

Relationship between sediment conditions and mangrove *Rhizophora apiculata* seedling growth and nutrient status

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ABSTRACT: The growth rate and nutritional status of *Rhizophora apiculata* seedlings were analyzed across mangrove stands with different sediment composition in The Philippines and Southern Thailand. Plant growth differed 10-fold and the production of new leaves, roots and branches varied between 50- and 100-fold across sites. Most (>60%) of the variance in mangrove growth rate across systems could be accounted for by differences in the nutrient concentration of the leaves, which was in turn related to the interstitial nutrient concentration and the silt plus clay content of the sediments. Nutrient-poor coarse sediments were characteristic of mangroves located in the mouths of rivers draining small watersheds, while sediments at the mouths of large rivers had high silt, clay, and nutrient contents, thus allowing the development of nutrient-sufficient, fast-growing *R. apiculata* seedlings. The growth of *R. apiculata* seedlings increased significantly when the plants grew adjacent to rivers draining areas >10 km². The results provide evidence that growth of *R. apiculata* seedlings at the edge of the progressing mangrove forests is often nutrient limited, and that the extent of nutrient limitation depends on the delivery of silt and nutrients from the rivers. The coastal zones adjacent to small (<10 km²) drainage areas seem unsuitable to support adequate growth of *R. apiculata* seedlings, and afforestation programmes should, therefore, target mud flats adjacent to large rivers instead.

KEY WORDS: SE Asia · Mangrove growth · Nutrient status · Sediment nutrients · Watershed size

INTRODUCTION

The development of large mangrove forests depends on warm air temperatures, high (>0.75) values of the mean annual rainfall/potential evapotranspiration ratio (Blasco 1984), and the generation of vast intertidal substrata by coastal geomorphic processes (Thom 1984). The climate in Southeast (SE) Asia, which is characterized by high rainfall, and rivers with high silt loads (Milliman & Meade 1983, Milliman & Syvitski 1992) combine to provide favourable conditions for

mangrove development, and mangrove forests cover large areas in the deltaic areas along the coasts of SE Asia (Mcnae 1968). Water hydrology is a major determinant of mangrove productivity, and the highest productivity values are usually reported in mangroves associated with rivers (Twilley et al. 1986). River flow and tides are powerful mechanisms for the transfer of matter between ecosystems and they cause a large fraction of mangrove production (on average 29.5%; Duarte & Cebrián 1996) to be exported from the ecosystem as leaf litter and propagules (e.g. Twilley et al. 1986, Hemminga et al. 1994, Panapitukkul et al. 1998). In addition, a substantial fraction of the mangrove production is buried in the sediments (10.4% on average;

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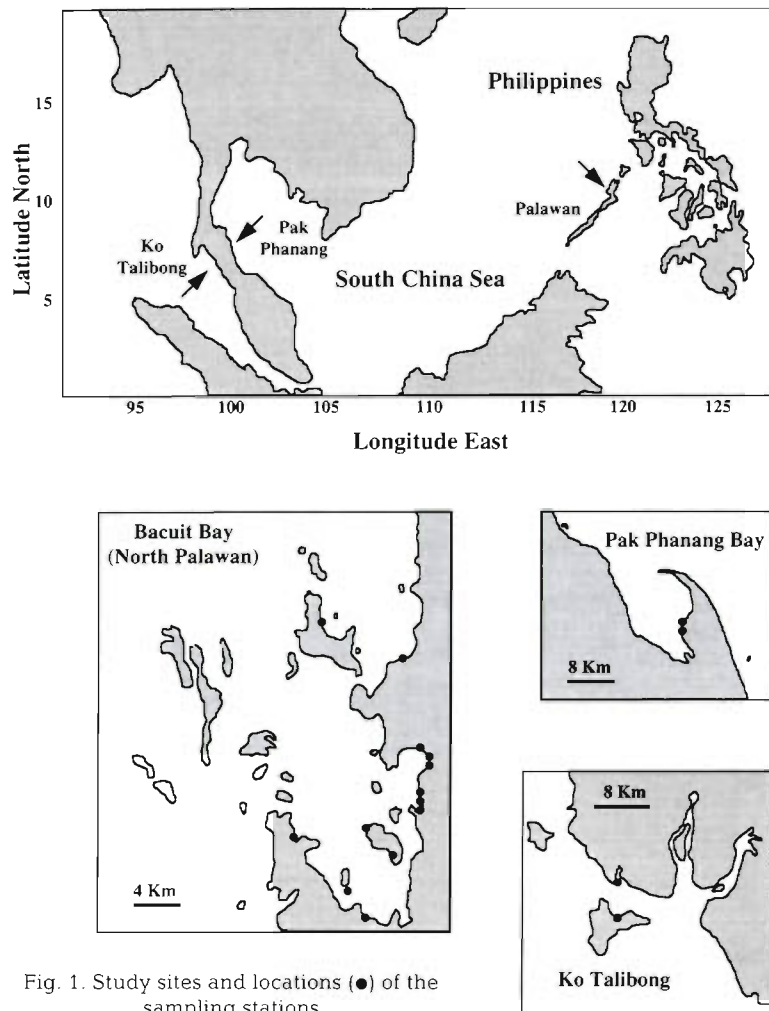


