286	668	1·57	12·22
2	15·7	3446	508	2·93	8·50
3	14·3	2471	460	3·44	13·93
4	10·3	2579	421	2·98	11·55
5	14·7	2933	564	2·99	10·21
6	6·3	1106	677	0·74	6·69
7	7·7	1910	729	1·23	6·44
8	15·9	3650	650	2·73	7·48
9	25·1	5197	1009	7·42	14·28
10	21·2	4392	769	5·60	13·21
11	10·9	1918	511	2·59	13·52
12	12·4	3093	713	1·80	5·82
13	11·4	2942	707	1·82	6·19
14	12·0	2977	727	1·75	5·88
15	16·5	3296	505	5·68	17·23
16	9·0	1762	373	1·87	10·61
17	13·1	2564	689	3·16	12·34
18	11·2	2428	719	2·96	12·20
19	10·9	2220	408	3·85	17·35
20	15·0	2748	351	3·10	11·28
Mean	13·1	2746	608	3·02	10·85
Standard deviation	4·5	980	165	1·65	3·62

from elsewhere using different methods (Table 6). The value for the tall mangrove of the creek banks lies between 86·0 t ha^{-1} for *Avicennia* in Westernport Bay (Clough & Attiwill, 1975) and the 128·4 t ha^{-1} for *Avicennia* in Sydney (Briggs, 1977). It is similar to values recorded for *Rhizophora* forests in Florida (Lugo & Snedaker, 1974) and for *Rhizophora* and *Bruguiera* forests in Japan (Suzuki & Tagawa, 1983). The value for the stunted mangroves is slightly lower than for dwarfed mangrove in Florida. As 94% of the basin is covered by low and generally sparse mangrove, the estimated total above-ground biomass for the entire basin is only 153 t. This is an average of 7·6 t ha^{-1}, below the biomass recorded for mangroves anywhere else in the world (Table 6).

The estimated rate of litter-fall beneath the tall mangrove is 7·6 ± 2·5 t ha^{-1} a^{-1} while that beneath the low mangrove is 3·3 ± 0·5 t ha^{-1} a^{-1}. Clough and Attiwill (1982) have drawn attention to the similarity of litter-fall rates beneath mangroves around the world of about 7 to 8 t ha^{-1} a^{-1} and Woodroffe (1982) has indicated that the taller creek bank mangroves can be as productive in terms of litter-fall as mangroves in Florida and Queensland (Pool *et al.*, 1975, Duke *et al.*, 1981). A similar value is reported beneath mangroves in the Central Pacific (Woodroffe & Moss, 1984) and higher values have been recorded in the structurally and floristically diverse mangroves of South-east Asia (Proctor *et al.*, 1983; Leach & Burgin, 1983).

TABLE 6. Total above-ground mangrove biomass

Location	Latitude	Mangrove species	Structure or average height (m)	Above-ground biomass (t ha^{-1})	Source
Panama	9°N	*Rhizophora brevistyla*	30–40	279·2	Golley *et al.* (1975)
Thailand	8°N	*Rhizophora apiculata*	11	159·0	Christensen (1978)
Puerto Rico	18°N	*Rhizophora mangle*	8	62·9	Golley *et al.* (1962)
Philippines	12°N	Mixed mangrove species	—	45·9	de la Cruz & Banaag (1967)
Florida	26°N	*Rhizophora mangle*	overwash	124·6	Lugo & Snedaker (1974)
		Rhizophora mangle	riverine	136·0	Lugo & Snedaker (1974)
		Rhizophora mangle	fringe	118·9	Lugo & Snedaker (1974)
		Rhizophora mangle	scrub	7·9	Lugo & Snedaker (1974)
		Mixed mangrove species	island	49·0	Lugo & Snedaker (1974)
		Laguncularia racemosa	succession	8·1	Lugo & Snedaker (1974)
Japan	24°N	*Rhizophora mucronata*	5–6	108·1	Suzuki & Tagawa (1983)
		Bruguiera gymnorhiza	5–6	97·6	Suzuki & Tagawa (1983)
		Rhizophora + Bruguiera	5–6	78·6	Suzuki & Tagawa (1983)
Australia					
Sydney	34°S	*Avicennia marina*	6–8	128·4	Briggs (1977)
Westernport Bay	38°S	*Avicennia marina*	2–4	86·0	Clough & Attiwill (1975)
New Zealand	37°S	*Avicennia marina* var. *resinifera*	2·5–4	104·1	this study
		Avicennia marina var. *resinifera*	<1	6·8	this study

