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Nutrient capital in different aged forests of the mangrove *Rhizophora apiculata*

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Abstract

Partitioning and storage of mineral nutrients and trace elements were examined in tree components and soils of differently aged (3-, 5- and 25-year-old) forests of the mangrove *Rhizophora apiculata* in southern Thailand. Despite lack of replication of forests, three patterns of element partitioning and forest nutrient capital emerged: (1) concentrations of most (but not all) elements in various tree parts declined with increasing tree age; (2) the soil pool size of most elements decreased with increasing stand age; and (3) the proportion of C, N, Na, Mn, Zn and Mo in total living biomass increased with increasing forest age. Most elements were stored in soils and dead roots, supporting the concept that wet tropical forests do not store proportionally more nutrients in their biomass than in soils, as compared to temperate and boreal forests. The large element pools stored in dead roots may serve as a conservation mechanism. Our data suggest that the proportion of element capital stored in forest biomass increases, but decreases in soils as forests age, suggesting net accumulation with forest maturity. Mean residence time for total forest N increased from 0.3 years for the 3-year-old forest to 0.5 years for the 5-year-old forest to 0.6 years for the 25-year-old forest. Compared with other forests, N turnover is very rapid, mirroring the tight coupling between production and decomposition processes in these wet tropical ecosystems.

Keywords: forest; mangrove; nutrient; *Rhizophora apiculata*; trace element.

Introduction

Tropical mangrove forests are often highly productive ecosystems with correspondingly high requirements for nitrogen, phosphorus, minerals and trace elements. Rates of nutrient cycling within mangrove ecosystems indicate that most fixed carbon and organic nitrogen is efficiently conserved, with proportionally little export of labile matter to adjacent coastal waters (Boto 1992, Twilley et al. 1992, Alongi 2002). Carbon budgets for mangrove forests in Southeast Asia show that these ecosystems are net autotrophic, with excess fixed carbon probably being buried in soils and stored in tree biomass (Kristensen et al. 1995, Alongi et al. 2000). Nitrogen is tightly coupled to tree production with approximately 70–90% of the nitrogen supplied to the forest floor being shunted back to trees via the ammonium pool, sustaining rapid rates of canopy production (Alongi et al. 2002).

Whether or not the net storage of carbon and nitrogen accumulated in biomass and soils in these forests translates into preferential allocation and accumulation of minerals and trace elements is unknown. A recent study of element partitioning and storage in arid-zone mangrove forests in Western Australia (Alongi et al. 2003) revealed two patterns in element behaviour. First, most elements were stored in green leaves and live roots, consistent with data from other trees. Second, only a small percentage ($<$1% for most elements) of the total forest nutrient capital was vested in tree biomass. Most elements were stored below-ground in soil and in dead fine roots. Similar data are lacking for mangroves of the wet tropics.

Various factors come into play in determining patterns of element use and storage in forested ecosystems, including soil fertility, species composition and forest age (Proctor 1989, Drechsel and Zech 1993, Gower et al. 1996, Ryan et al. 1997). In terrestrial forests, it is well known that as forests age to maturity, their productivity declines, and so does their requirement for nutrients. In contrast, the influence of forest age on element use, turnover and storage in mangrove ecosystems is unknown. In Southeast Asia, net canopy production for *Rhizophora apiculata* Blume increases from seedling stage to approximately 20 years, and does not level off until at least 65 years (Alongi 2002). This implies that some mangrove species show a post-climax stage decline in production much later than in many other trees. In southern Thailand, we examined nutrient cycling in three *Rhizophora apiculata* forests aged 3, 5, and 25 years (Alongi et al. 2001, 2002, 2004) and found that the percentage of nitrogen buried in soils declined with forest age from 10–12% in the 3–5-year-old stands to $<$4% in the 25-year-old forest. Also, the percentage of total N input removed by denitrification decreased from 6% in the youngest forest to 3% in the oldest forest. These nitrogen patterns suggest that rates of nutrient accumulation in trees increase with age. Study of these sites offered us the opportunity to further examine the influence of forest age on the partitioning and storage of mineral and trace element capital in *Rhizophora apiculata* forests, which are dominant along many sheltered coasts throughout Southeast Asia and northern Australia.

Materials and methods

Study sites

The study was conducted in Sawi Bay, southern Thailand, located on the south western coast of the Gulf of Thailand. Three mangrove forests within the bay were sampled in October 1999 and April 2000. Stations (Stns) S1 and S2 were located on opposite sides of Khlong Sawi, a small tidal river in the southern part of the bay. Station S1 (10°16.8'N, 99°9.8'E) was a mid-intertidal *Rhizophora apiculata* forest partially clear-felled 15 years ago, and allowed to regenerate naturally. The mature trees sampled in this stand were approximately 25 years old. Station S2 (10°16.7'N, 99°9.8'E) was a high-intertidal *R. apiculata* plantation, manually planted 5 years ago by the Royal Forestry Department, Thailand. Station S3 (10°22.4'N, 99°13.2'E) was located on a plantation that was originally the site of a failed shrimp farm. The plantation was located in a small tidal estuary, Khlong I Laet, in the northern part of Sawi Bay. Station S3 was a *R. apiculata* stand manually replanted 3 years ago within the mid-intertidal zone. Allometric data and productivity estimates for these forests can be found in Alongi and Dixon (2000). There was no replication for the factor "forest age" which, therefore, is confounded with spurious differences among sites.

