

# Mangrove growth in New Zealand estuaries: the role of nutrient enrichment at sites with contrasting rates of sedimentation

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**Abstract** Mangrove forest coverage is increasing in the estuaries of the North Island of New Zealand, causing changes in estuarine ecosystem structure and function. Sedimentation and associated nutrient enrichment have been proposed to be factors leading to increases in mangrove cover, but the relative importance of each of these factors is unknown. We conducted a fertilization study in estuaries with different sedimentation histories in order to determine the role of nutrient enrichment in stimulating mangrove growth and forest development. We expected that if mangroves were nutrient-limited, nutrient enrichment would lead to increases in mangrove growth and forest structure and that nutrient enrichment of trees in our site with low sedimentation would give rise to trees and sediments that converged in terms of functional characteristics on control sites in our high sedimentation site. The effects of fertilizing with nitrogen (N) varied among sites and across the intertidal zone, with enhancements in growth, photosynthetic carbon gain, N resorption prior to leaf senescence and the leaf area index of canopies being

significantly greater at the high sedimentation sites than at the low sedimentation sites, and in landward dwarf trees compared to seaward fringing trees. Sediment respiration (CO<sub>2</sub> efflux) was higher at the high sedimentation site than at the low one sedimentation site, but it was not significantly affected by fertilization, suggesting that the high sedimentation site supported greater bacterial mineralization of sediment carbon. Nutrient enrichment of the coastal zone has a role in facilitating the expansion of mangroves in estuaries of the North Island of New Zealand, but this effect is secondary to that of sedimentation, which increases habitat area and stimulates growth. In estuaries with high sediment loads, enrichment with N will cause greater mangrove growth and further changes in ecosystem function.

**Keywords** *Avicenna marina* · Leaf area index · Nutrient resorption efficiency · Photosynthesis · Soil respiration · Waikopua · Whangapoua

## Introduction

Sedimentation and nutrient enrichment are major threats to the coastal ecosystems of the world (Thrush et al. 2004). In New Zealand, land-use change associated with agricultural development and urbanization has resulted in an increased sedimentation in estuaries, which has been followed by an expansion of mangroves into estuaries that were previously dominated by coarse sandy sediments with benthic diatom communities (Burns and Ogden 1985; de Lange and de Lange 1994; Ellis et al. 2004). Although high rates of sedimentation (in excess of 1 cm year<sup>-1</sup>) are detrimental to mangroves, causing dieback and death (Ellison 1998), moderate rates of

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sedimentation can lead to enhanced growth (Pezeshki et al. 1992; Ellison and Farnsworth 1996; Ellis et al. 2004). Increased sedimentation is often associated with increases in the availability of nutrients (de Olf et al. 1997; Hemminga et al. 1998; Alongi et al. 2005). Given that mangroves have strong growth responses to nutrient additions (Feller et al. 1995, 2003; Lovelock et al. 2004, 2006), the recent expansion of mangroves in New Zealand could be partially driven by nutrient enrichment of coastal sediments, which would result in increased growth of mangrove trees.

In addition to enhanced nutrient availability, sediments delivered to the coastal zone are often very fine and can have high concentrations of terrestrial organic carbon and other pollutants (Howarth et al. 1991; Thrush et al. 2004). The deposition of fine sediments reduces oxygen concentrations (Thrush et al. 2004), and carbon deposition increases heterotrophic production which can compete for nutrients with primary producers (Gattuso et al. 1998; Orwin et al. 2006). Thus, while nutrient enrichment enhances plant growth by reducing the allocation to roots relative to aboveground tissues (Tilman 1988; van der Werf et al. 1993; McKee 1996; Koch and Snedaker 1997), reductions in sediment oxygen concentrations and carbon-rich materials may decrease plant growth by increasing relative allocation to roots (McKee 1996; Weisner 1996; Eschen et al. 2006). Nutrient enrichment and sedimentation could therefore have opposing effects on ecosystems: nutrient enrichment could stimulate autotrophic production, while the addition of fine sediments could reduce plant growth. For these reasons we would expect mangrove communities to be affected by nutrient availability in different ways in environments with different levels of sedimentation.

