NUTRIENT LIMITATION OF TREE SEEDLING GROWTH IN THREE SOIL TYPES FOUND IN SABAH

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NILUS R, MAYCOCK CR, MAJALAP-LEE N & BURSLEM DFRP. 2011. Nutrient limitation of tree seedling growth in three soil types found in Sabah. Variation in soil nutrient may contribute to species–habitat associations and landscape-scale plant diversity in tropical forests. A nutrient bioassay experiment was used to test the hypotheses that (a) plant growth rate would be greater in more nutrient-rich alluvial soil than in soils taken from low mudstone and sandstone hills in the Sepilok Forest Reserve, Sabah and that (b) P would be the main limiting nutrient for plant growth in all three soil types. Seedlings of the pioneer tree *Neolamarckia cadamba* were grown for 45 to 52 days in pots of soil taken from alluvial, mudstone hill and sandstone hill habitats. The experiment comprised six macronutrient addition treatments and a control, with 10 replicates for each treatment. The growth rate of *N. cadamba* seedlings increased in response to P addition in sandstone hill soil and in response to K in alluvial soil. Relative growth rates were highest in alluvial soil, which had the highest concentrations of available nutrients. We conclude that alluvial, mudstone hill and sandstone hill soils provide contrasting soil chemical environments that are sufficient to induce differential growth rates for *N. cadamba* seedlings in pots. Phosphorus availability was non-limiting for *N. cadamba* seedlings in the alluvial forest soil, which unmasked limitation by K.

Keywords: Habitat specialisation, nutrient addition, soil fertility

NILUS R, MAYCOCK CR, MAJALAP-LEE N & BURSLEM DFRP. 2011. Pengehadan nutrien bagi pertumbuhan anak benih pokok dalam tiga jenis tanah di Sabah. Variasi dalam nutrien tanah mungkin menyumbang kepada hubung kait spesies–habitat dan kepelbagaian tumbuhan pada skala landskap di hutan tropika. Satu uji kaji bioasai nutrien digunakan untuk menguji hipotesis bahawa (a) kadar pertumbuhan tumbuhan lebih tinggi dalam tanah aluvium yang kaya dengan nutrien berbanding tanah daripada bukit batu lumpur dan bukit batu pasir di Hutan Simpan Sepilok, Sabah dan (b) fosforus (P) merupakan nutrien utama yang mengehadkan pertumbuhan tumbuhan dalam ketiga-tiga jenis tanah. Anak benih pokok perintis *Neolamarckia cadamba* ditanam di dalam pasu yang mengandungi tanah daripada habitat aluvium, bukit batu lumpur dan bukit batu pasir selama 45 hari hingga 52 hari. Eksperimen ini merangkumi rawatan tambahan enam makronutrien dan satu kawalan dengan 10 ulangan setiap rawatan. Kadar pertumbuhan anak benih *N. cadamba* meningkat dengan tambahan P dalam tanah bukit batu pasir dan tambahan kalium (K) dalam tanah aluvium. Kadar pertumbuhan relatif paling tinggi dalam tanah aluvium yang mengandungi nutrien sedia ada yang paling banyak. Sebagai kesimpulan, tanah aluvium, bukit batu lumpur dan bukit batu pasir menunjukkan keadaan kimia tanah yang berbeza yang dapat mempengaruhi kadar pertumbuhan anak benih *N. cadamba* di dalam pasu. Apabila P sedia ada dalam tanah aluvium tidak terhad, K akan mengehadkan pertumbuhan anak benih *N. cadamba*.

INTRODUCTION

Climate and soil conditions are the most important factors controlling the distribution of tropical forest trees and tropical forest formations (Whitmore 1984, Townsend et al. 2008). Studies in the lowland dipterocarp forests of South-East Asia have frequently demonstrated strong associations of floristic variation and tree species distribution with soil resource availability at multiple spatial scales (Baillie et al. 1987, De Walt et al. 2006, Paoli et al. 2006). For example, at Sepilok Forest Reserve (SFR) in Sabah, two distinct floristic associations of lowland mixed dipterocarp forest occur in close proximity, and their distributions are associated with contrasting parent materials and differences in biogeochemical cycling (Dent et al. 2006). These floristic associations are broadly defined as lowland dipterocarp forest on alluvial and mudstone soils, and sandstone hill dipterocarp forest on sandstone-derived soils (Fox 1973).

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The soils underlying these forest types have contrasting chemical and physical properties (Dent et al. 2006). In seeking to understand the mechanisms that drive differentiation of forest composition on different soil types, it is necessary to determine the effects of both the physical and chemical properties of the soils, and in particular the spatial heterogeneity and temporal dynamics of plant nutrient availability. Since plant distribution may be closely related to site conditions and nutrient availabilities, it is important to understand which nutrient(s) are limiting to plant growth on both soil types.