Field and laboratory measurements

Trees cut for allometry were also used for elemental analysis. Three trees were cut randomly from each of three replicate plots (5×5 m in area) at each site. Trees were cut and divided into green leaves, live branches, stem, and prop roots. Prop roots were cut where they joined a stem or the butt, and at ground level. Some trees were multi-stemmed, so stems were cut at the point where they attached to a common butt. Each above-ground component of the tree was then weighed with a 50-kg spring scale. Other forest biomass (e.g., coarse woody debris) was not measured because washout by tides removed most tree debris on the forest floor (Alongi et al. 2001). Animal biomass was not measured, but visual observations suggested that it would be insignificant compared to tree biomass. Soils and fine roots below ground were sampled by taking triplicate cores to the maximum depth of root penetration (usually 80–100 cm) at each site (Alongi and Dixon 2000). Sub-samples (n=9 for each tree part per site, except n=3 for roots per site) of each tree component were taken to determine fresh weight:dry weight ratio and element concentration.

All tree and soil samples were kept frozen until returned to the laboratory. Thawed tree parts (including fine roots) were washed briefly with double distilled water, and, with the soil samples, oven-dried to constant weight at 80°C. Individual samples of each tree part and soils were ground to a fine powder and analysed separately for total organic carbon on a Shimadzu TOC-5000 analyser (Kyoto, Japan) with solid-sampler and for total nitrogen on a Perkin Elmer 2400 CHNS/O series II analyser (Norwalk, CT, USA). The soils and tree samples were further analysed for Fe, Mn, S, Na, Mg, K, Ca, P, Zn, Cr, Ni, Cu, Co, Pb, Mo, Cd, Hg and As. Except for Cd measured on a Zieman atomic absorption spectrometer (Melbourne, Australia), the other elements were determined on a Liberty ICP-AES (Melbourne, Australia) following a modified acidification procedure (Loring and Rantala 1992). Briefly, 0.5 g of each dried (80°C for 24 h) and ground sample was weighed into a 50-ml digestion tube, digested with HNO_3 and $HClO_4$ at 120°C for 3 h, then refluxed at 180°C for 3 h, and made up to 50 ml in a volumetric tube. The resulting complex was analysed sequentially. Analytical performance was monitored with standard reference materials NBS 1646 (estuarine sediment) from the National Institute of Standards Technology and MESS-2 (marine sediment) obtained from the National Research Council of Canada. Values were always within the certified range. Analytical precision was 5% for C and N, and within 3% for the other elements.

Data analysis

The data for each element in each tree part from the triplicate plots per site were averaged prior to further analysis. The averaged data (n=3 per site) were compared using the non-parametric Kruskal-Wallis (KW) test (Sokal and Rohlf 1995). H values (df=2) calculated from the KW tests were compared with critical values in Siegel and Castellan (1988). Where necessary, multiple comparisons among stands were tested using the Student-Newman-Keuls (SNK) procedure. Levels of significance were $p=0.004$ for the KW tests and $p<0.05$ for the SNK tests, except where noted.

For estimation of total forest nutrient capital, element concentrations in each tree part were scaled up to forest level by multiplying the mean concentration of each element by the total biomass of each tree component for each of the three replicate plots at each site.

Results

Element concentration in trees

Concentrations of C (in leaf, H=7.2), Ca (in stem and branch, H=7.2), Mg (branch and stem, H=7.5), K (stem, H=7.5 and prop root, H=7.2), Na (branch, stem, prop root, H=7.2), Mn (leaf, H=5.96; p=0.025; branch, stem, prop root, H=7.2), Cu (leaf, H=6.25; p=0.011; stem, H=7.45; prop roots and live fine roots, H=6.88), Pb (live and dead roots, H=7.2), Cd (leaf, H=7.45) and As (live roots, H=6.88; dead roots, H=7.2) declined in the various tree parts, apparently with increasing tree age (Tables 1–3); for all significant SNK tests for the above treatments, site differences were: Stn S3>Stn S2>Stn S1 (q-values ranged from 2.8–3.8). Concentrations of S (leaf, H=7.2) and Fe and Cr (leaf, branch, H=7.2) increased in particular tree components with age (all SNK tests: Stn S1>Stn S2>Stn S3 (q-values ranged from 2.8–3.8). Other elements either showed no significant change (e.g., Zn, Co) or concentration varied significantly among stands (e.g., Hg, dead roots), but not with increasing tree age. For instance, prop roots of the 25-year-old forest

Table 1 *Rhizophora apiculata*: concentration (mean±1 SE) of elements in various parts of trees (n=3) at the 3-year-old forest, Stn S3.