Fig. 1. Study sites and locations (●) of the sampling stations

Duarte & Cebrián 1996), so that the production available for recycling within the ecosystem is reduced (50% on average; Duarte & Cebrián 1996). Accordingly, a large fraction of the mangrove production is lost from the ecosystem (Boto & Bunt 1981, Twilley et al. 1986), leading to an associated high loss of nutrients. Mangrove ecosystems tend to be, therefore, autotrophic communities (Duarte & Cebrián 1996, Gattuso et al. 1998) whose primary production should, therefore, depend on continuous nutrient supply from land or sea.

The continuous export of nutrients from mangrove ecosystems led us to hypothesize that the growth of mangrove trees may often be nutrient limited, as already shown by some nutrient addition experiments (Boto & Wellington 1983, Feller 1995), and that the extent of nutrient limitation should depend on the input of nutrients from land. Moreover, we suggest that nutrient limitation may be most pronounced at the edge of the mangrove forest, where the higher exposure leads to an

increased likelihood of export losses, and where nutrient availability in the sediment is lower (Tam et al. 1995). These considerations suggest that mangrove seedlings established at the edge of the mangrove forest may have reduced growth, which would represent an important bottleneck for the sustained expansion of the mangrove forest (e.g. Panapitukkul et al. 1998).

In order to test these hypotheses, we assessed the nutrient (C, N and P) status of mangrove seedlings growing along the forest edge across a range of sites in SE Asia. The sites receive discharge from rivers representing a gradient of watershed sizes, which vary from creeks in small islands to large rivers (e.g. Pak Phanang river, Nakhon Si Thammarath, Southern Thailand). In the present study we focused on the seedlings of *Rhizophora apiculata*, a common species throughout the region, and one that is particularly relevant because of its importance as the target species in afforestation plans (Aksornkoae 1993). Growth of the seedlings was calculated from measurements of height and estimates of age derived from counts of internodes as described by Duke & Pinzón (1992) for *Rhizophora mangle* and modified by Duarte et al. (unpubl.) for *R. apiculata*. The nutrient status of the plants was described from the C, N and P content in their leaves (Chapin 1980), while the nutrient availability at the study sites was represented by the nutrient concentrations within the sediments.

METHODS

Study sites. The study was conducted under the framework of a large, interdisciplinary project aimed at elucidating effects of siltation on SE Asian coastal ecosystems (CERDS project, funded by the European Commission). The study extended across sites in The Philippines (Bacuit Bay, Palawan) and Thailand (Trang coast, adjacent to Ko Talibong island, and Pak Phanang estuary), encompassing a broad range of conditions (Fig. 1). Bacuit Bay is a large, open bay with numerous islands of different sizes, which receives freshwater discharges from a couple of medium-sized rivers that support significant mangrove forests at their mouths. Although the Bay is still largely surrounded by forests, the watersheds of the larger rivers are now

experiencing deforestation and increased erosion resulting from road construction and slash and burn practices, which have led to increased silt loading (Hodgson 1989). In contrast, the islands present in the bay are still almost fully covered by vegetation, and pockets of mangroves grow near the mouth of the small streams and creeks draining the islands.

The coastal areas in Pak Phanang and Trang in Thailand both receive the discharge of large rivers (15 to 120 and 2.5 to 51.5 m³ s⁻¹, respectively), and mangrove forests develop in the proximity of these river mouths (Fig. 1). The watersheds of both rivers have suffered major changes in land use over the past century, including a recent proliferation of shrimp ponds, which have led to a major increase in the silt loads of these rivers (CORIN 1991). The Pak Phanang river discharges into a semi-enclosed Bay, where a thick mangrove forest (92 km²; CORIN 1991) progresses at rates of about 40 to 50 m yr⁻¹ along the mud flat formed by river deposits (cf. Panapitukkul et al. 1998). Additional details on the sites can be found in Panapitukkul et al. (1998) and Terrados et al. (1998).