In a review of nutrient limitation in tropical forest soils, Vitousek (1984) suggested that P and not N limited the productivity of lowland tropical forests on oxisols and ultisols. In support of this finding, several bioassay experiments of seedling growth in pots have confirmed that P is the primary limiting nutrient in tropical forest soils (Denslow et al. 1987, Burslem et al. 1994, Raaimakers & Lambers 1996, Lawrence 2001, Wan Juliana et al. 2009). However, not all species show responses to N or P addition in pot bioassay experiments (Turner et al. 1993, Burslem et al. 1995, 1996), which may be because they are limited by nutrient cations such as K or Mg rather than P (Burslem et al. 1996) and because test species with relatively shade-tolerant seedlings are less responsive to nutrient addition (Brearley et al. 2007). Similarly, Amir and Miller (1990) suggested that K was the primary limiting nutrient for productivity in two lowland mixed dipterocarp forests in Peninsular Malaysia. This conclusion was derived from a correlation between soil and foliar nutrient concentrations, and because the accumulation of tree basal area was related to the availability of K. However, they did not show that the basal area growth of the two forest stands responded to inputs of K. Therefore, their study was inconclusive.

We hypothesised that plant growth in forest soils taken from SFR would be greatest on alluvial forest soil and lowest on sandstone hill forest soil, and that growth would be limited primarily by the low availability of P in all soil types. In this study, we used a nutrient addition bioassay experiment to determine systematically which nutrient(s) are limiting growth of the pioneer species *Neolamarckia cadamba* (Rubiaceae) in the contrasting soils underlying lowland dipterocarp forests in Sepilok.

MATERIALS AND METHODS

A bioassay experiment was conducted in the nursery of the Forest Research Centre (5° 10' N, 117° 56' E), Sandakan, Malaysia. During the period 1976–1995 Sandakan had mean (± SEM) annual rainfall of 2929 ± 134 mm and mean annual temperatures between 26.7 and 27.7 °C, with no month receiving < 100 mm of rainfall on average (Malaysian Meteorological Services 1976–1995). April is generally the driest month and December or January the wettest; 45% of the annual precipitation falls between early November and mid-February (Fox 1973).

The parent materials underlying SFR are sedimentary sandstone, shale and mudstone originating from the Miocene period (Fitch 1958). Two broad soil associations, classified locally as Silabukan and Lokan can be recognised within the study area (Acres & Folland 1975). The soils of the Silabukan association consist of alluvium derived from low mudstone and sandstone hills. These soils are well drained and imperfectly drained red yellow podzolic soils between 15 and 30 m asl (Fox 1973). The topography of the alluvial habitat is flat with gently undulating low mudstone hills rising to a maximum elevation of approximately 15 m. By contrast, the soils of the Lokan association are confined to sandstone hills, which run from the northern to the western parts of the reserve. These soils are derived largely from the dominant sandstone bedrock interbedded with mudstone. This area has strongly dissected topography comprising a series of spurs with steep and occasionally sheer slopes, narrow crests and valley bottoms between 30 and 90 m asl. Furthermore, red yellow podzolic soils dominate in this habitat with lithosols restricted to the upper slopes (Fox 1973).

A survey of the soil chemical and physical conditions at SFR showed that alluvial soils had greater cation exchange capacity, base saturation, pH as well as concentrations of nitrate, total N, available P and exchangeable Mg and K than soils sampled from sandstone hills (N Majalap-Lee, personal communication). Alluvial soils also had significantly greater percentages of clay and silt but lower sand contents than sandstone hill soils. In general, the chemical and physical properties of mudstone hill soils are intermediate or similar to both alluvial and sandstone hill soils, especially in soil cation exchange capacity, base saturation,

pH, concentrations of nitrate, total N, available P and exchangeable Mg and K, and percentage of soil clay, sand and silt fractions.

Soils from representative alluvial and mudstone hill sites in SFR were collected in mid-August 2001, while sandstone hill soil was collected in February 2002. Soil was collected from five randomly located sites in each forest type. In all cases, the litter layer was removed and discarded before the soil was collected from a depth of 0–15 cm and mixed thoroughly with soils from the same collection site. A detailed description of the floristic associations and their relationship to site conditions is presented in Nilus (2004).