	Leaf	Branch	Stem	Prop root	Live root	Dead root
C$^{\alpha}$	466±4	447±2	466±1	467±1	371±4	410±7
N$^{\alpha}$	12±1	3.3±0.2	2.3±0.3	2.6±0.3	6.4±0.3	6.4±0.1
Mg$^{\alpha}$	5.0±0.05	1.9±0.03	1.0±0.08	0.7±0.0	4.2±0.5	5.0±0.3
Ca$^{\alpha}$	18.9±0.1	19.1±0.6	9.5±0.1	3.8±0.0	4.1±0.2	4.8±0.2
S$^{\alpha}$	4.0±0.1	0.5±0.08	0.5±0.0	0.5±0.05	34.9±2.8	49.3±1.0
K$^{\alpha}$	6.9±1.1	3.0±0.6	2.0±0.3	2.9±0.2	2.5±0.2	1.4±0.1
Na$^{\alpha}$	19.6±4.0	8.2±0.1	4.2±0.3	9.3±0.5	14.1±2.6	6.8±1.0
P$^{\beta}$	970±19	413±40	287±5	383±58	435±38	434±31
Mn$^{\beta}$	1079±227	457±43	177±13	78±1	64±5	189±12
Fe$^{\beta}$	87±2	37±3	54±2	66±6	6720±560	23800±1288
Zn$^{\beta}$	5.0±0.3	2.0±0.0	4.0±1.1	1.8±0.2	23.5±3.5	30.9±1.6
Cu$^{\beta}$	2.4±0.2	1.1±0.2	1.1±0.0	1.1±0.3	9.8±4.3	6.5±0.4
Mo$^{\beta}$	<0.5	<0.5	<0.5	<0.5	21.5±2.5	40.0±6.0
Cr$^{\beta}$	1.3±0.2	1.3±0.1	1.3±0.2	1.3±0.3	10.8±0.4	10.8±0.8
Ni$^{\beta}$	2.4±0.6	1.1±0.3	0.6±0.0	1.1±0.2	4.8±0.3	9.0±0.6
Pb$^{\beta}$	<2.0	<2.0	<2.0	<2.0	5.0±0.8	12.8±0.2
Co$^{\beta}$	<0.25	<0.25	<0.25	<0.25	2.5±0.3	8.0±0.5
Cd$^{\chi}$	170±13	173±42	<75	<75	124±22	225±11
As$^{\chi}$	53±1	12±3	6.0±0.4	8±1	11925±1350	29775±2700
Hg$^{\chi}$	25±2	7±1	<5	<5	24±6	28±4

α=mg g^{-1}; β=μg g^{-1}; χ=ng g^{-1}.

showed significantly higher Ca, but lower N, P and Ni concentration compared with 3- and 5-year-old prop roots. Similarly, live below-ground roots showed significantly lower concentration of C, N, P, and Ni in the 25-year-old forest than in the two younger forests (Tables 1–3).

Soil element pool size

The soil pool size of most elements (C, N, Mg, S, K, Na, P, Fe, Zn, Mo, Cr, Ni and Pb) decreased with increasing forest age (Table 4). Only the Cu soil pool increased with stand age. The remaining elements (Ca, Mn, Co, Cd, As and Hg) showed no clear trends.

Total forest nutrient capital

Total forest pools (Figure 1a,b) indicated that C, N, S, Na, Mn, Zn and Mo vested in total living tree biomass, as a percentage of the respective total forest pool of each element, increased with increasing forest age (Table 5). For instance, the percentage of the total forest C pool tied up in living *R. apiculata* biomass increased from 10% (3-year-old forest) to 13% (5-year-old forest) to 53% (25-year-old forest).

Few elements showed a proportional increase in tree parts with increasing forest age; none showed a decrease (data not shown). For example, the percentage of Mn increased from 21% to 29% to 32% in branches,

Table 2 *Rhizophora apiculata*: concentration (mean±1 SE) of elements in various parts of trees (n=3) at the 5-year-old forest, Stn S2.