Sampling and analyses. Several sampling stations, located along the fringes of mangrove formations in the mouths of rivers of contrasting catchment sizes, were established in March-April 1996 following a preliminary survey conducted in 1995. The mangroves ranged from large forests, associated with large rivers, to small groups of seedlings with a few adult trees growing on the shores of small islands. The size of the watersheds of the different rivers was obtained from national geographic databases and reports. Whenever these estimates were unavailable, the watershed of the rivers was delineated on a topographic map and digitized to estimate the size of the riverine watershed associated with the mangrove stands sampled.

At each sampling site, the height of 30 to 40 *Rhizophora apiculata* seedlings, spanning the broadest possible range in size (<1 to 3.5 m), was recorded, and the number and individual lengths of internodes along the main axis were measured. We also counted the number of roots developed by the plants, the total number of standing leaves and the number of branches. A sample of about 12 fully grown leaves was collected from several of the seedlings examined at each station for subsequent analysis of nutrient contents. Leaf carbon and nitrogen were determined using a Carlo-Erba CHN analyzer, while leaf phosphorus was analyzed as phosphate (Parsons et al. 1984) after Kjeldahl digestion. Duplicate sediment cores (4.5 cm internal diameter, 25 cm long) were collected to a sediment depth of about 15 cm at each site and kept refrigerated until processed within 1 to 3 h. The upper 10 cm of the cores was transferred to a GF-C fiber glass filter, and 5 to 20 ml of porewater was extracted under vac-

uum directly into 20 ml vials and preserved with 100 µl of concentrated sulfuric acid until later analysis. After neutralization with sodium hydroxide, the samples were analyzed for dissolved reactive phosphate, ammonium and nitrate on an Alpkem RAF autoanalyzer following standard methods (Parsons et al. 1984). The silt plus clay content of sediments was analyzed by weighing the fraction of a subsample of sediment material dried at 105°C for 24 h which passed through a 63 µm screen in a sieve-shaker.

Seedling growth determinations. Seedling age was estimated from counts of the number of internodes and knowledge of the number of internodes produced annually. Duke & Pinzón (1992) reported that seedling age of the mangrove *Rhizophora mangle* can be determined from the presence of distinct seasonal changes in the length of the internodes, which was also recently confirmed for SE Asian mangrove species, including *R. apiculata* (Duarte et al. unpubl.). In essence, the sequence of the internodal length is first filtered to remove short (<seasonal) and long (interannual) term variability, respectively. Interannual variability is removed using a low-pass filter (running average of 11 internodes), while sub-seasonal variability was removed by filtering the residuals through a high-pass filter (running average of 3 internodes). The remaining signal has a clear periodicity with period length representing the number of internodes produced in a year (Duarte et al. unpubl.). In the present study, annual internode production was estimated from the examination of >12 annual cycles per sampling site, and seedling age was determined as the ratio between the number of internodes produced over the life span of the seedling and the average number produced annually.

The rate of seedling growth was subsequently calculated from linear regression between the height of the seedlings, the number of roots, branches and standing leaves, and their estimated age. The slope of the regression equations represents the centimeters grown and the increment in the number of roots, branches, and standing leaves per year. Whenever examination of the relationships suggested these to be nonlinear, we fitted an allometric ($y = a x^\mu$) model to the height or number of standing roots, branches or leaves (y) and the estimates of age (x) to describe the exponential growth rates (μ , yr⁻¹). The significance of the relationship between seedling growth and leaf nutrient and sediment properties was tested using linear correlation analyses, for which the data were log-transformed when necessary to comply with the assumptions of the analysis. In a few instances, cores containing porewater samples were damaged during transportation to the laboratory, and the samples were lost, resulting in an uneven number of observations for the different paired statistical analyses conducted.

