Nitrogen limitation of dwarf *Avicennia marina* mangroves

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Introduction

Variation in tree height and productivity along environmental gradients is common in mangrove systems. Usually, trees fringing shorelines and rivers are tall and highly productive, while those occurring inland are dwarfed and often referred to as scrub mangroves. These mangroves usually occur at high elevation in the intertidal zone where tidal influence is infrequent and high evapotranspiration contributes to hypersalinity conditions. Differences in tree height and productivity have been attributed to a variety of edaphic factors such as salinity, waterlogging, tidal frequency, surface hydrology, sulphide concentrations, soil redox potentials and nutrient limitation. Nutrient enrichment studies suggest that dwarf mangrove sites may be N or P limited, and that species respond differentially to nutrient enrichment. It is unclear whether the responses of dwarf mangroves to N and P enrichment are due to nutrient limitation *per se*, or secondary to other co-occurring stressors such as salinity and waterlogging.

In this investigation, *A. marina* plants in a hypersaline (58±8 psu) dwarf zone were fertilized with N, P or N+P, or remained unfertilized, and growth and physiological responses monitored over a period of two years. It was hypothesized that at high salinities mangroves allocate more resources to roots than shoots, and that nutrient enrichment with N and P will shift resource allocation to shoots and enhance growth and productivity.

Materials and Methods

This study was conducted in Richards Bay Harbour (28°48'S, 32°05'E),172 km north of Durban on the Indian Ocean coast, South Africa, which is fringed by extensive mangroves (Fig. 1).

Five sites, 30 meters apart, were randomly selected in the dwarf zone of a monospecific *A. marina* stand. At each site, four large volume, open-ended pots, 75 cm long and 25 cm in diameter, constructed from PVC drainpipe (Fig. 2), were inserted into the soil to a depth of 70 cm.

One-year old seedlings of *A. marina*, previously cultured in the glasshouse and watered with full strength sea water, were planted into each pot (one per pot) with minimum disturbance to the soil. Each pot was enriched bimonthly with N, P, N+P, or remained unfertilized (control-C). At each site, one pot was fertilized with 1.05 g N supplied as urea (459 kg ha^{-1}), the second with 0.16 g P, supplied as phosphorus pentoxide (P_2O_5) (73 kg ha^{-1}), the third received both N (1.05 g) and P (0.16 g), while the fourth was the unfertilized control (C). These levels of nutrient dosing were based on preliminary experiments. Fertilizers were in powder form and were broadcast on the soil surface inside the pot.

Use of open-ended pots permitted tidal flooding, drainage, and water percolation through the soil profile. Fertilizers were applied bimonthly for two years during neap tides when the substrate was not inundated. There were 4 treatments (C, N, P, N+P) replicated at five sites. All plants were fully exposed to direct sunlight. At each of the five sites, treatments were located about 2 m apart in a randomized block design (Fig. 3).

Photosynthetic gas exchange was measured with a portable gas exchange system (LiCor 6400), chlorophyll fluorescence with a field portable, pulse amplitude, modulated fluorometer (PAM – 2100) and leaf chlorophyll content with a hand-held chlorophyll content meter, CCM-200 (Opti Sciences). Inorganic ions were determined by atomic absorption, P by the molybdenum blue procedure and N by the automated Dumas dry combustion method using a CNS analyzer.

Data analysis

All data were subjected to one-way analysis of variance (ANOVA) and Tukey-Kramer Multiple Comparisons Test using GraphPad Instat, Version 3.

Fig. 1. Richards Bay mangroves.

Fig. 2. Long, open-ended plastic pots.

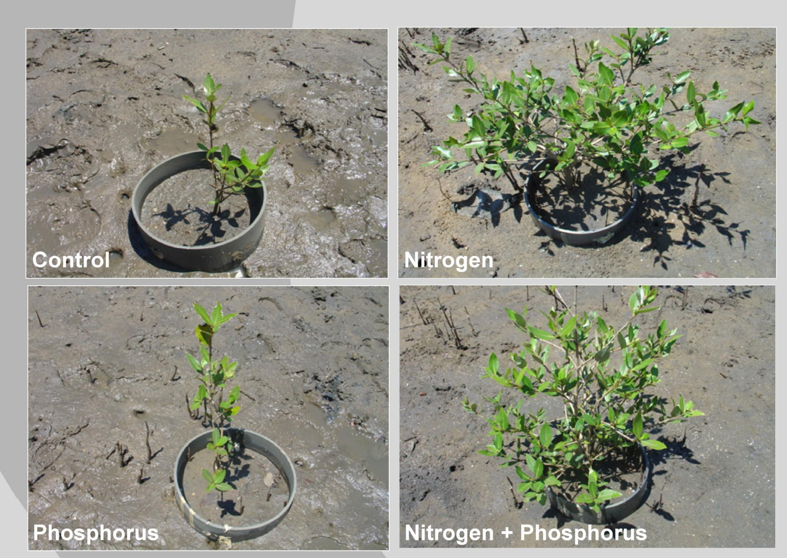

Fig. 3. Nitrogen and phosphorus enrichment after 2 years

Table 1. Soil conditions in the dwarf *A. marina* stand in Richards Bay. Values are mean ± S.E., n = 4