	Leaf	Branch	Stem	Prop root	Live root	Dead root
C$^{\alpha}$	438±3	460±2	472±0.5	464±0.4	352±11	389±16
N$^{\alpha}$	10±0.6	3.4±0.4	1.7±0.2	2.3±0.3	5.2±0.6	6.4±0.1
Mg$^{\alpha}$	6.7±0.1	1.8±0.0	0.8±0.05	0.9±0.01	4.9±0.5	5.0±0.5
Ca$^{\alpha}$	14.5±2.3	16.5±0.2	7.4±0.1	3.8±0.01	11.7±2.7	8.2±1.6
S$^{\alpha}$	4.3±0.04	0.5±0.0	0.5±0.05	0.5±0.05	25.9±2.6	61.6±3.8
K$^{\alpha}$	6.1±0.1	2.1±0.1	1.1±0.08	1.7±0.2	3.5±1.1	1.3±0.0
Na$^{\alpha}$	17.9±0.2	7.4±0.5	3.3±0.5	6.2±0.1	19.6±1.7	6.1±0.3
P$^{\beta}$	1015±6	257±5	208±5	279±2	434±42	527±186
Mn$^{\beta}$	498±17	349±12	113±10	74±1	118±18	380±68
Fe$^{\beta}$	116±10	56±15	59±5	130±20	8024±885	38763±4660
Zn$^{\beta}$	7.0±0.07	2.0±0.0	1.3±0.3	1.0±0.0	23.5±1.7	47.3±5.5
Cu$^{\beta}$	2.2±0.04	0.7±0.1	0.8±0.06	0.7±0.1	2.6±0.2	5.6±0.4
Mo$^{\beta}$	<0.5	<0.5	<0.5	<0.5	8.3±5.5	14.6±3.6
Cr$^{\beta}$	2.4±0..2	2.0±0.09	1.0±0.14	1.8±0.1	16.7±2.1	34.2±1.6
Ni$^{\beta}$	2.5±0.2	1.7±0.05	0.8±0.04	0.7±0.1	4.4±0.8	8.5±0.6
Pb$^{\beta}$	<2.0	<2.0	<2.0	<2.0	3.6±0.3	9.3±0.8
Co$^{\beta}$	<0.25	<0.25	<0.25	<0.25	2.8±0.3	10.4±0.3
Cd$^{\chi}$	114±4	<75	91±7	<75	56±10	202±34
As$^{\chi}$	91±1	21±3	10±1	32±4	5100±1050	24150±1950
Hg$^{\chi}$	16±3	<5	<5	<5	20±6	34±1

α=mg g^{-1}; β=μg g^{-1}; χ=ng g^{-1}.

Table 3 *Rhizophora apiculata*: concentration (mean±1 SE) of elements in various parts of trees (n=3) at the 25-year-old forest, Stn S1.

	Leaf	Branch	Stem	Prop root	Live root	Dead root
C^{α}	419±1	465±2	471±1	472±1	335±9	397±6
N^{α}	13.0±0.7	4.0±0.1	1.4±0.2	1.8±0.0	4.1±0.1	7.8±0.1
Mg^{α}	7.3±0.5	1.2±0.01	0.5±0.0	0.9±0.0	4.8±0.06	6.5±0.6
Ca^{α}	19.6±0.1	14.5±0.2	4.7±0.01	5.4±0.1	3.4±0.04	7.5±0.1
S^{α}	4.7±0.2	0.7±0.07	0.4±0.08	0.45±0.2	25.9±2.4	45.7±3.4
K^{α}	8.2±0.1	2.6±0.4	0.8±0.0	1.2±0.1	1.8±0.11	1.2±0.1
Na^{α}	25.1±1.0	4.8±0.5	2.5±0.1	5.7±0.2	19.3±1.1	19.3±1.1
P^{β}	964±7	548±65	197±8	200±4	341±38	558±62
Mn^{β}	482±3	268±12	58±2	57±4	60±2	232±13
Fe^{β}	141±5	82±6	38±3	65±3	4032±616	24640±3764
Zn^{β}	6.0±0.05	3.0±0.5	1.3±0.6	1.0±0.0	14.5±2.4	32.1±3.2
Cu^{β}	1.5±0.2	0.9±0.0	0.4±0.05	0.25±0.1	2.3±0.1	5.3±0.01
Mo^{β}	<0.5	<0.5	<0.5	<0.5	4.4±0.7	18.4±3.5
Cr^{β}	3.2±0.05	3.0±0.2	1.3±0.4	1.3±0.7	6.5±0.1	10.4±1.7
Ni^{β}	2.7±0.3	2.3±0.5	0.5±0.1	0.4±0.0	3.3±0.1	7.7±0.4
Pb^{β}	<2.0	<2.0	<2.0	<2.0	2.9±0.04	7.0±0.8
Co^{β}	<0.25	<0.25	<0.25	<0.25	2.1±0.3	7.5±0.9
Cd^{χ}	<75	<75	94±8	<75	90±11	281±44
As^{χ}	63±2	12±3	6±1	8±2	3450±600	20250±1250
Hg^{χ}	36±1	8±1	<5	<5	20±5	44±10

α=mg g^{-1}; β=μg g^{-1}; χ=ng g^{-1}.

and from 3% to 10% to 11% prop roots, from stations S3 to S1. Also, the percentage of Mo in leaves (1%→2%), branches (1%→6%), stem (8%→33%) and prop roots (1%→10%) increased with increasing stand age, as did Fe in prop roots (0.4%→3%) and Mg in prop roots (4%→13%).