Table 1. Mean (\pm SE) and range of the variables measured or derived in this study

	N	Minimum–maximum	Mean \pm SE
Leaf C (% DW)	17	36.87–46.15	41.16 \pm 0.59
Leaf N (% DW)	17	0.78–1.66	1.05 \pm 0.05
Leaf P (% DW)	17	0.057–0.117	0.075 \pm 0.004
Growth (cm d ⁻¹)	17	0.015–0.15	0.059 \pm 0.010
Internode production (internodes yr ⁻¹)	17	5.2–8.9	7.3 \pm 0.2
Net leaf production (leaves seedling ⁻¹ d ⁻¹)	17	0.005–0.445	0.062 \pm 0.026
Branch production (branches d ⁻¹)	17	0.00004–0.016	0.004 \pm 0.001
Root production (roots d ⁻¹)	17	0.0005–0.018	0.004 \pm 0.001
Allometric coefficient of growth in height	17	0.17–0.71	0.38 \pm 0.04
Allometric coefficient of leaf production	17	0.42–2.28	0.99 \pm 0.13
Watershed size (km ²)	17	0.1–100	21.85 (median)

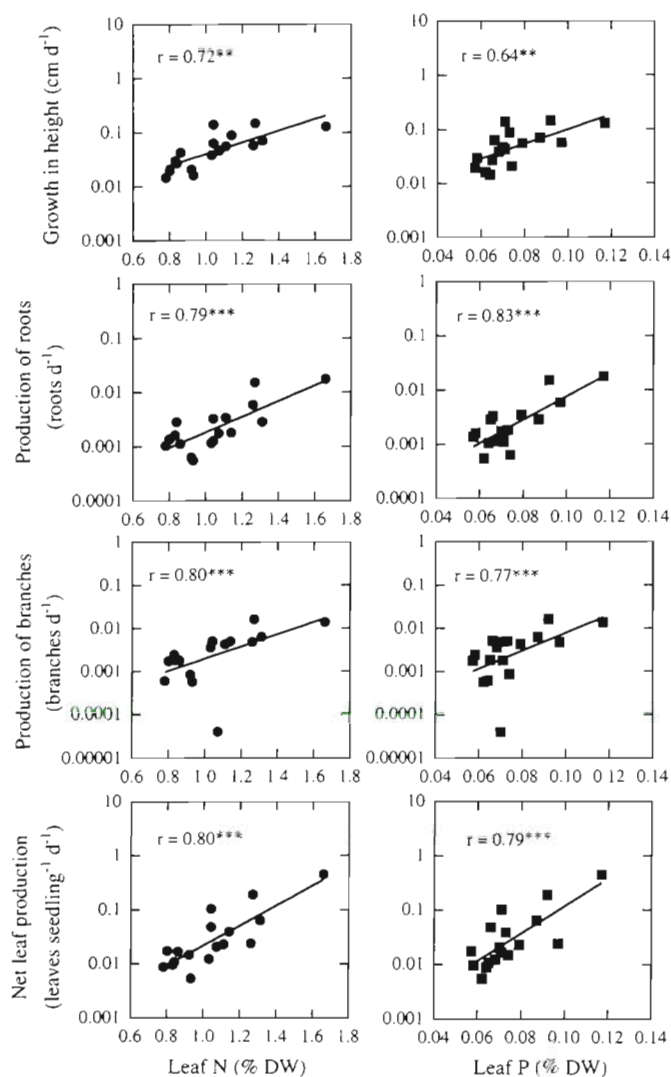


Fig. 2. *Rhizophora apiculata*. Relationship between the growth rate of mangrove seedlings and the nitrogen and phosphorus concentrations of their leaves (as % DW). Solid lines represent the fitted regression equations, and r is the corresponding linear correlation coefficient. ** $p < 0.01$, *** $p < 0.001$

RESULTS

The number of internodes produced per year did not vary much among mangrove stands and averaged 7.3 ± 0.2 (mean \pm SE) internodes yr⁻¹ (Table 1). Internode production was independent of sediment conditions and nutrient status of the plants (Pearson linear correlation coefficient, $p > 0.05$), suggesting that the number of internodes produced per seedling per year is a rather conservative feature of *Rhizophora apiculata*. In contrast, the growth rates varied 10-fold among sites (Table 1), with the fastest growth (0.15 cm d^{-1}) recorded for seedlings from the mud flat of the Pak Phanang River and the slowest growth (0.015 cm d^{-1}) for seedlings growing on the shores of the smaller islands in Bacuit Bay. The relationship between seedling height and age was nonlinear and best described by an allometric relationship. The slope of the allometric relationship averaged 0.38 ± 0.04 , indicating seedling height to increase as the third power of age (Table 1). The seedlings produced, on average, 1 new stilt root and a new branch every 250 d but with considerable differences among stands (Table 1). The canopy of the seedlings increased with age, with the plants gaining a new leaf every 2 wk, on average. The canopy of seedlings growing on the shores of small islands only gained a new leaf every 200 d, because of high leaf loss rate, while that of seedlings growing on the rich mud flat of the Pak Phanang gained a new leaf every other day (Table 1), as a result of extensive branching and longer leaf life spans.