To understand the influence of sedimentation and nutrient availability on the growth of mangroves, we conducted an experiment where we artificially enhanced nutrient availability in mangrove forests at two sites in New Zealand: one in a highly modified catchment with high sedimentation rates and another in a less modified catchment that has comparatively lower sedimentation rates. Our aim was to understand the relative effects of sedimentation and nutrient enrichment on mangrove growth and ecosystem function. We tested three hypotheses: (1) mangrove encroachment with sedimentation is mainly due to enhanced growth caused by nutrients arriving with sediments; (2) increased nutrient availability, in the absence of increased sedimentation, has similar effects on mangrove trees as sedimentation; (3) increasing the availability of nutrients will have different effects on plant growth at sites with differing sedimentation rates.

## Materials and methods

### Site description

Two sites from the North Island of New Zealand are used in this study, both having monospecific stands of *Avicennia marina*. Waikopua (Lat. 36°56'E, Long. 174°57'E) is close to the city of Auckland. The site is muddy, with high rates of sediment deposition due to land-use change that includes urban development within the catchment. A general site description of Waikopua can be found in Ellis et al. (2004). The second site was situated in the Whangapoua estuary (Lat. 36°43'E, Long. 175°37'E). This site is less heavily impacted by land-use change than Waikopua, with plantation forestry being the major activity in the catchment. Sediments are coarse to fine sands, and mangroves form open stands without closed canopies. A general site description can be found in Schwarz (2004). The density and basal area of the trees was measured at both sites in October 2003 using the Point Centre Quarter method (Cintron and Schaffer-Noveli 1984). At the low sedimentation site (Whangapoua), tree density was 836 individuals trees ha<sup>-1</sup> with a basal area of 1.08 m<sup>2</sup> ha<sup>-1</sup>, and at the high sedimentation site, (Waikopua) tree density was 16,672 individuals trees ha<sup>-1</sup> with a basal area of 10.4 m<sup>2</sup> ha<sup>-1</sup>.

### Experimental design

At both sites there is a distinctive tree height gradient from taller fringing trees approximately 2–3 m in height along the channel edges, decreasing to very short dwarf trees 0.5–1.2 m in height toward the landward edges. At each site, 18 trees that were approximately 5–10 m apart were selected in both the fringe and dwarf stands. Individual trees were then randomly assigned a treatment. In each zone, six replicate trees were fertilized with nitrogen (N) and six with phosphorus (P), and six were designated as unfertilized controls for a total of 36 trees per site. At Waikopua, trees were fertilized first in October 2001; in Whangapoua, fertilization was started in January 2003. Thereafter, the trees were fertilized at 12-month intervals with 300 g of N fertilizer as urea (N:P:K, 45:0:0), or P fertilizer as P<sub>2</sub>O<sub>5</sub> (N:P:K, 0:45:0), as described in Feller (1995). Briefly, fertilizer was encased in dialysis tubing (Spectropor; Spectrum, Gardena, Calif.) and inserted into 30-cm-deep holes cored on either side of the tree. After inserting the fertilizer, the holes were then plugged with the extracted sediment core. The same extraction and replacement of the core was carried out for the control trees.

Sediment porewater salinity and redox potential were sampled from all trees at both sites in 2005 using the

**Table 1** Sediment characteristics at each of the study sites. Values for salinity are in practical salinity units (PSU) and are the means of 18 measurements  $\pm$  standard errors for each forest type within each site

	Whangapoua, low sedimentation		Waikopua, high sedimentation	
	Fringe	Dwarf	Fringe	Dwarf
Salinity (PSU)	22.2 $\pm$ 1.2	19.6 $\pm$ 0.9	29.8 $\pm$ 0.3	22.8 $\pm$ 1.0
Redox potential at 10 cm (mV)	100 $\pm$ 40	128 $\pm$ 20	76 $\pm$ 47	-34 $\pm$ 39

methods of McKee (1993). Table 1 summarizes the porewater salinity and redox potentials of the sediments. In dwarf forest stands, Whangapoua sediments are more oxidized and less saline than those at Waikopua, while porewater salinity and sediment redox potential in fringing forests are similar at both sites.