The soil pools constituted the vast bulk of the total forest pool, usually accounting for >90% of the total forest capital of each element (cf. Table 4 with Tables 1–3). The bulk of the elements in mangrove material were stored in dead roots (Figure 1A,B). The dead root pool of nearly all elements was greater than their respective pool in total living tissue.

In living tissue, most of the C, N, Mn, and P were vested in stems, and most of the K, Ca, and Mg were stored equally in stems and live roots. The remaining elements were stored in live roots, especially Fe, Cu, Mo, Zn, S, Pb, Co, Ni, Cd, As and Hg.

Table 4 *Rhizophora apiculata*: mean total standing amounts of soil elements to the depth of maximal live root penetration.

	S3	S2	S1
C^{α}	337.1	189.4	162.8
N^{α}	12.9	6.5	6.1
Mg^{α}	32.3	22.3	17.1
Ca^{α}	11.7	22.2	4.6
S^{α}	102.3	100.8	64.3
K^{α}	34.9	30.0	21.8
Na^{α}	55.7	30.0	19.5
P^{β}	1039	1018	672
Mn^{β}	1203	2302	897
Fe^{α}	127.5	118.8	75.7
Zn^{β}	198.2	191.7	126.9
Cu^{β}	28.1	30.0	38.9
Mo^{β}	41.3	30.8	15.9
Cr^{β}	140.4	101.1	87.7
Ni^{β}	91.0	68.0	49.7
Pb^{β}	115.8	57.4	48.3
Co^{β}	41.1	48.2	26.8
Cd^{χ}	0.5	0.4	0.5
As^{χ}	62.3	75.6	38.7
Hg^{χ}	0.2	0.1	0.1

Values include contribution from live and dead roots. Element concentration data taken from Alongi et al. (2004) multiplied by soil dw values of 5300, 7700 and 5300 t dw ha^{-1} at Stns S3 (3 years old), S2 (5 years old), and S1 (25 years old), respectively. $^{\alpha}$=t ha^{-1}; $^{\beta}$=kg ha^{-1}; χ=g ha^{-1}.

Discussion

The *Rhizophora apiculata* forests of Sawi Bay were very productive (17–53 tC ha^{-1} y^{-1}), but the increase in production and biomass accumulation with age was nonlinear: the 25-year-old forest was the largest and most productive stand, but the replanted 3-year-old stand exhibited greater rates of photosynthesis and was larger than the 5-year-old forest (Alongi and Dixon 2000). This variability can be most directly related to confounding site differences in human impacts on soil fertility, as the youngest forest was planted in reclaimed shrimp ponds containing soils with residual organic matter from previous aquaculture production and that also received an initial amount of fertiliser (Ratanasermpong et al. 2000). Intertidal position also played a role in forest production: the two most productive forests were situated at the seaward edge, whereas the 5-year-old forest was located at a higher elevation, receiving less tidal inundation and sediment influx, and hence less nutrients, than the other two forests (Alongi et al. 2001).

In all cases, the factor "age" for the forests was confounded through pseudoreplication. Hence, the experimental effects cannot be considered definitive.

Despite biomass and productivity variations with age, intertidal position, and other confounding factors (e.g., human impacts), some patterns of element partitioning and forest nutrient capital did emerge from the data. First, concentrations of most (but not all) elements in var-

