

NUTRIENT LIMITATION OF SEEDLING GROWTH ON CONTRASTING SOILS FROM PASOH FOREST RESERVE, PENINSULAR MALAYSIA

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WAN JULIANA WA, BURSLEM DFRP & SWAINE MD. 2009. Nutrient limitation of seedling growth on contrasting soils from Pasoh Forest Reserve, Peninsular Malaysia. A pot bioassay experiment was established to test the hypotheses that different soil types represented on a 50 ha plot in Pasoh Forest Reserve supply different amounts of nutrients for plant growth, and that phosphorus (P) is the main limiting nutrient. Seedlings of the tree *Lagerstroemia floribunda* were grown for 54 days in pots of alluvial, shale or laterised-shale soil. The experiment comprised six nutrient addition treatments and an unmanipulated control, with five replicates for each treatment. The growth of seedlings of *L. floribunda* was limited by the availability of P but not by the other nutrients (N, K, Ca or Mg) added singly in the experiment. Relative growth rates were highest on alluvial and shale-derived soils, which had higher available P concentrations than the laterised shale-derived soils in the absence of nutrient addition. Shifts in biomass allocation and changes to specific leaf area were the mechanisms responsible for the increase in plant growth in response to nutrient addition.

Keywords: Bioassay, pot experiment, nutrient addition, phosphorus, seedling growth rate, biomass allocation, specific leaf area

WAN JULIANA WA, BURSLEM DFRP & SWAINE MD. 2009. Nutrien terhadap bagi pertumbuhan anak benih dalam tanah yang berbeza dari Hutan Simpan Pasoh, Semenanjung Malaysia. Satu eksperimen bioasai pasu dijalankan untuk menguji hipotesis bahawa tanah berbeza dari plot 50 ha di Hutan Simpan Pasoh membekalkan jumlah nutrien yang berbeza untuk pertumbuhan pokok dan fosforus (P) ialah nutrien terhadap yang utama. Anak benih pokok *Lagerstroemia floribunda* ditanam selama 54 hari di dalam pasu yang berisi tiga jenis tanah iaitu aluvium, syal atau syal berlaterit. Eksperimen ini terdiri daripada enam rawatan nutrien tambahan dan satu kawalan. Setiap satu rawatan mempunyai lima replikasi. Pertumbuhan anak benih *L. floribunda* didapati terhadap oleh P tersedia dan tidak oleh nutrien lain (N, K, Ca atau Mg) yang ditambah secara berasingan dalam eksperimen ini. Tanpa kehadiran nutrien tambahan, kadar pertumbuhan relatif anak benih didapati paling tinggi dalam tanah jenis aluvium dan tanah berasaskan syal yang mempunyai kandungan P tersedia yang lebih tinggi berbanding tanah laterit berasaskan syal. Peralihan dalam pengagihan biojisim dan perubahan luas permukaan spesifik daun ialah mekanisme yang berhubung kait dengan peningkatan dalam pertumbuhan akibat penambahan nutrien.

INTRODUCTION

Soil resource availability is often correlated with local-scale variation in tree species distribution in tropical forests (John *et al.* 2007). At the Pasoh Forest Reserve, Peninsular Malaysia, these studies suggest that species may be competing for nutrients as a limiting resource (Wan Juliana 2001, Davies *et al.* 2003, Potts *et al.* 2004). However, studies that provide direct tests of the nutrient limitation hypothesis are rare. It is well known that nutrient availability limits forest productivity on old, highly weathered tropical

soils (Grubb 1989, Elser *et al.* 2008, Lambers *et al.* 2008). However, direct experimental tests of local-scale differences in plant growth in response to natural variation in soil resource availability have not been conducted.

A study of nutrient limitation of leaf litter production at 55 lowland tropical forest sites suggested that P is more limiting than N in the lowland tropics (Vitousek 1984). Limitation by low P availability is prevalent in soils that have high concentrations of Al and Fe, and

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therefore a high capacity to bind phosphates as insoluble Al and Fe sesquioxides. Soils with these characteristics are common in many tropical regions (Binkley 1986), including Pasoh Forest Reserve in Peninsular Malaysia (Allbrook 1973). A direct test showed that P was the main limiting nutrient for non-mycorrhizal seedlings of the shrub *Melastoma malabathricum* growing in soil from a lowland dipterocarp forest in Singapore (Burslem *et al.* 1994). In this experiment, other nutrients became limiting only when the supply of P was sufficient for growth. Raaimakers (1995) also showed that P rather than N was the major growth-limiting nutrient for saplings of the legume *Dicymbe alstonii*, in white sand soil in Guyana. These findings are supported by a pot study in Sri Lanka (Gunatilleke *et al.* 1997) and field experiment in Malaysia (Raja Barizan & Appanah 2000) demonstrating a significant positive effect of P addition on dipterocarp seedling growth rates.