We used seedlings of the fast-growing pioneer tree *N. cadamba* to assess nutrient limitations within the three soil types. This species was selected because it is common in disturbed sites on relatively nutrient-rich soils in Sabah and because the fast growth of its seedlings would ensure that the experiment would deliver results within a short period. However, we acknowledge that it would be desirable to repeat the experiment with a broader sample of species, including slow-growing shade-tolerant species that are typically less responsive to nutrient addition (Brearley et al. 2007). On January 2002, 2–3-week-old *N. cadamba* seedlings were transplanted into cylindrical polyethylene bags filled with 2 litres of either alluvial or mudstone hill soil. Initial stem heights were 5.4 ± 1.2 cm and 6.6 ± 1.5 cm for seedlings planted in alluvial and mudstone hill soils respectively. Ten days after transplanting, seedlings of uniform size within each soil type were selected and used in the experiment. A third batch of seedlings was transplanted into polyethylene bags (as above) containing 2 litres of sandstone ridge soil on 4 February 2002. Four days later, seedlings of uniform size (4.9 ± 0.9 cm in height) were selected and used in the experiment. There was significant difference in initial stem height between seedlings transplanted in the three soil types (ANOVA, $p < 0.05$). The seedlings were watered twice daily using rain water.

A randomised block design was used with 10 individual shade screens of width 1.2 m, length 2.4 m and height 1.5 m. These shade screens were covered in double layer neutral density shade material that transmitted approximately 18–33% of full sunlight. These 10 shade screens were designed as replicate blocks. A replicate block comprised three soil type treatments with seven individuals per soil type (3 soil types × 7 individuals/soil type = 21 plants/block; 21 plants/block × 10 blocks = 210 plants) to give one individual per species per soil type in each of the six macronutrient addition treatments (N, P, K, Mg, Ca and S) plus a control (distilled water). Seedlings were allocated at random to the 10 shade screens and to nutrient addition treatments. The positions of seedlings in the shade screens were re-randomised every four weeks.

Treatments involved addition of the following solutions to seedlings growing in each soil type: 1, control, i.e. distilled water with no added nutrients; 2–7, with additions of 0.037 M NH_4NO_3, 0.037 M Na_2HPO_4, 0.032 M KCl, 0.009 M $MgCl_2$, 0.005 M $CaCl_2.2H_2O$ or 0.009 M Na_2SO_4. The concentrations of all nutrient solutions in treatments 2–7 followed Denslow et al. (1987) and Burslem et al. (1994). Nutrient additions, comprising 30 ml/individual, were carried out weekly from 1 February till 22 March 2002. Therefore, the seedlings growing in alluvial and mudstone hill soils received eight sets of nutrient additions, while those growing in sandstone hill soils received only seven.

The initial height, stem diameter and leaf number were measured on 23 January 2002 for seedlings growing in alluvial and mudstone hill soils and on 4 February 2002 for seedlings growing in sandstone hill soil. Additional measurements were conducted on 28 February 2002 and 22 March 2002 for all seedlings. An initial harvest of 20 seedlings was made on 23 January 2002 for seedlings growing in alluvial and mudstone hill soils, and on 5 February 2002 for those growing in sandstone hill soil. The final harvest was carried out for all seedlings on 25–26 March 2002. Above-ground plant parts were severed from the roots at the soil surface and all leaves were removed from the stem. Leaf area was determined for all seedlings at the initial and final harvests by photocopying leaves on paper (80 g m^{-2}) and applying a conversion factor (surface area (cm^2) = weight of paper (g) × 125) relating the mass of the image to its area. The leaves were then oven dried. Soil was removed from the roots by soaking and carefully washing the roots in water in order to minimise root loss. All harvested plant parts were oven dried at a constant temperature of 60 °C for a week and then weighed separately.

Plant materials, i.e. leaves and stems plus roots, were analysed for N, P, K, Mg and Ca concentrations of oven-dried plants in the initial harvest and

in the control treatment of the final harvest. All plant materials were ground and dried at 50 °C before acid digestion. Some samples had to be bulked to provide sufficient sample for acid digestion. Samples of 0.3 mg were digested using concentrated sulphuric acid and hydrogen peroxide following the protocol described by Allen et al. (1974). The concentrations of N and P were measured colometrically using a continuous flow method (auto analyser) and flow injection auto analyser respectively. K, Mg and Ca concentrations were measured by atomic absorption spectrophotometry.

Statistical analysis

The effects of soil type, nutrient addition and their interaction on plant growth measures were determined using ANCOVA with initial plant size as the covariate. Comparisons of the effect of each nutrient addition treatment with the control were made using Bonferroni post hoc tests. Some variables were subjected to Box–Cox transformation to normalise the distribution of residuals. The normality of the distributions of residuals was determined using the Anderson–Darling test.

Relative growth rate (RGR) values were calculated as follows (Evans 1972):

$$RGR = \log_e W_2 - \log_e W_1 \; / \; t_2 - t_1$$

where W_2 is the growth measurement at time t_2 and W_1 is the growth measurement at t_1.