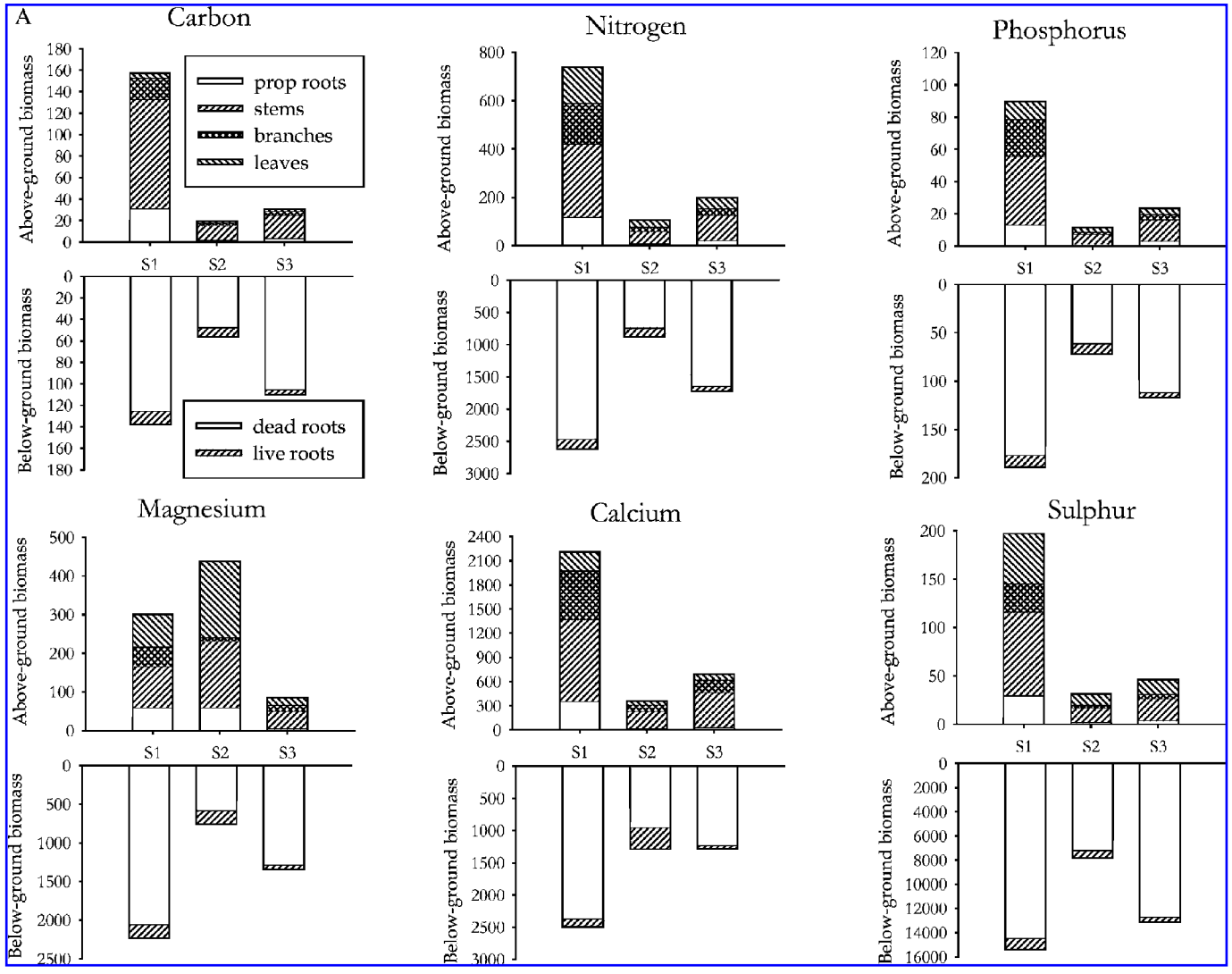

Figure 1A *Rhizophora apiculata.*
Partitioning of C, N, P (top row), Mg, Ca, and S (bottom row) in leaves, branches, stems, prop roots, and live and dead fine roots of trees. Standing amounts of soil elements are in Table 4. Forest sites as station numbers (S1, S2 and S3) are identified between the above- and below-ground plots. Station ages: Stn S1=25 years old, Stn S2=5 years old, and Stn S3=3 years old. Note differences in scaling between above- and below-ground plots and between elements. Carbon units are tC ha^{-1} and ka ha^{-1} for the other elements.