pH	8.24 ± 0.03
Bulk density (g cm^{-3})	1.65 ± 0.03
Electrical conductivity (mS m^{-1})	9426 ± 178
Redox potential (mV) 15 cm depth	-31 ± 3.2
Soil ψ (MPa)	-7.62 ± 0.06
Salinity (PSU)	56.8 ± 2.4
Phosphorus (mg l^{-1})	12.8 ± 1.3
Sodium (meq l^{-1})	1621 ± 37
Calcium (meq l^{-1})	49.3 ± 3.4
Magnesium (meq l^{-1})	318 ± 15.2
Potassium (meq l^{-1})	20.3 ± 0.8

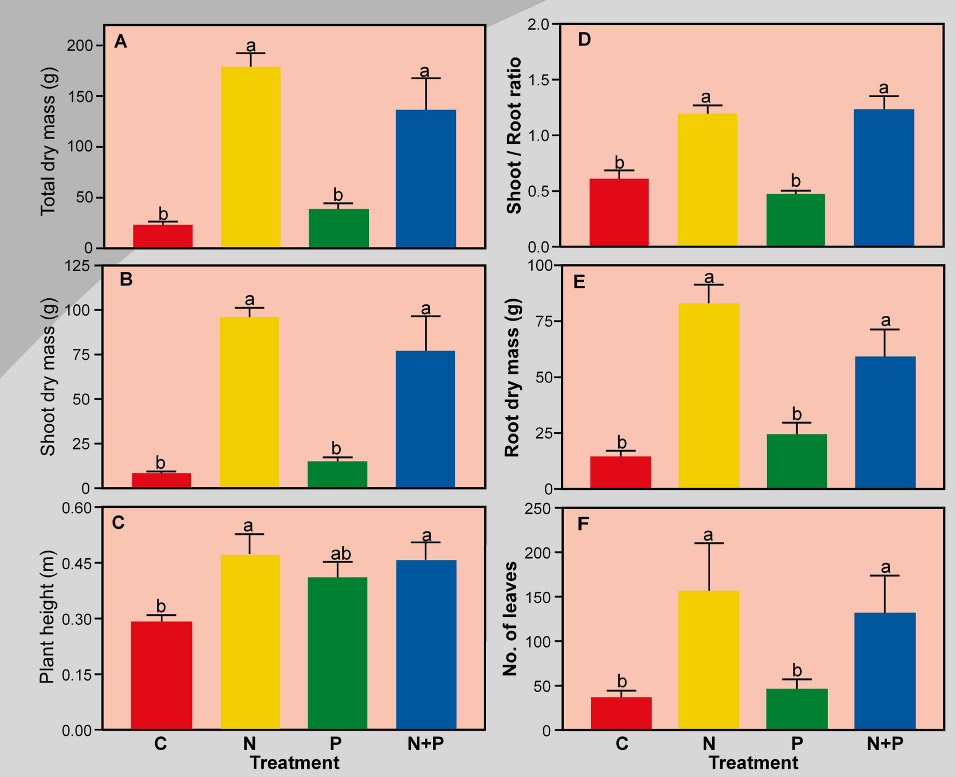

Fig. 4. Effects of N and P enrichment on total (A), shoot (B) and root (E) biomass accumulation; shoot/root ratios (D), plant height (C) and number of leaves (F) in dwarf *A.marina*. Plants were subjected to treatment for 2 years.