The nitrogen content of *Rhizophora apiculata* leaves varied from 0.78 to 1.66% of dry weight (DW) (Table 1). The phosphorus concentration in leaves ranged from 0.057 to 0.117% of DW and was significantly correlated to foliar nitrogen content ($r = 0.93$, $p < 0.001$). In general, *R. apiculata* seedlings had rather balanced N:P ratios (31.2 ± 0.6 atomic ratio). The ratio of total inorganic nitrogen (TIN) to phosphate in the sediment porewaters

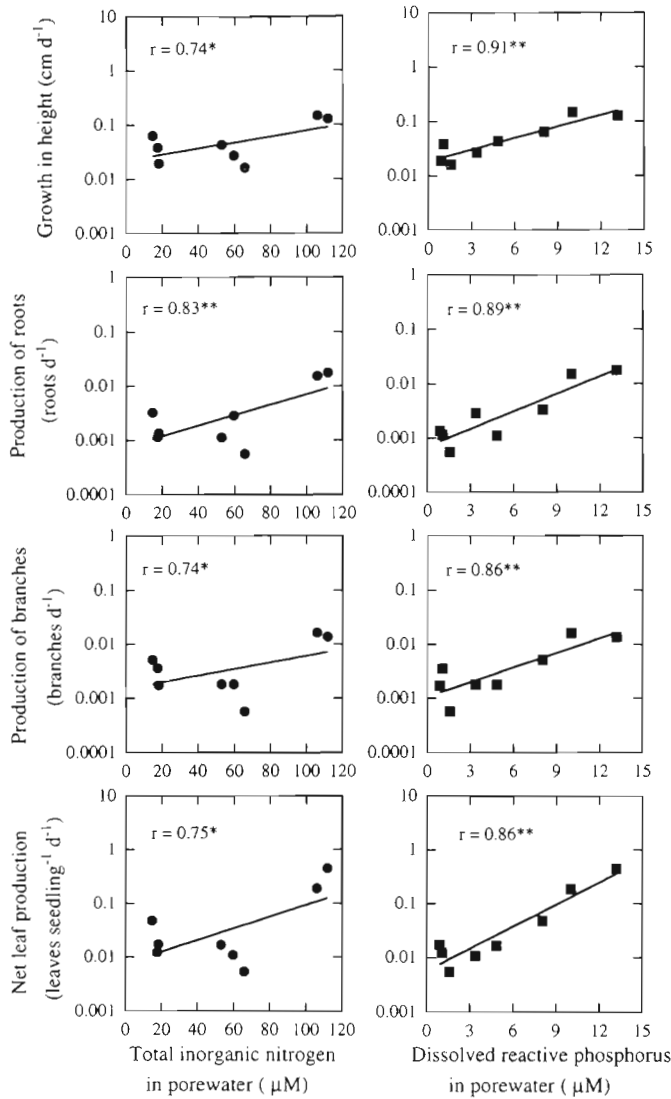


Fig. 3. *Rhizophora apiculata*. Relationship between the growth rate of mangrove seedlings and the total inorganic nitrogen and dissolved reactive phosphorus concentrations in the sediment porewaters. Solid lines represent the fitted regression equations, and r is the corresponding linear correlation coefficient. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

was relatively low (molar N:P ratio = 7.2 ± 1.3), suggesting a deficit in nitrogen availability relative to that of phosphorus in the sediment porewaters.