### Plant growth

As a bioassay of the effects of nutrient treatment on plant growth, we monitored the number of shoots and the length of shoots on five, initially unbranched, shoots (first order) in sunlit positions in the outer part of the canopy of each tree. To distinguish the growth produced over each interval, we labeled the leaves in the apical position on each of these shoots at each sampling period. Shoot length and number of new leaves (one leaf pair per node) were measured from the previously marked apical position to the base of the current apical bud along the main axis and any shoots. A demographic growth analysis was used to determine the effect of nutrient enrichment on plant growth rates (McGraw and Garbutt 1990; Feller 1995). Demographic absolute growth rates (DAGR) were calculated for monthly increases in shoot length in both the winter period (from May 2004 to October 2004) and summer months (from October 2005 to April 2005) using the formula:

$$\frac{\text{Shoot length}_{\text{time}_1} - \text{Shoot length}_{\text{time}_0}}{\text{time}_1 - \text{time}_0} = \text{DAGR (cm month}^{-1}\text{)}.$$

Stem extension was found to be highly correlated with leaf production over both sites and, therefore, only stem extension is presented here. In winter, the number of leaves month<sup>-1</sup> = 0.396 + 0.933  $\times$  stem extension month<sup>-1</sup>,  $R^2 = 0.924$ ; in summer, the number of leaves month<sup>-1</sup> = 0.714 + 0.894  $\times$  stem extension month<sup>-1</sup>,  $R^2 = 0.910$ .

The heights of all trees were measured at each measurement interval with a telescoping pole. In August 2004, the leaf area index (LAI) was measured using a gap fraction method. A hemispherical photo was taken with a Nikon Coolpix digital camera (model 995; Nikon, Tokyo, Japan) fitted with a fisheye lens under the canopy of each of the trees in the experiment. Images were processed

using the HEMIVIEW CANOPY ANALYSIS computer software program (ver. 2.1; Delta-T Devices Ltd., Cambridge, UK).

### Photosynthetic gas exchange and leaf N

The rates of photosynthetic gas exchange were measured with a Li-Cor 6400 photosynthesis measuring system (Li-Cor, Lincoln, Neb.) in January 2005. Photosynthesis was measured on sunny days with little or no cloud cover using natural light. Light levels were generally saturating for photosynthesis (>800  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), and thus photosynthetic rates were assumed to be close to maximal. Measurements were made on the youngest, fully expanded leaves that were exposed to full sunlight at the time of the measurement. After each measurement was completed (usually in approximately 1 min), the leaf was harvested. Leaf area was measured using a Li-Cor leaf area meter (Li-Cor). The leaves were then dried in an oven at 60°C and subsequently weighed. Dried leaf material was ground to a fine powder in a small mill, and N concentrations of the dried tissue were determined with near-infrared spectroscopy (NIRS; model 5000; Foss NIRS Systems, Silver Springs, Md.) calibrated for *A. marina* leaf tissue using a CHN Analyzer (model 2400; Perkin Elmer, Norwalk, Conn.) at the Smithsonian Environmental Research Center, Edgewater, Md. The P concentration in the leaves was measured by inductively coupled plasma mass spectrometry at the Analytical Services Unit within the School of Land and Food at the University of Queensland.

Resorption efficiency (RE%) was calculated for each experimental tree in January 2005 as the percentage of N or P recovered from senescing leaves before leaf fall (Chapin and Van Cleve 1989):

$$\frac{\text{N (mg cm}^{-2}\text{)}_{\text{green leaves}} - \text{N (mg cm}^{-2}\text{)}_{\text{senescent leaves}}}{\text{N (mg cm}^{-2}\text{)}_{\text{green leaves}}} \times 100 = \text{RE}\%.$$

### Sediment respiration

In January 2005, sediment respiration was measured at low tide, at both sites, using a Li-Cor 6400 portable photosynthesis system configured with the LiCor Soil Respiration chamber. The chamber was set to penetrate only

0.5 cm into the sediment to avoid damaging surface roots. Settings for the measurement were determined at each site following the procedure described by the manufacturer. Sediment temperature was measured simultaneously with sediment respiration at a depth of 2 cm.