RESULTS

All five measures of seedling growth were higher in alluvial forest soil than sandstone hill soil (Table 1). For seedlings grown in mudstone hill soil, the RGR of stem diameter and height did not differ significantly from those growing in sandstone hill soil, while relative leaf production rate and RGR of leaf area and dry mass were similar to values for seedlings grown in alluvial forest soil (Table 1). Seedlings grown in sandstone hill soil had a net loss of leaf number and virtually zero accumulation of leaf area. In all cases, sandstone hill soil had lower mean RGR than seedlings grown in alluvial forest soil.

There were significant main effects of nutrient addition on RGR of stem diameter (F = 2.74, $p < 0.05$, result not shown), leaf number and leaf area of *N. cadamba* seedlings (Figure 1). Relative leaf production rate increased by 26% in comparison with the unfertilised treatment in response to the addition of S ($p < 0.05$), although the response to S differed between soil types. However, the significant main effects of nutrient addition on RGR of stem diameter and leaf area could not be attributed to significant contrasts between the control treatment and any one or more nutrient addition treatments.

There is evidence that relative leaf production rate and RGR of leaf area and total dry mass responded differently to nutrient addition treatments between soil types (Figure 1). The mean relative leaf production rate for seedlings grown in mudstone hill soil was reduced by 52% in response to the addition of N (Figure