The hypothesis that *Rhizophora apiculata* growth may be nutrient limited in the area was supported by the finding of strong positive correlations between seedling elongation rate, leaf, root and branch formation and leaf N concentrations ($r \geq 0.72$, $p > 0.005$; Fig. 2). Seedling growth was also positively correlated with leaf P concentrations ($r \geq 0.64$, $p > 0.005$; Fig. 2). Nutrient concentrations in the leaves were, in turn, associated with the porewater inorganic nutrient concentrations ($r = 0.72$

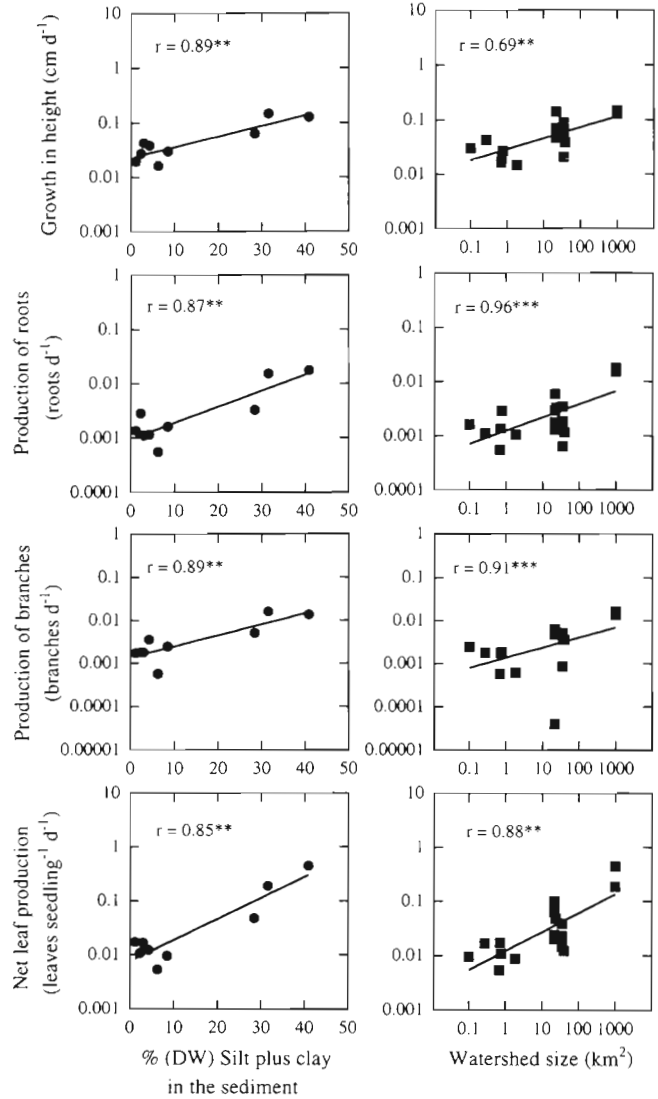


Fig. 4. *Rhizophora apiculata*. Relationship between the growth rate of mangrove seedlings and the silt plus clay content of the sediments, and the area drained by adjacent rivers or streams. Solid lines represent the fitted regression equations, and r is the linear correlation coefficient. ** $p < 0.01$, *** $p < 0.001$

and $r = 0.88$ for N and P, respectively, $p < 0.005$). As a result, there were strong, significant positive correlations between seedling growth and nutrient concentrations in the sediment porewaters ($r \geq 0.74$ and $r \geq 0.86$ for total inorganic nitrogen and phosphorus, respectively, $p < 0.005$; Fig. 3).

Leaf nitrogen and phosphorus concentrations were positively ($p < 0.01$) correlated with the percent of silt plus clay in the sediment ($r = 0.89$ and $r = 0.82$, respectively), and seedling growth was also positively correlated with the percent of silt plus clay in the sediment (Fig. 4, $r \geq 0.85$, $p < 0.01$). The sediments with low

nutrient concentrations and low contents of silt and clay occurred in association with rivers draining small (<10 km²) watersheds, whereas higher nutrient concentrations were found in the sediments containing high contents of silt and clay delivered by rivers draining large watersheds. Hence, there was a strong positive correlation ($r = 0.69$, $p < 0.01$) between seedling growth and the size of the watershed drained by the rivers (Fig. 4). The relationships were, however, non-linear and suggest a critical watershed size of about 10 km² before the growth of *Rhizophora apiculata* is enhanced in the river mouth (Fig. 4).