The litter-fall rate beneath the low mangroves is greater than that observed beneath low *Avicennia* in Westernport Bay, Australia (Clough & Attiwill, 1975) but less than observed beneath *Avicennia* in Sydney, Australia (Goulter & Allaway, 1979). The production of fruit varied considerably between the two years. Similar variation has been noted in other mangroves; Clough and Attiwill (1975) recorded that *Avicennia* in Westernport Bay only set fruit once in two or three years.

A storm in April 1981 led to high litter-fall in that month, particularly in the taller mangrove (Woodroffe, 1982). In view of the fact that the total litter-fall for 1981–1982 was of the same order of magnitude as the collection year in which the storm event was recorded it appears that the storm did not contribute disproportionately to the annual total.

The total fall of litter in Tuff Crater is estimated to be 53·7 t a^{-1}. This value is low because such a large percentage of the basin is covered by stunted and sparse mangrove. It gives an average rate of 2·66 t ha^{-1} a^{-1}; a rate much lower than from any mangroves studied other than those at the southernmost occurrence of mangroves in Westernport Bay, Australia. This rate of litter-fall implies that 35% of the total above-ground biomass falls annually as litter.

Leaf biomass on the 12 trees felled averaged 44% of the total above-ground biomass and on this basis leaves accounted for 45·8 t ha^{-1} in the tall mangroves while the leaf component of litter-fall averaged 4·4 t ha^{-1} a^{-1}. In the low mangrove leaf biomass was 3·0 t ha^{-1} and leaf fall 2·5 t ha^{-1} a^{-1}. It appears from these figures that leaf turnover is far more rapid in the stunted mangrove than in the tall. In the low mangrove it is close to the annual turnover of leaves of 0·88 suggested by Pool *et al.* (1975).

The structure of a mangrove ecosystem is shown schematically in Figure 4. Nutrients can be recycled *in situ* but organic matter is also lost from the system in a number of ways. In some mangrove stands herbivory may be important and Johnstone (1981) has recorded up to 20% consumption of leaves in mixed mangrove stands in New Guinea. Herbivory is relatively unimportant in the mangroves in Tuff Crater; Johnstone recorded low levels of leaf consumption of *Avicennia* in New Zealand and in Shoal Bay, adjacent to Tuff Crater, he recorded a site where 0% of the leaf area had been eaten (Johnstone, 1981, table 5).

The decomposition of litter is an important stage in its utilisation in the estuarine system. Rates of decomposition vary according to oxygen availability, substrate characteristics, and micro-organism and scavenger activity, but are generally high in mangrove swamps (Hesse, 1961). It has been shown that *Avicennia* leaves in Tuff Crater lose approximately half their weight in 10 weeks, a decomposition rate very similar to that found elsewhere in New Zealand by Albright (1976) and in Sydney by Goulter & Allaway (1979). In Thailand, Boonruang (1978) recorded a much more rapid rate of degradation with *Avicennia* leaves losing half their weight in 20 days.

The degradation rates may be artificially low because the method used excludes some organisms which may accelerate the breakdown. The amphipod, *Orchestia* sp. was observed to be numerous in litter decomposition bags and evidently plays an important role in the breakdown process. Crabs are known to assist with degradation of mangrove litter in the tropics (Malley, 1978) and the New Zealand mangrove crab, *Helice crassa* Dana, which would generally have been too big to have entered the bags, may be important in breaking down mangrove tissues faster.