Table 1   Mean (and standard error) relative growth rates of stem diameter, stem height, leaf number, leaf area and total dry mass of *N. cadamba* seedlings grown in alluvial, mudstone hill and sandstone hill soils taken from Sepilok Forest Reserve in Sabah, Malaysia

Relative growth rate (week^{-1})	Alluvial	Mudstone hill	Sandstone hill	F	p
RGR$_{Stem\ diameter}$	0.097 a (0.005)	0.077 b (0.005)	0.060 b (0.006)	13.13	< 0.001
RGR$_{Stem\ height}$	0.095 a (0.005)	0.067 b (0.005)	0.050 b (0.006)	15.49	< 0.001
RGR$_{Leaf\ number}$	0.038 a (0.004)	0.039 a (0.004)	-0.052 b (0.005)	118.76	< 0.001
RGR$_{Leaf\ area}$	0.345 a (0.009)	0.326 a (0.009)	0.076 b (0.011)	202.70	< 0.001
RGR$_{Total\ dry\ mass}$	0.315 a (0.009)	0.305 a (0.009)	0.154 b (0.011)	73.58	< 0.001

Means with different letters in the same row are significantly different ($p < 0.05$, Bonferroni's post hoc test); F and p values for the soil type are also presented (two-way ANOVA).
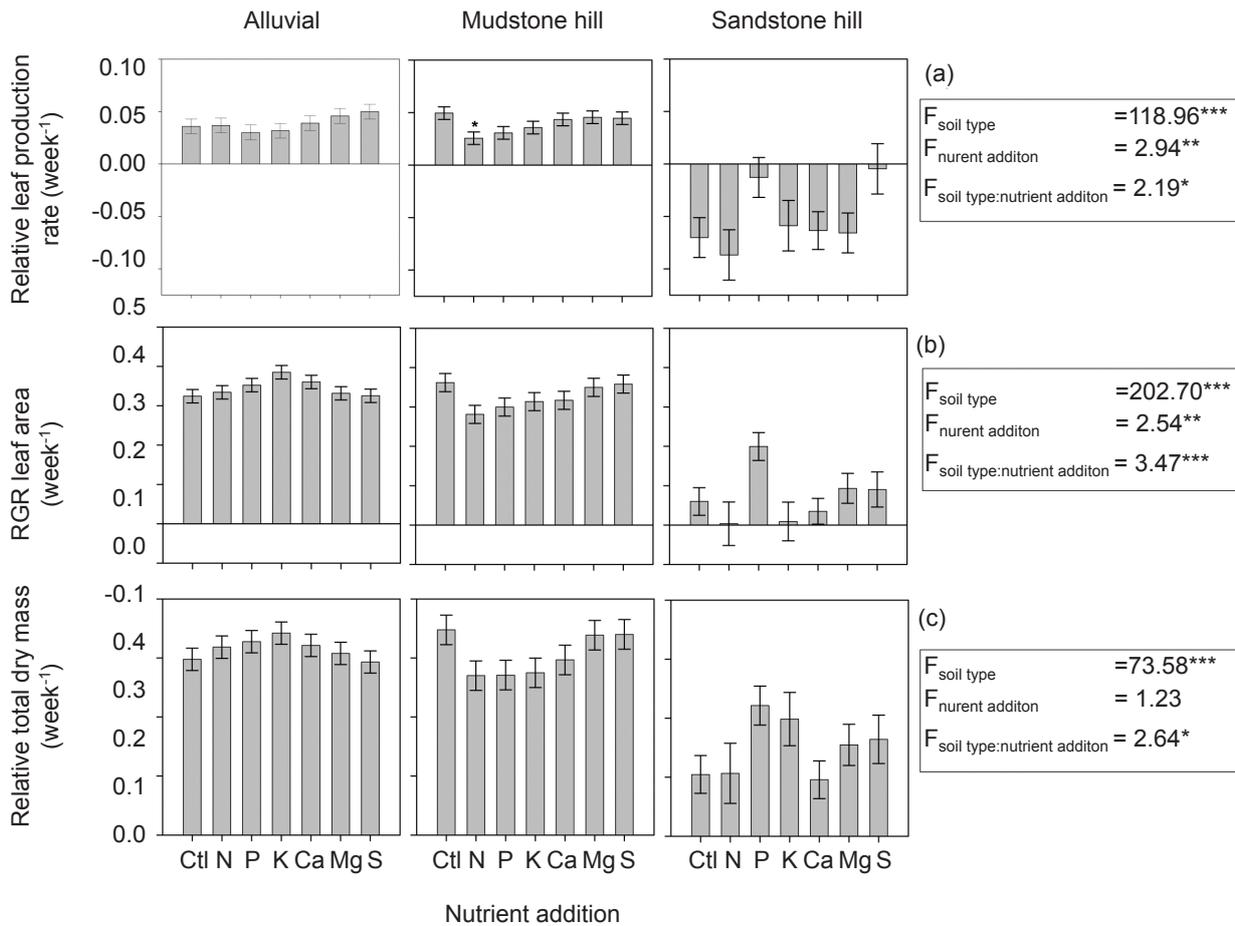
Figure 1 Means and standard errors of (a) relative leaf production rate, and relative growth rates of (b) leaf area and (c) total dry mass of *N. cadamba* seedlings grown in alluvial, mudstone hill and sandstone hill soils taken from Sepilok Forest Reserve in Sabah, Malaysia. The significance of the difference between mean values for each nutrient addition treatment and the unfertilised treatment (Ctl) was obtained using Bonferroni's post hoc test. F and p values for soil type, nutrient addition and the interaction between soil type and nutrient addition from a two-way ANOVA are presented. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