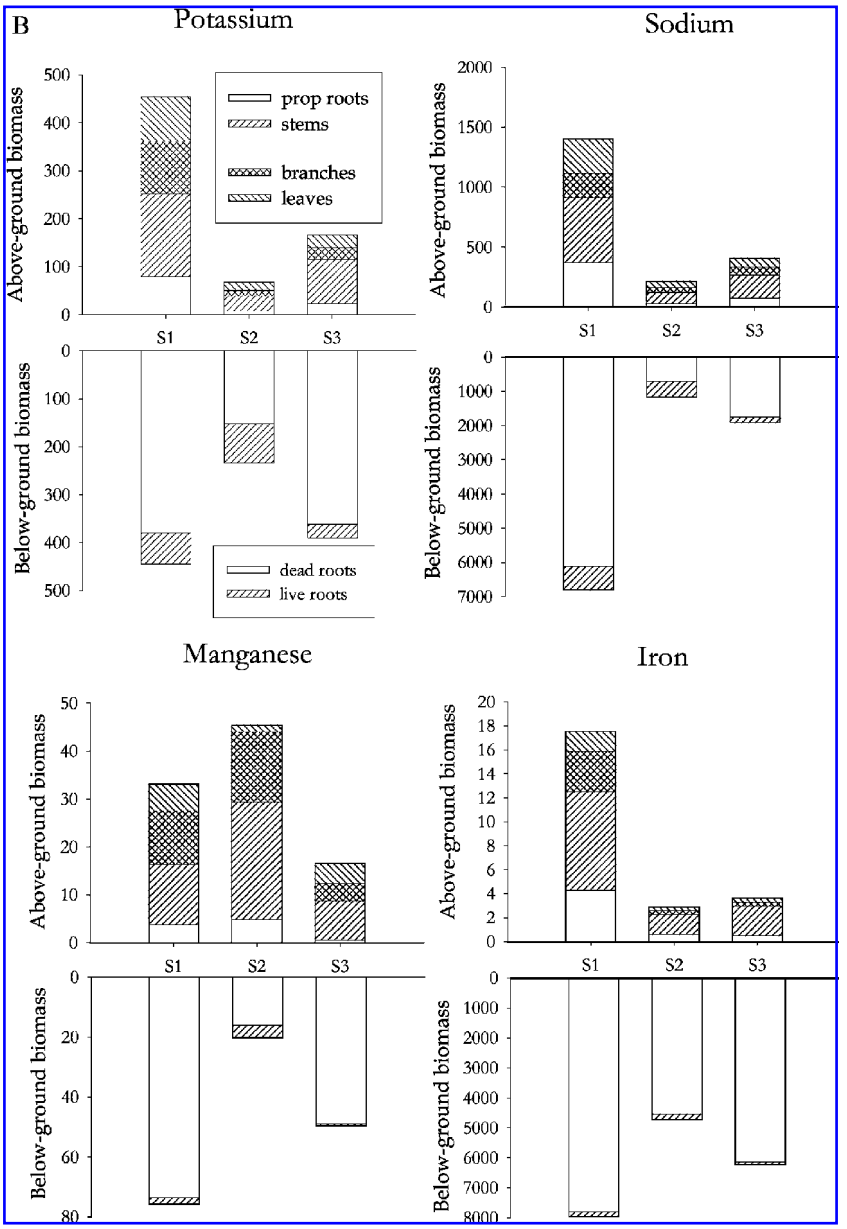

Figure 1B *Rhizophora apiculata*.
Partitioning of K, Na (top row), Mn and Fe (bottom row) in leaves, branches, stems, prop roots, and live and dead fine roots of trees. Standing amounts of soil elements are in Table 4. Forest sites as station numbers (S1, S2 and S3) are identified between the above- and below-ground plots. Station ages: Stn S1=25 years old, Stn S2=5 years old, and Stn S3=3 years old. Note differences in scaling between above- and below-ground plots and between elements. Units are kg ha^{-1} for each element.

ious tree parts declined with increasing tree age. Second, the soil pool size of most elements decreased with increasing stand age. Finally, the proportion of C, N, Na, Mn, Zn and Mo in total living biomass of the total respective forest pools increased with increasing forest age (Table 5).

These patterns must be considered with caution owing to the lack of replication among sites of the same age, but data from many other forested ecosystems indicate that element concentrations in tree components decline with age (Golley et al. 1975, Nwoboshi 1984, Folster and Khanna 1997). The reasons for this pattern are complex, owing to synergistic/antagonistic interactions of climate, successional state, soil fertility and leaching, nutrient-use efficiency, and net ecosystem and canopy production (Gower et al. 1996, Ryan et al. 1997, Barnes et al. 1998). The same reasons can be offered here, but the available nutrient elements appear to accumulate in tree biomass over time. The bulk of the remaining mineral and trace elements in these soils probably reside in organically and inorganically bound forms (i.e., metal oxides) that are unavailable to plants. The dissolved pore water pools for all elements were several orders of magnitude smaller than solid-phase pools and exhibited a sharp decline in the wet monsoon due to percolation and dilution by rainwater and less saline tidal water (Alongi et al. 2004). The behaviour of dissolved and solid-phase elements in soils is influenced by physical and biological reworking, and

Table 5 *Rhizophora apiculata*: percentage of the total pool of each major element vested in total living mangrove biomass at each location.

	S3	S2	S1
C	10	13	53
N	2	3	12
Mg	0.4	3	3
Ca	6	3	34
S	0.4	0.6	2
K	0.6	0.5	2
Na	1	2	10
P	3	2	13
Mn	1	2	4
Fe	0.06	0.2	0.2
Zn	0.2	0.3	0.8
Cu	0.7	0.3	0.6
Mo	0.6	0.7	2

Values are rounded. S3 (3 years old), S2 (5 years old), S1 (25 years old).

by tidal pumping and infiltration acting with roots to foster a biogeochemical profile that is periodically exposed to surface waters and atmospheric conditions. These phenomena may have a stronger impact on soil chemistry, or act more rapidly, than uptake by tree roots.

All elements were stored mostly in soils and dead fine roots. The storage of elements below ground has been observed in other mangrove forests (Alongi et al. 2003). This phenomenon was attributed to the slow decomposition rates of mangrove roots due to their refractory nature. These subsurface pools may act as a mechanism to conserve nutrients and other elements (Alongi et al. 2003). In terrestrial forests, a large proportion of nutrient capital is stored in floor litter (Barnes et al. 1998), but in mangroves, tidal flow and crab foraging prevent accumulation of litter on the forest floor, necessitating storage beyond the direct impact of tidal action and surface water flow. If large subsurface pools of dead roots are typical of most mangrove forests, mangrove soils are implicated as prime sites for carbon sequestration, and should be managed in such a way as to conserve the soil horizon.