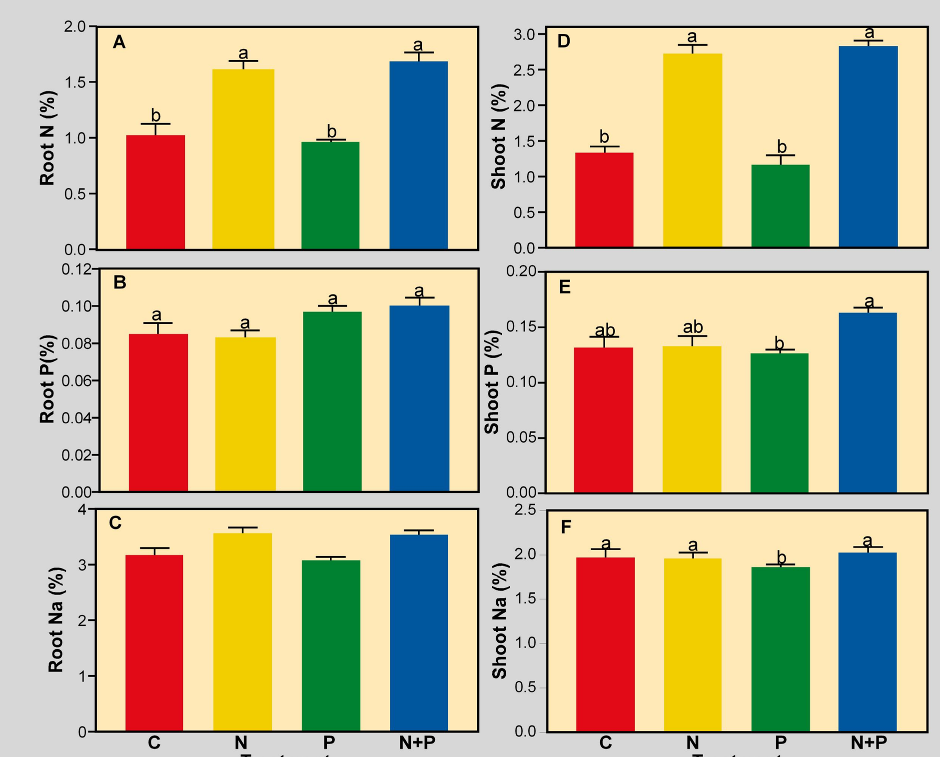

Fig. 5. Effects of N and P enrichment on accumulation of N, P and Na (% dry mass) in roots (A-C) and shoots (D-F) of dwarf *A.marina*.

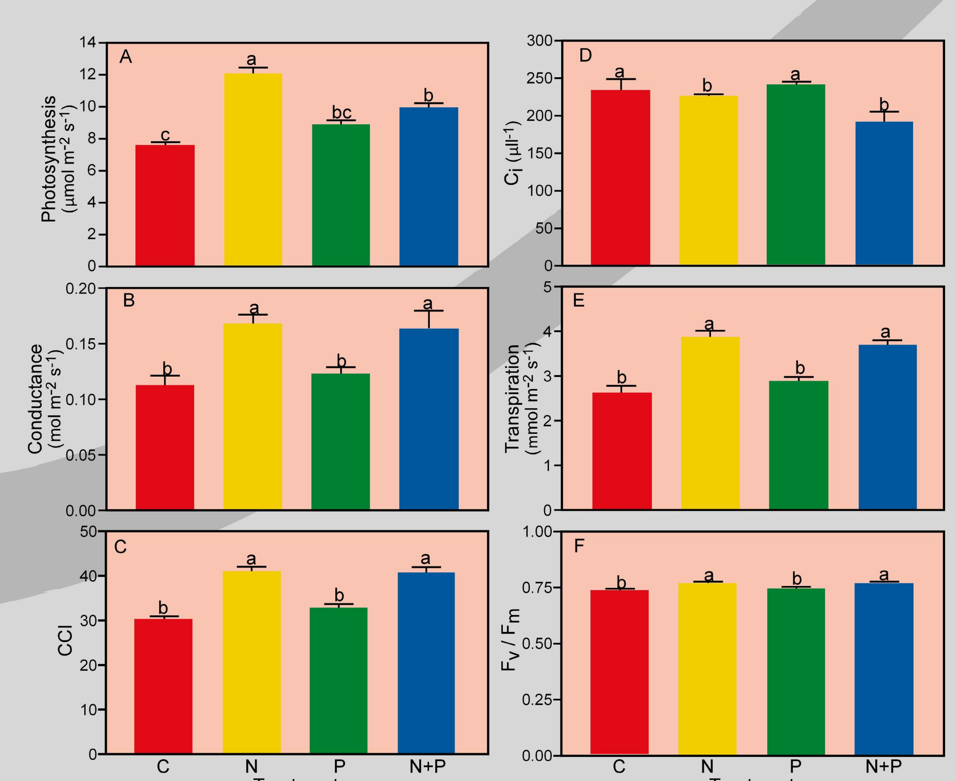

Fig. 6. Effects of N and P enrichment on photosynthesis (A), conductance (B) chlorophyll content index (CCI) (C), intercellular CO_2 concentrations (c_i)(D), transpiration (E) and photochemical efficiency of PSII (F_w/F_m) in dwarf *A.marina*.