1). The significant effect of nutrient addition treatments on RGR of leaf area for seedlings grown in the sandstone hill soil could not be attributed to a significant contrast between any nutrient treatment and the control treatment. It is noteworthy to mention that there was a marginally non-significant effect of P addition on RGR of leaf area ($p = 0.0504$) and a three-fold increase in mean leaf area compared with the control treatment in these seedlings (Figure 1). For all growth measures, there was a tendency for growth to decline in response to the addition of N, P and K for seedlings grown in mudstone hill soil, and a potential for an increase in growth in response to the addition of P for seedlings grown in sandstone hill soil.

Absolute growth rates of *N. cadamba* seedlings were significantly affected by nutrient addition for at least one growth measure in each soil type (Figure 2). In alluvial soil, stem diameter increased by 32% in response to the addition of K. The addition of N reduced leaf number by 20% for seedlings grown in mudstone hill soil. A similar but marginally non-significant ($p = 0.0501$) reduction in growth occurred in response to the addition of P. In sandstone hill soil, P addition increased seedling stem diameter growth by 44% over the control and had a marginally non-significant ($p = 0.0504$) effect on leaf area.

In the absence of nutrient addition, seedlings grown in alluvial soil had significantly greater concentrations of N, P, Mg and Ca in their
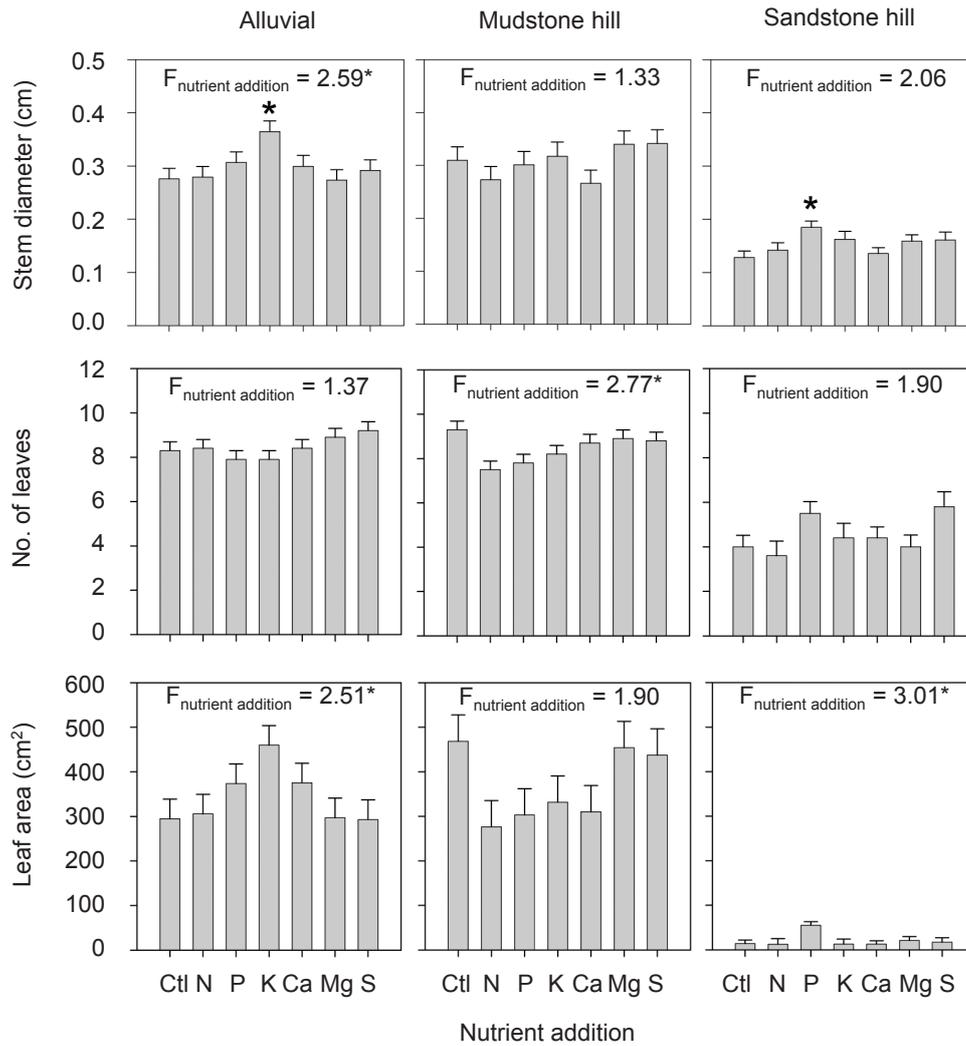
Figure 2 Means and standard errors of (a) stem diameter, (b) leaf number and (c) leaf area of *N. cadamba* seedlings grown in alluvial, mudstone hill and sandstone hill soils taken from Sepilok Forest Reserve, Sabah, Malaysia. The significance of the difference between mean values for each nutrient addition treatment and the unfertilised treatment (Ctl) was obtained using Bonferroni's post hoc test. F and p values for soil type, nutrient addition and the interaction between soil type and nutrient addition from a two-way ANOVA are presented. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

leaves but no significant difference in foliar K concentrations than seedlings grown in mudstone hill or sandstone hill soil (Figure 3). The stems and roots of these seedlings showed a similar difference between soil types in concentrations of N, P and Ca. When grown in mudstone hill soil, seedlings also had significantly higher foliar concentrations of all nutrients, except for K compared with seedlings grown in sandstone hill soil. Nutrient concentrations in the stem plus root fraction of these seedlings demonstrated a similar difference for N, P and Ca but not for K and Mg.