Geochemical processes occurring beneath the forest floor exert an important influence on storage and availability of soil elements. In the Sawi Bay forests, Alongi et al. (2004) analysed differences in concentrations of S and Fe between live and dead roots, and found evidence for extensive formation of pyrite and co-precipitation of trace metals associated with dead roots. Another explanation is that metal plaques form on mangrove roots, functioning as a protective layer to limit plant uptake of toxic solutes such as sulphides (Lacerda 1997). The geochemical evidence points to net immobilisation and storage of mineral and trace elements rather than uptake by plants or release to tidal waters. Little, if any, tidal flux of trace elements occurs across the sediment-water interface in these ecosystems (Alongi et al. 2004).

Foliar concentrations of C, N, P, K, S, Mg and Na were at the mid-range of values reported for other tropical trees, including mangroves (Spain and Holt 1980, Silva et al. 1990, Drechsel and Zech 1991, 1993, Jayasekera 1991). However, concentrations of foliar Ca, Mn, Pb, Cd and Hg were higher, and foliar levels of Zn, Cu, Fe, and Mo were lower, than concentrations in other tropical leaves. Laboratory studies (Silva et al. 1990, Jayasekera 1991) suggest that *Rhizophora* accumulates Ca in leaves, but concentrations of other highly mobile elements such as K and Na were mid-range compared with other tropical trees, implying selective bioavailability of some, but not all, mineral and trace elements. The trace element requirement of mangrove trees is very poorly understood. The comparatively high levels of heavy metals in these trees reflect the fact that a variety of human activities affect the catchment (Ratanasermpong et al. 2000). The fact that these forests are highly productive despite the high metal concentrations suggests tolerance to, or some mechanism within, the trees to ameliorate the effects of metal toxicity.

The foliar molar N:P ratio for these *Rhizophora apiculata* trees ranged from 21.8 to 29.9. Foliar N:P ratios >16 normally indicate that P is limiting (Aerts and Chapin 2000). We cannot verify that P limitation is occurring in Sawi Bay, but experimental studies in dwarf mangrove communities and in mature *R. stylosa* Griff. stands inhabiting soils with soil P concentrations and foliar N:P ratios equivalent to the Sawi Bay mangroves, have indicated P deficiency (Boto and Wellington 1983, Feller et al. 1999).

Our data do not support the view that wet tropical forests store proportionally more nutrients in the canopy or live roots than in their soils as compared with temperate and boreal forests (see references in Barnes et al. 1998). In mangroves, the vast bulk of most elements is stored in soils, probably in forms not readily available to plants (Alongi et al. 2003, this study). In forests of the mangroves *Rhizophora stylosa* and *Avicennia marina* (Forsk). Vierh. 1907, $>95\%$ of the total forest capital of nearly all elements was stored in soils, with little difference between forests of both species (Alongi et al. 2003).

The data from the *Rhizophora apiculata* forests of Sawi Bay suggest that the proportion of nutrient elements stored in tree biomass increases and decreases in soil as forests age. Only 2–3% of total forest N capital was vested in 3- and 5-year-old trees, but 12% was stored in 25-year-old trees (Table 5) suggesting net accumulation with forest maturity. This pattern was nearly identical for carbon, phosphorus, calcium, sulphur, potassium, sodium, manganese and molybdenum (Table 5). These percentages are not greatly different from other tropical forests, or from boreal and temperate forests (Golley et al. 1975, Barnes et al. 1988). The range of percentages within the tropical, temperate and boreal biospheres is as wide as those between forests of different latitude.

The rate of nutrient turnover does vary among forests of different latitude. Analyses of the mean residence time of nitrogen in the forest floor of tropical, temperate, and boreal forest ecosystems show that turnover of nitrogen increases with decreasing latitude (Vogt et al. 1986, Barnes et al. 1998). Residence times for nitrogen in temperate forests are usually calculated using only aboveground litter production, which accounts for only 28–56% of total litter input to the forest floor, underestimating total ecosystem N turnover. If root N turnover were considered (for which there are few data), residence times would be shortened considerably (Vogt

et al. 1986). We have no litter fall data for the Thai mangroves, but if we estimate mean residence time of total forest N by dividing total living forest N biomass (Figure 1A) by total soil N decomposition (data in Alongi et al. 2002) for each forest, we obtain the following values: 0.3 years for the 3-year-old forest (Stn S3), 0.5 years for the 5-year-old forest (Stn S2) and 0.6 year for the 25-year-old forest (Stn S1). These estimates suggest that (1) total ecosystem N turnover may slow down with increasing stand age; and (2) mean residence time for N is very short in these wet tropical mangrove forests compared with other forested ecosystems. This agrees with previous findings that mangrove ecosystems exhibit tight coupling between production and decomposition pathways, and is driven by high nutrient needs (Boto 1992, Clough 1992). We cannot directly compare our estimates with those compiled by Vogt et al. (1986) and Barnes et al. (1998), but it is clear that mangrove and other tropical forested ecosystems more rapidly cycle nitrogen (and probably other mineral and trace nutrients) than forests of higher latitude.

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