#### Data analysis

We used a  $2 \times 2 \times 3$  factorial (site  $\times$  zone  $\times$  nutrient treatment) analysis of variance (ANOVA) to test for differences in plant responses to fertilization treatments across sites. When an ANOVA found a significant main effect or interaction between nutrient treatment and zone, we used Fisher's Least Significant Difference post hoc hypothesis test to examine pairwise differences within and among the treatment levels. Plant growth in winter and summer was analyzed using a repeated measures design. To analyze for heteroscedasticity, we examined probability plots of all variables and residual plots. For heterogeneous variances, we transformed continuous data using logarithms prior to analysis.

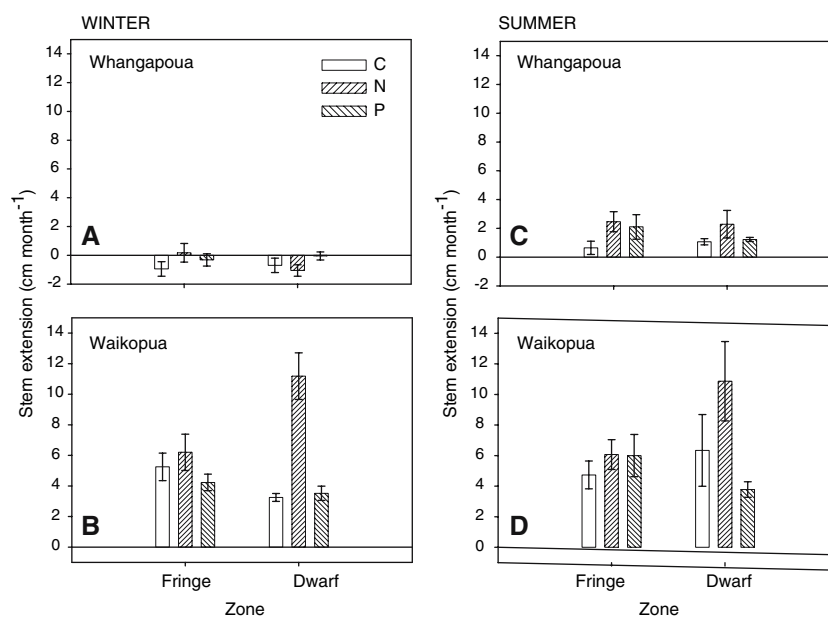
#### Results

Rates of stem extension differed among the two sites and seasonally (Fig. 1). Stem extension was greater at the high

sedimentation site (Waikopua) than at the low sedimentation site (Whangapoua) (main effect of site:  $F_{1, 57} = 174$ ,  $P < 0.0001$ ). Winter growth was less rapid than summer growth ( $F_{1, 57} = 28.0$ ,  $P < 0.0001$ ), with stem extension at Whangapoua in the winter being negative (twigs died back), particularly in dwarf trees. Over all sites and seasons, stem extension was significantly influenced by fertilization ( $F_{2, 57} = 10.3$ ,  $P = 0.0002$ ). N fertilization led to significant enhancements in the growth of dwarf trees at Waikopua and to a lesser extent at Whangapoua, but it did not significantly influence stem extension in fringe trees.

Mean tree height was similar in the fringe zones at both sites, but dwarf trees were taller at the Whangapoua site (Fig. 2a, b). Fertilization had no significant effect on tree height over the course of the experiment. LAI of the trees at Whangapoua was higher than for the trees at Waikopua (Fig. 2c, d). Within 2 years, N fertilized dwarf trees at Waikopua had doubled their LAI.