DISCUSSION

The study clearly documents that the growth of *Rhizophora apiculata* seedlings living at the edge of progressing mangrove forests is directly correlated to the nutrient and silt contents within the sediments of SE Asian mangrove sites. Seedlings growing over nutrient-poor, coarse sediments had very low growth rates, to the point that their canopy only gained a couple of new leaves per year, while the highly branched canopy of seedlings growing over nutrient-rich, silty sediments gained a new leaf every other day. Experiments with fertilization suggest that the growth of mangrove trees is constrained by insufficient nutrient supplies (Onuf et al. 1977, Boto & Wellington 1983, Feller 1995), which seems to be a general trend for tropical rainforests (Tanner et al. 1998). Twilley et al. (1986) found that tree production is higher (i.e. nutrient limitation less important) in riverine and fringe mangroves than in mangroves with slower water exchange despite the larger export of litter and nutrients from the former. For seedlings growing in the outermost fringes of mangroves, however, variable exposure may markedly change the balance between export and import of silt and nutrients, resulting in highly variable nutrient and silt contents in the sediment. It is, therefore, not a surprise that the growth of newly established seedlings in the mangrove progression zone is variable and strongly controlled by local differences in sediment nutrient content.

The relationships we found between seedling growth, foliar nutrient contents and sediment nutrient status cannot unambiguously distinguish between the roles of different nutrients in the limitation of growth in *Rhizophora apiculata* seedlings. Growth in height and production of roots, branches and leaves were all significantly correlated to both nitrogen and phosphorus in leaves and in sediment porewater. The nitrogen concentrations in *R. apiculata* leaves (range: 0.78 to 1.66% of DW) were similar to, or in the lower end of, those found in other studies of tropical and subtropical

mangroves (0.7 to 2.5% of DW; Onuf et al. 1977, Boto & Wellington 1983, Twilley et al. 1986, Rao et al. 1994, Feller 1995) and were also comparable to foliar nitrogen in different types of tropical rainforests (0.6 to 1.6% of DW; Tanner et al. 1998). Foliar phosphorus of *R. apiculata* seedlings (0.06 to 0.12% of DW) was similar to, or in the higher end of the range of, the levels usually found in both mangroves and tropical rainforests (0.03 to 0.11% of DW; Boto & Wellington 1983, Feller 1995, Tanner et al. 1998), so there seems to be a tendency for younger trees growing at mangrove edges to be primarily nitrogen limited, while older mangroves growing at higher elevations tend to be more limited by phosphorus (Boto & Wellington 1983). In our study there was a weak tendency for nitrogen to be deficient relative to phosphorus both in the leaves and within the sediments, suggesting nitrogen limitation to be most important. Nutrient addition experiments are needed to elucidate the relative roles of nitrogen, phosphorus and other essential sediment components in regulating seedling growth.

The correlations presented suggest strong links between the size of the watersheds drained by the rivers where the mangrove stands develop, and sediment composition, foliar nutrient contents, and mangrove growth. Mangrove soils receive high inputs of organic matter from the mangrove itself (Boto & Bunt 1981, Boto 1984, Twilley et al. 1986), and inorganic nutrients are imported from the sea (Kristensen et al. 1995, Rivera-Monroy et al. 1995). However, a substantial fraction of the fine particulate material and the associated nutrients originate from land and are responsible for the continuous accretion of sediment, allowing sustained progression of the mangrove. The silt plus clay content of the sediments deposited at the mouths of large rivers, such as the Pak Phanang river, was very high, while sediments supporting mangroves near creeks were mainly coarse, marine carbonates. Hence, slow-growing, nutrient-deficient mangrove stands were associated with small rivers, while fast-growing mangroves, with a more balanced nutritional status, were found in association with rivers draining watersheds larger than 10 km².

Southeast Asian mangroves are ecologically and commercially important ecosystems, which have declined dramatically during the last 50 yr due to human exploitation (Chou 1994). While high silt loads caused by changes in land use have a negative impact on most coastal ecosystems (e.g. coral reefs and seagrass beds; Hodgson 1989, Terrados et al. 1998), they can be beneficial for mangrove progression. High silt loads in the rivers cause increased sediment accretion and thus the formation of new habitat suitable for natural mangrove colonization and continuous development of extensive mangrove forests (Panapitukkul et

al. 1998). Our results show that increased siltation will enhance seedling growth, which likely helps the seedlings to outbalance the high mortality rates encountered by newly established unprotected seedlings (Clarke & Myerscough 1993). In order to promote mangrove progression and compensate for earlier losses of forest area, various programmes have been initiated to protect expanding mangrove fringes and afforestation programmes have also been conducted. The nonlinear relationship between seedling growth performance and watershed size found in this study identifies mangroves next to rivers draining watersheds larger than 10 km² as the most profitable target areas in the efforts promoting natural and artificial colonization of *Rhizophora apiculata*.

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