DISCUSSION

Pot experiments have often been criticised for not providing an exact simulation of the natural forest environment and because seedling responses to treatments cannot be assumed to be similar to those of large trees (Sollins 1998). Factors that may directly or indirectly influence plant growth in pots are pot size, soil moisture availability, irradiance, plant growth stage and the presence of mycorrhizas (Burslem et al. 1994, 1995). In this experiment, we took steps to minimise the effects of these limitations by
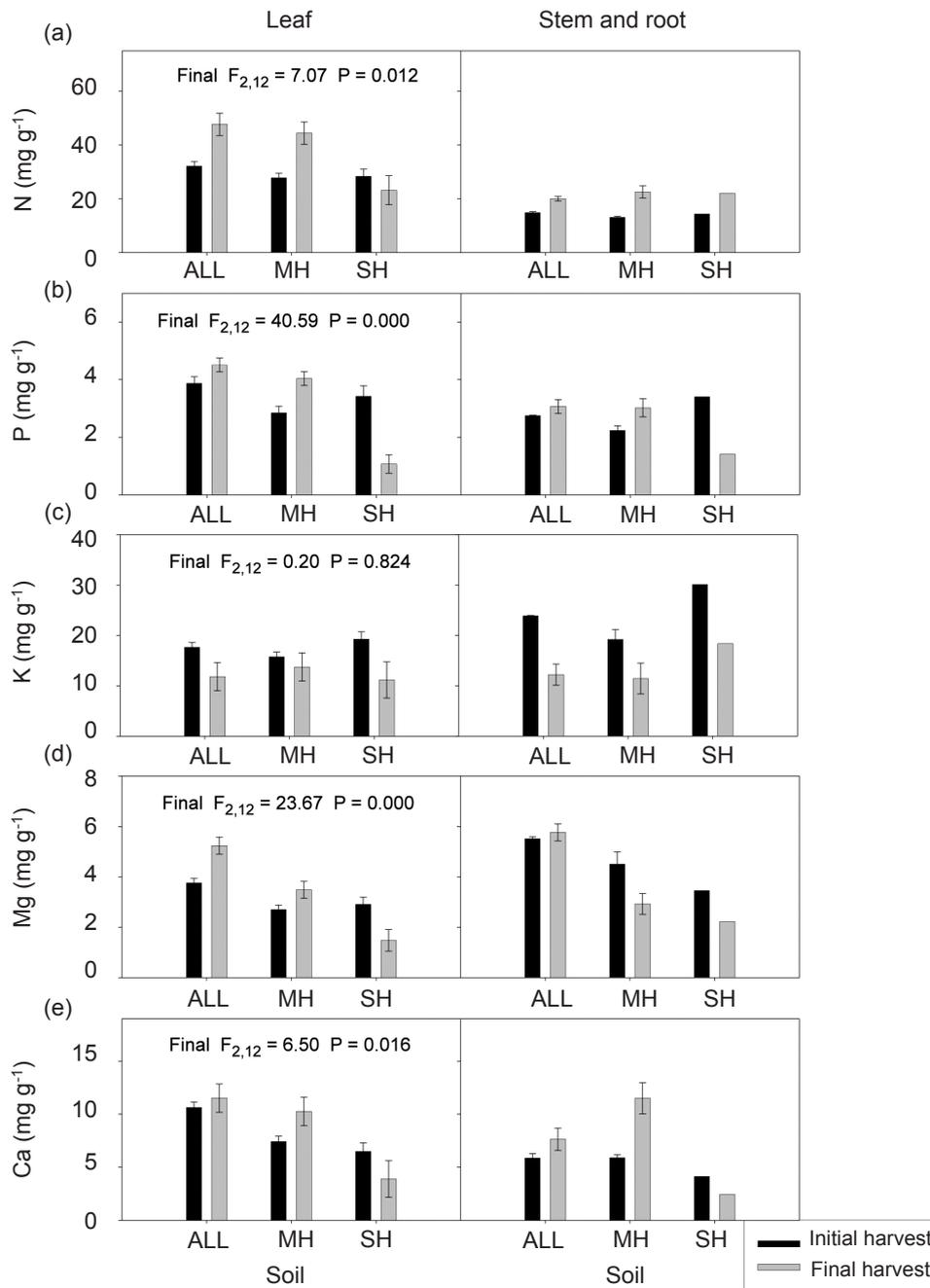
Figure 3 Mean and standard error concentrations of (a) N, (b) P, (c) K, (d) Mg and (e) Ca for leaf and stem plus root samples of *N. cadamba* seedlings grown in soils (ALL = alluvial, MH = mudstone hill, SH = sandstone hill) taken from Sepilok Forest Reserve in Sabah, Malaysia. The F-ratios and degree of significance following one-way ANOVA of leaf nutrient concentrations between soil types at the final harvest are presented.

using the fast-growing native pioneer tree species *N. cadamba* as a tool to determine limitations to plant growth in three soil types. To address the different durations of growth between soil types (approximately eight weeks for seedlings grown in alluvial and mudstone soils vs. six weeks for seedlings grown in sandstone soil), the comparison of growth between soil types was based on values

of relative growth only. However, it is possible that this difference in experimental duration may have also affected the likelihood of limitation by N vs. P between soil types because increasing root length density reduces the potential for limitation by P relative to more mobile nutrients such as nitrate (Cornforth 1968). We minimised the likelihood of this problem by harvesting before seedlings

became large relative to the soil volume in the pot. However, the results should be interpreted with caution.

The responses of *N. cadamba* seedlings suggest that P availability is only limiting its growth in the sandstone hill soils, which have lower available P concentrations than alluvial or mudstone hill forest soils (Dent et al. 2006). Previous bioassays of nutrient limitation have demonstrated that P was the primary limiting nutrient for growth of the non-mycorrhizal herb *Phytolacca rivinioides* in a relatively nutrient-rich soil derived from volcanic parent material in Costa Rica (Denslow et al. 1987), non-mycorrhizal seedlings of the shrub *Melastoma malabathricum* growing in an ultisol taken from a coastal hill dipterocarp forest in Singapore (Burslem et al. 1994), seedlings of the riverine species *Lagerstroemia floribunda* growing in alluvial, shale and laterite soils taken from lowland dipterocarp forest at Pasoh Forest Reserve, Peninsular Malaysia (Wan Juliana et al. 2009), seedlings of the early successional tree species *Persea rimosa* and *Melicope glabra* growing in soils taken from a rubber estate in West Kalimantan, Indonesia (Lawrence 2001), and seedlings of the non-pioneer tree species *Shorea johorensis* growing in lowland secondary forest at Danum Valley Conservation Area, Sabah, Malaysia (Bungard et al. 2002). All these species have potentially high RGR and therefore a high demand for nutrients to sustain vegetative growth (Aerts & Chapin 2000).