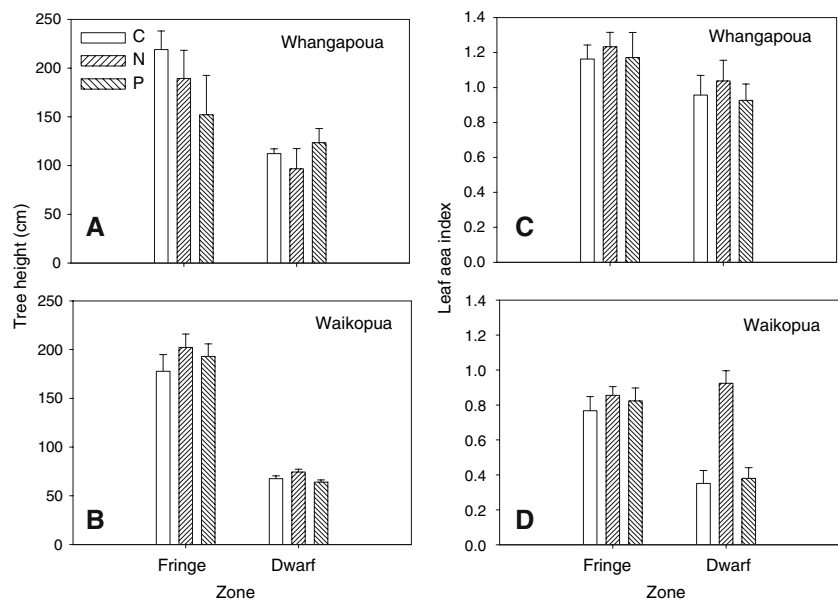
Rates of photosynthetic carbon gain were similar over sites and over zones (Fig. 3a, b). Small effects due to fertilization were evident, with N fertilization increasing photosynthetic carbon gain in dwarf trees at Waikopua, and both N and P fertilization enhancing photosynthetic carbon gain in fringing trees at Whangapoua. Sediment  $\text{CO}_2$  exchange (respiration) measured at low tide was higher at Waikopua than at Whangapoua (Fig. 3c, d). Sediment respiration was similar over both zones and showed no



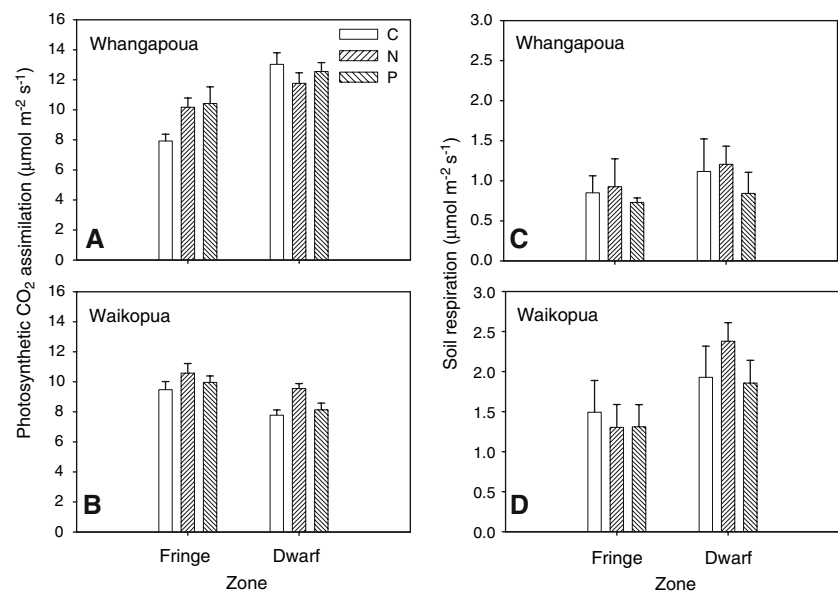
**Fig. 1** Stem extension ( $\text{cm month}^{-1}$ ) of fertilized trees of the mangrove *Avicennia marina* at two sites with contrasting sedimentation – a, c Whangapoua (= low sedimentation), b, d Waikopua (= high sedimentation) – in both winter (a, b) and summer (c, d). Trees were either fertilized with nitrogen (N) or phosphorus (P) or were designated as controls (C). Values are the mean and standard

error of stem extension rate for eight trees derived from following the extension of five individual shoots per tree. Stem extension is highly correlated with leaf production. In winter, the number of leaves  $\text{month}^{-1} = 0.396 + 0.933 \times \text{stem extension month}^{-1}$ ,  $R^2 = 0.924$ ; in summer, the number of leaves  $\text{month}^{-1} = 0.714 + 0.894 \times \text{stem extension month}^{-1}$ ,  $R^2 = 0.910$

**Fig. 2** Tree height (a, b, cm) and leaf area index (c, d,  $m^2 m^{-2}$ ) of fertilized trees of the mangrove *A. marina* at two sites with contrasting sedimentation: a, c Whangapoua (= low sedimentation), b, d Waikopua (= high sedimentation). Trees were either fertilized with nitrogen (N) or phosphorus (P) or were designated as controls (C). Values are the mean and standard error for eight trees