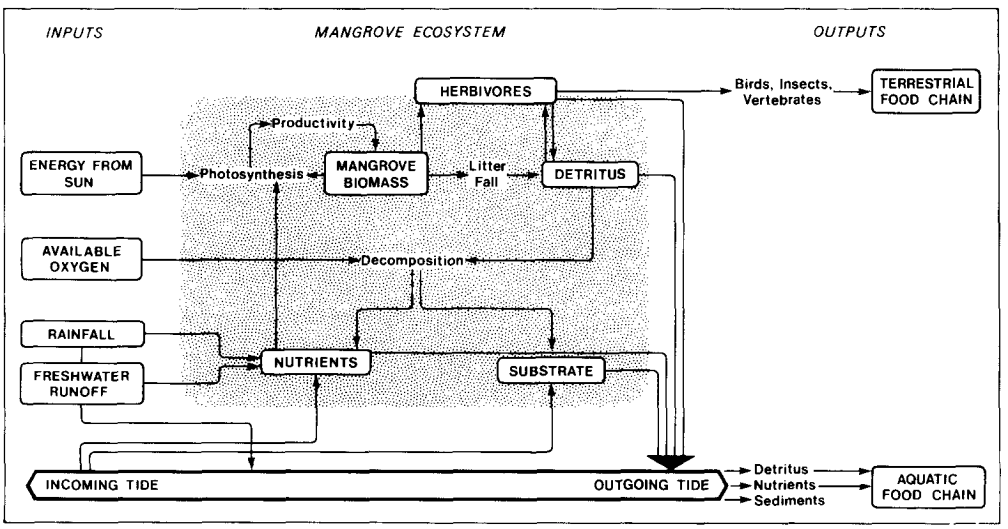

Figure 4. A schematic model of the mangrove ecosystem.

One of the unknown factors in the functioning of the mangrove ecosystem (Figure 4) is the proportion of the litter or detrital fragments which become incorporated into the substrate as opposed to that which is flushed from the system by tidal action. The rate of accumulation of detritus on and in the substrate is difficult to measure. It is likely to vary in relation to substrate characteristics, the frequency of tidal inundation and the stage and hence energy of the tide, as well as seasonally with the pattern of production and supply of mangrove litter. Boto and Bunt (1981) observed that in Coral Creek, Queensland there was no accumulation of litter in the mangrove swamp as litter falling in the area was effectively removed by the subsequent high tide. In Tuff Crater, leaves and detrital fragments have been observed with a thin cover of mud which prevents their suspension at high tide. The organic content of the sediments is high but variable and although not all of this organic matter is derived from mangrove detritus, a proportion of the detrital production is evidently retained on and in the sediment and recycled *in situ*. On the other hand the concentration of particulate matter in the tidal creek, both detritus floating on the surface and microscopic material in suspension, is high and some material is flushed from the system by tidal action. Two subsequent papers attempt to estimate the tidal flux and derive a particulate matter budget for the mangroves in Tuff Crater (Woodroffe, 1985*a*, *b*).

Conclusions

The above-ground biomass (excluding pneumatophores) of the taller mangroves, up to 4 m tall beside the tidal creek in Tuff Crater, is estimated to be 104·1 t ha^{-1} and that of the lower mangroves, less than 1 m tall on the mudflats, is estimated to be 6·8 t ha^{-1}. The litter-fall beneath the taller mangroves is estimated to be $7{\cdot}6 \pm 2{\cdot}5$ t ha^{-1} a^{-1} and that beneath the lower mangroves $3{\cdot}3 \pm 0{\cdot}5$ t ha^{-1} a^{-1}. When these estimates are compared with data from mangroves from elsewhere it is found that the taller *Avicennia*, though close to the southern latitudinal limit of mangroves, is comparable both in terms of biomass and litter-fall with mangroves from more tropical sites. The estimates for the low mangroves are similar to those for stunted mangroves elsewhere. However, as 94% of Tuff Crater is covered with low generally sparse mangroves, the total above-ground biomass in the basin is estimated to be 153·1 t and the total litter-fall 53·7 t a^{-1}. These estimates suggest average biomass of 7·6 t ha^{-1} and average litter-fall of 2·7 t ha^{-1} a^{-1}, which are very low when compared with mangroves from elsewhere.

Decomposition has been shown to occur relatively rapidly, with leaves of *Avicennia* losing half their weight in approximately 10 weeks, after which degradation continues at a slower rate. Sediment samples indicate that the substrate has a high organic content and although the observation of detritus in the tidal creek implies some tidal flushing of organic matter from the basin, a proportion of the detrital production is evidently recycled *in situ*.

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