C=control, N=nitrogen, P=phosphorus, N+P=nitrogen plus phosphorus. Means ± S.E. are given, n=5. Bars with different letters differ significantly at *P*<0.05 using Tukey-Kramer Multiple Comparisons Test.

Results

Soils : Soils in the dwarf zone were slightly alkaline with high concentrations of cations, dominated by Na^+, which contributed to a high electrical conductivity (Table 1). Soils were highly saline with very low soil water potential compared to sea water which has a salinity of about 35 psu and a water potential of about -2.5 MPa

Growth : Plants fertilized with N and N+P had a significantly higher (P<0.001) total dry biomass than those of the control and P treatments (Fig. 4A). There was no difference in total dry biomass between the control and P-fertilized treatments.

Shoot (P< 0.001) and root (P<0.001) dry biomass accumulation and shoot-root ratios (P<0.001) followed trends similar to total dry biomass (Fig. 4B, E, D). In the control and P-fertilized treatments, about 62% of dry weight was allocated to roots and 38% to shoots. Fertilization with N and N+P shifted allocation from roots to shoots, with about 45% directed to roots and 55% to shoots

Plants fertilized with P, N+P and N, were taller than those of the control at harvest by 41%, 57% and 62% respectively (Fig. 4C). P-fertilized plants had few branches (4±1), while those enriched with N and N+P were profusely branched (20±3) with a broad canopy. The number of leaves in plants fertilized with P, N+P and N was greater than the control (Fig. 4F).

Mineral Elements : The concentrations of N and P in shoots were consistently greater than those in roots (Fig. 5). Plants fertilized with N and N+P had significantly higher concentrations of N in roots (P<0.001) and shoots (P<0.001) compared to the control and P treatments. Root concentrations of N in the N and N+P treatments were about 60% higher than the control value, while in shoots, these were twice as high (Fig. 5A, D). In contrast to N, there were no differences in root P amongst treatments (Fig. 5B), while in shoots, plants fertilized with N+P had significantly higher P concentrations (P<0.03) than those in the P treatment (Fig. 5E). Shoot N:P ratios were 10±1, 9±2, 20±2 and 17±2 in the C, P, N and N/P treatments. In the N and N+P treatments, N:P ratios were significantly higher (P< 0.02) than those in the control by 102% and 71% respectively. There were no differences in N:P between shoots in the C and P treatments. Fertilization with N and N+P produced vigorous growth compared to the C and P treatments.

The concentration of Na^+ in tissues (Fig. 5C, F) was high, being higher in roots (3.1-3.6%) than in shoots (1.9-2.4%). Concentrations of other inorganic ions such as K^+, Ca^{2+}, Mg^{2+}, Cu^{2+}, Fe^{2+} and Mn^{2+} were generally higher in roots than shoots with no differences among treatments.

Photosynthesis : Carbon dioxide exchange, leaf conductance and transpiration in the N and N+P treatments were generally higher than those in the C and P treatments (Fig. 6A, B, E). In the N and N+P treatments, CO_2 exchange was higher (P<0.001) than the control by 59% and 31% respectively. There were no differences in CO_2 exchange, conductance, transpiration or ci between the C and P treatments. The intrinsic photochemical efficiency of PSII (*Fv/ Fm*) was higher in the N and N+P treatments (Fig. 6F) compared to the others (P<0.001). The leaf chlorophyll content index (CCI) values were about 35% higher in the N and N+P treatments than the others (P<0.001). There were no differences in CCI between the C and P treatments (Fig. 6C).

Discussion

1. At high salinities, about 65% of the dry plant biomass in control plants was allocated to roots, thereby supporting the hypothesis that salt stressed plants allocate most of their biomass to roots. Increasing allocation of biomass to roots is an important survival strategy to meet the higher requirements for water and nutrients at high salinities, but it appears to occur at the cost of leaf biomass, photosynthesis and thus growth.

2. The most dramatic effect of N enrichment was a change in biomass allocation, which supports the hypothesis that enrichment with N, but not P, shifts allocation from roots to shoots.

3. Increased photosynthesis with N enrichment at high salinities was strongly associated with increased stomatal conductance and leaf chlorophyll content. Increased photosynthesis with N additions at high salinities may also be attributed to increased sink strength as a result of greater biomass allocation to shoots and leaves, and the greater number of growing points.

Conclusions

1. Growth enhancement of dwarf *A. marina* with N and N+P enrichment and significant increases in the concentration of N in roots and shoots, as well as in N: P ratios indicate that the dwarf zone is N limited.

2. Plants fertilized with P did not exhibit the vigorous growth responses observed in the N and N+P treatments. These plants were similar in appearance to those of the control, albeit slightly taller, with no differences in total, root or shoot dry biomass accumulation, shoot/root ratios or number of leaves.