**Fig. 3** Photosynthetic  $CO_2$  assimilation of leaves (a, b,  $\mu mol m^{-2} s^{-1}$ ) and soil respiration (c, d,  $\mu mol m^{-2} s^{-1}$ ) of fertilized trees of the mangrove *Avicennia marina* at two sites with contrasting sedimentation: a, c Whangapoua (= low sedimentation), b, d Waikopua (= high sedimentation). Trees were either fertilized with nitrogen (N) or phosphorus (P) or were designated as controls (C). Values are the mean and standard error for eight trees



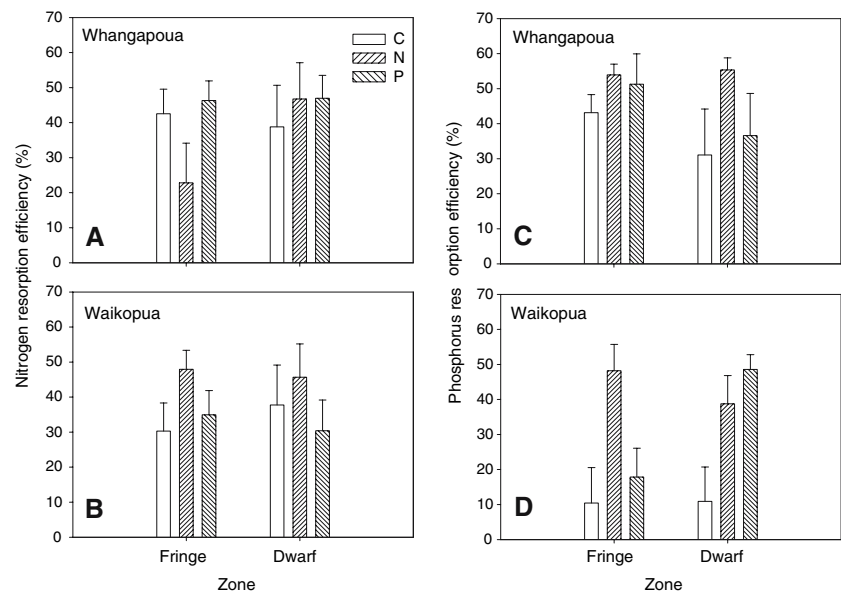
significant increase in response to fertilization at Whangapoua. In contrast, sediment respiration at Waikopua was higher in the dwarf forests than in the fringing forest and increased with N fertilization in the dwarf forest.

In order to explore the relationship between above-ground and belowground processes across sites and treatments, we calculated the ratio of sediment respiration to canopy LAI. The ratio ( $\mu mol m^{-2} leaf area s^{-1}$ ) was not affected by fertilization treatments, but it was significantly higher in the high sedimentation site than in the low sedimentation one ( $1.79 \pm 0.24$  vs.  $0.75 \pm 0.13$ ,  $n = 18$ ), and in the landward dwarf forests than in the seaward fringing forests ( $5.17 \pm 0.75$  vs.  $1.07 \pm 0.18$ ,  $n = 18$ ). To obtain an

indication of the proportion of photosynthetically fixed  $CO_2$  that is respired by roots and root and sediment microbial communities over sites and treatments, we compared the sediment respiration:LAI ratio to measured maximum photosynthetic rates. Sediment respiration per unit canopy leaf area was approximately 8–9% of photosynthetic carbon fixation at the low sedimentation site. At the high sedimentation site, sediment respiration per unit canopy leaf area was 18% in the fringe and 60% in the dwarf trees.