The absence of response to the addition of P on alluvial and mudstone hill soils suggests that growth of *N. cadamba* may not be limited by P availability on these soils. Alternatively, it is possible that the addition of P led to no effective increase in soil P availability because of the high buffering capacity of these clay-rich soils (Brady & Weil 1999). This phenomenon has been demonstrated in experiments using oil palm that have shown wide variations in the response of oil palm yield to P addition dependent on soil buffering capacity (Foster & Goh 1977).

There was a suggestion that seedling growth in the alluvial soils was limited by K. In agricultural systems, K is an important component of fertilisers for increasing yield and growth of crops, and in Malaysia, it is used to increase girth increment of rubber trees (Pusparajah 1969) and in the early establishment of oil palm (Ng et al. 1968), in both cases planted on former primary rainforest soils. The basal area of lowland tropical rainforest stands at Pasoh and Jengka Forest Reserves in Peninsular Malaysia were reported to correlate significantly with the availability of K in soil and leaves (Amir & Miller 1990). Nonetheless, this correlation might be construed as poor evidence that K was the primary limiting nutrient in these forest soils because the studies did not demonstrate that basal area growth of those two forest stands responded to inputs of K. In contrast, Wan Juliana et al. (2009) found that seedlings of the riverine tree species, *L. floribunda* growing in forest soils taken from Pasoh Forest Reserve were limited by P but not K.

Limitation of *N. cadamba* seedling growth by K in the alluvial forest soil may have been induced by an absence of primary limitation by P availability. Alluvial forest soils have significantly higher concentrations of available P than soils taken from the sandstone hill environment (Dent et al. 2006) and the higher P concentrations may have been sufficient to prevent P from limiting growth of *N. cadamba* seedlings. Previous studies have suggested that plant growth in a tropical forest soil with high available P concentration may be limited by other macronutrients such as N and K (Burslem et al. 1994). Limitation by N and nutrient cations for plants that had been relieved of primary limitation by P was observed in seedlings of *M. malabathricum* growing in ultisol in Singapore (Burslem et al. 1994). Limitation of growth by the supply of K, Mg and Ca was also observed for seedlings of the non-mycorrhizal herb *P. rivinioides* growing in nutrient-rich soils derived from volcanic parent material in Costa Rica (Denslow et al. 1987), while seedlings of *Antidesma cuspidatum* and *Vatica maingayi* grown in ultisol were limited by Mg and by one or more macronutrient respectively (Burslem et al. 1995).

Seedlings of *N. cadamba* grown on mudstone hill soil had lower growth rate of leaf number in response to the addition of N than in the control. It is known that high inputs of inorganic N fertilisers such as ammonium nitrate may induce soil acidification and loss of exchangeable cations through leaching (Wild 1988). In addition, an excess of ammonium ions in soil solution may lead to ammonia toxicity that can retard plant growth (Schenk & Wehrmann 1979). The addition of small quantities of N was also toxic to seedlings of *Chlorocardium rodiei* tree growing naturally on white sand soils at the Tropenbos research site in the Mabura region in central Guyana

(Raaimakers 1995) and seedlings of *L. floribunda* growing in soil taken from lowland dipterocarp forest in Pasoh Forest Reserve, Peninsular Malaysia (Wan Juliana et al. 2009). However, this finding may also relate to the specialised habitat requirements of the test species because adult trees of *N. cadamba* are rarely found in mudstone hill habitats (R Nilus, personal observation). This was supported by the observation that seedlings grown in mudstone hill soil demonstrated growth rates that were intermediate between those of seedlings grown in alluvial and sandstone hill soils. The retardation in seedling growth in response to nutrient addition may have been caused by an imbalance of the cation–anion ratio in the soil, which may have affected the availability of one or more nutrients essential for plant development (Marschner 1995).

CONCLUSIONS

The differences in nutrient limitation between soil types at SFR are likely to be associated with the differences in parent material. We have provided preliminary evidence that seedling growth of the pioneer tree species *N. cadamba* is limited by P in soil from the sandstone hill habitat and by K in alluvial soils. This experiment has determined that P and not N limits growth of *N. cadamba* in the sandstone hill soil. The alluvial soils have higher concentrations of available nutrients and the experiment suggests that P is not limiting to plant growth. In the absence of limitation by P, growth became limited by the availability of K.

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