Nutrient resorption efficiency (nitrogen, NRE%; phosphorus, PRE%; Fig. 4) gives an indication of the internal nutrient conservation of plants. NRE% ranged between 20

**Fig. 4** Nitrogen resorption efficiency (**a, b**, NRE%) and phosphorus resorption efficiency (**c, d**, PRE%) in leaves of fertilized trees of the mangrove *A. marina* at two sites with contrasting sedimentation: **a, c** Whangapoua (= low sedimentation), **b, d** Waikopua (= high sedimentation). Trees were either fertilized with nitrogen (N) or phosphorus (P) or were designated as controls (C). Values are the mean and standard error for eight trees



and 60% over the sites and did not differ significantly over sites or with vegetation zone or fertilization treatment ( $P > 0.05$ ). In contrast, PRE% was significantly higher at Whangapoua (low sedimentation) than at Waikopua (high sedimentation) ( $F_{1, 53} = 9.52$ ,  $P = 0.0032$ ). At the low sedimentation site fertilization with N increased PRE% in the dwarf trees relative to the controls ( $P = 0.046$ ), but overall PRE% did not differ between dwarf and fringe trees (main effect of site  $P > 0.05$ ). At the high sedimentation site, PRE% was low in the controls (approx. 10%) but was significantly enhanced with fertilization with N in the fringe trees ( $P < 0.0001$ ) and with fertilization with N and P in the dwarf trees ( $P = 0.0015$  and  $P = 0.0202$ ).

## Discussion

The objective of this study was to determine whether nutrient enrichment plays an important role in facilitating encroachment by the mangrove *A. marina* in New Zealand's estuaries. One of our initial hypotheses was that mangrove encroachment with sedimentation was mainly due to enhanced growth caused by nutrients arriving with the sediments. To test this, we used experimental nutrient enrichment at both a high sedimentation and at a low sedimentation site, expecting that with nutrient enrichment, the forest characteristics of the low sedimentation site would converge on those of the high sedimentation site. Our data do not support this hypothesis.

We observed that stem extension (and leaf production) at the low sedimentation site was lower than that at the high sedimentation site, indicating that sedimentation enhances growth rates, as has been observed in other studies

(Pezeshki et al. 1992; Ellison 1998; Ellison and Farnsworth 1996; Ellis et al. 2004; Walls et al. 2005, but see Ewing 1996 and Weisner 1996). Contributing to this pattern was negative growth in the winter period at the low sedimentation site, but sustained growth at the higher sedimentation site (Fig. 1). *Avicennia marina* is at the edge of the biogeographic range in New Zealand; consequently, cool temperatures and frosts may limit mangrove growth (Beard 2006). Although the two sites were situated at similar latitudes, they may have differed subtly in terms of climate or sedimentation, and urban development may have improved the climate for growth and provided more favorable hydrology at the high sedimentation site, thereby contributing to the enhanced growth observed. The role of herbivores could also be important in reducing the observed growth rates at the high sedimentation site as evidence of wood boring Longhorn beetles were common, particularly in the fringing forests (I.C. Feller, personal observation). At the low sedimentation site, where the effects of nutrient addition were expected to be greatest, fertilization with nutrients led to only slight increases in growth rates in dwarf trees and no significant enhancement in growth of the fringing trees (Fig. 1). Nutrient enrichment also had only small effects on photosynthetic carbon gain, nutrient resorption efficiency (NRE% and PRE%), canopy structure and sediment respiration at the low sedimentation site. Our observations show that: (1) growth of *A. marina* trees is slow in sites with low sedimentation compared to sites with high sedimentation, and (2) the effects of sedimentation on tree growth rates cannot be solely attributed to nutrient enrichment, but that other factors must be responsible for enhanced growth, sediment respiration and canopy development at the high sedimentation site. In an earlier study,

soil texture was shown to influence mangrove growth (McMillan 1971), but other factors may also be important in stimulating the growth of mangroves. Although our study cannot identify with certainty which factors are important, given our results, we propose that the expansion of mangroves in New Zealand's estuaries is likely to be primarily due to an increased availability of a suitable habitat with sedimentation and less likely to be due to direct nutrient enrichment.

Although the expansion of mangroves can be attributed to sedimentation, sedimentation appears to alter the sensitivity of tree growth to nutrient enrichment and alters nutrient and carbon cycling. In both sites, N enrichment stimulated growth, but enhancements in growth were greater at the high sedimentation site than at the low one (Fig. 1). Internal nutrient conservation indicated that P availability was also higher at the high sedimentation site than at the low one. PRE%, which reflects plant internal P recycling, was lower at the high sedimentation site (10% in controls) than at the low one (approx. 50%), as would be expected if the plants at the high sedimentation site were P-replete and those at the low sedimentation site were deficient (Aerts 1996; Feller et al. 2003). These data suggest that sedimentation enhances P availability, either directly or due to the more anaerobic soil conditions (Nye and Tinker 1977), which would then allow for further enhancements in tree growth with N enrichment from pollution. Contributing to the greater sensitivity to N enrichment at the high sedimentation may be the release from intense belowground competition due to the much higher stem densities at the high sedimentation site compared to the low sedimentation site. Additionally our observation that fertilization with limiting N increased PRE% at the high sedimentation site in both the fringe and dwarf forests (Fig. 4) may indicate that continued N enrichment may give rise to a switch from N to P limitation, following a successional sequence described by Walker and Syers (1976) and Vitousek (1993). Overall, our data indicate that nutrient enrichment could play an important role in enhancing mangrove growth in New Zealand estuaries that are already impacted by sedimentation.

Sedimentation also influenced the CO<sub>2</sub> fluxes from sediments. We observed higher rates of sediment respiration in the high sedimentation site than in the low sedimentation site (Fig. 3), which is indicative of enhanced microbial mineralization of sediment carbon (i.e. heterotrophy) (Jonasson et al. 1996; Orwin et al. 2006). In a study over a range of mangrove sites experiencing differing sedimentation regimes, Alongi et al. (2005) found the highest rates of carbon and N mineralization in sites with high sedimentation rates. At our high sedimentation site (Waikopua), this effect seemed to be the greatest in the

dwarf forest, which also showed the strongest growth response to N fertilization (Fig. 1). Dwarf stands have lower sedimentation rates compared to the fringing forests, thus factors in addition to sedimentation are influencing the rates of CO<sub>2</sub> efflux in the dwarf forest at this site. Enhanced belowground carbon allocation by the dwarf trees (e.g. Baudion et al. 2003) or changes in the microbial community and its activity associated with anaerobic soils (Table 1) may also increase sediment respiration. Because CO<sub>2</sub> efflux from soils is a large component of ecosystem carbon budgets (Raich and Schlesinger 1992), enhanced CO<sub>2</sub> efflux from mangrove sediments with sedimentation may indicate a shift from net autotrophy (sequestration of C), to ecosystems that are net heterotrophic (net loss of carbon).

#### Spatial patterns in nutrient limitation

Fringe trees in both sites showed little evidence of nutrient limitation, with shoot elongation, canopy structure, NRE% and sediment respiration showing no significant responses to fertilization treatments. %PRE in fringe trees was increased with N fertilization at the high sedimentation site, which may have been due to a developing P limitation (discussed above). Additionally, there was a slight increase in growth and photosynthetic carbon gain relative to control trees in both – and P-fertilized trees at the low sedimentation site (Whangapoua). In contrast, in dwarf landward stands, growth and photosynthetic carbon gain were stimulated by N fertilization at both sites, but the effect was larger at the high sedimentation site, leading to significant enhancements in LAI and tree height within the second year of the experiment. These data suggest that similar to other sites, dwarf stands are often more sensitive to nutrient enrichment than taller fringing forests (Lin and Sternberg 1992; Feller et al. 2002, 2003, 2007; Lovelock et al. 2006). This may reflect the influence of other environmental conditions often brought about by reduced hydrological connectivity that can place overall controls on growth and metabolic function (Lugo and Snedaker 1974; McKee et al. 2002).

#### Conclusion

Our goal was to assess whether nutrient enrichment with sedimentation was one of the key drivers for increasing mangrove growth in New Zealand estuaries. We found that tree growth and other parameters were relatively insensitive to N additions in an estuary with low sedimentation, but they were more sensitive to fertilization in an estuary with high sedimentation rates. Our experiments suggest that sedimentation enhances mangrove growth but that it also likely increases microbial mineralization of N leading

to nutrient limitation in mangrove tree communities and that mangrove forest growth can be greatly stimulated by the combined influences of sedimentation and nutrient enrichment. Mangrove encroachment in New Zealand's estuaries appears to be initiated by high rates of sedimentation which increase the extent and suitability of the habitat, with the direct effects of nutrient enrichment playing a role in estuaries that have already been affected by sedimentation.

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