Not all studies on nutrient limitation of plant growth in forest soils, however, provide evidence of limitation by P, and differences between sites must be considered when analysing nutrient availability to plants (Vincent & Davies 2003). For example Vitousek and Sanford (1986) suggested that temperate and tropical montane forests are more limited by N, whereas the evidence suggested that P is more limiting than N in lowland tropical forests. This contrast reflects the relatively low N mineralisation rates in temperate forest soils (Vitousek & Sanford 1986). Nevertheless, this generalization is yet to be tested in the field in the lowland tropics. In addition, there are some tropical montane and temperate sites where P is likely to limit growth as well as N (Tanner *et al.* 1990, Tanner *et al.* 1998, Cavelier *et al.* 2000, Stewart 2000, van den Driessche *et al.* 2003, Gradowski & Thomas 2006). Recently, Elser *et al.* (2008) proposed that simultaneous addition of N and P leads to increased primary production in terrestrial, freshwater and marine ecosystems.

Three major soil types have been identified on the permanent 50 ha forest dynamics plot at Pasoh Forest Reserve, Peninsular Malaysia (Wan Juliana 2001). These soil types are differentiated on the basis of parent material, and they vary in their chemical characteristics (Wan Juliana 2001). Variation in tree species floristic composition is strongly associated with available P concentrations in Pasoh forest soil (Wan Juliana 2001, Davies *et al.* 2003, Potts

et al. 2004), suggesting that the outcome of competition for P might be an important determinant of this pattern.

This paper reports an experimental test of the hypotheses that the three soil types occurring on the 50 ha plot at Pasoh supply different amounts of nutrients for plant growth, and that P is the main limiting nutrient. We examined differences in early seedling growth of *Lagerstroemia floribunda* in pots containing the three major soil types underlying the Pasoh forest dynamics plot, and the differential responses to nutrient addition of forest seedlings growing in those three soil types.

MATERIALS AND METHODS

The test species was *L. floribunda* (Lythraceae), which is indigenous to the northern part of Peninsular Malaysia. *Lagerstroemia floribunda* is an understory tree with a maximum height of about 18 m. It produces good quality, light hardwood and is suitable as an ornamental tree. It is abundant on riverbanks in low open country and is sometimes gregarious (Everett & Whitmore 1983).

Soil from 0 to 20 cm depth was collected after surface litter and the organic F layer was removed. The soils were of the Bukit Tuku (BTU), Musang–Durian (MSG–DRN) and Padang Besar–Batu Lapan (PBR–BLN) soil series (references to soil map of the plot). The three soil series were chosen to represent typical soils overlying the three main parent materials (alluvium, shale and laterised-shale respectively) on the 50 ha plot (Amir 1989). Soil of the Bukit Tuku series (alluvial soil) was collected from a site halfway between the research station and the 50 ha permanent plot, Musang–Durian series (shale) from a seasonally-flooded site in the Pasoh research station arboretum and Padang Besar–Batu Lapan series (laterised shale) was collected near the Japanese research tower. Soil samples were taken at three randomly located points at each site using an auger. The replicates were bulked, mixed, subsampled and transported to Aberdeen University, UK, for chemical analysis.

Soil chemical characteristics were determined to allow comparison with soils collected on the 50 ha forest dynamics plot at Pasoh. pH was analysed using a pH meter in a 1:2 paste of soil: distilled water; total and available P by

the molybdenum-blue method using a flow injection auto-analyser—total P was extracted with sulphuric acid-hydrogen peroxide reagent and available P with negatively charged resin in Cl⁻ form resin bags; exchangeable bases and Al were extracted with 1M ammonium acetate at pH 7; K by flame emission spectrophotometry; Mg and Ca by atomic absorption spectrophotometry and Al by graphite furnace atomic absorption spectrophotometry; cation exchange capacity was determined by leaching the ammonium saturated soil with acidified 1M sodium chloride solution; total organic nitrogen and carbon concentrations by a flash combustion technique using an NCS auto-analyser. Further details of these analyses are provided by Wan Juliana (2001).

Soils for the bioassay experiment were air dried and sieved through a 5 mm mesh to remove roots and litter. The soils were then mixed 50:50 by volume with fine river sand to improve their drainage characteristics. The pH of the soil/sand mixture was measured and only slight, non-significant increases were found (results not shown). One experimental unit comprised a standard 554 g of soils in a square polythene pot 8.5 cm × 8.5 cm and 12.5 cm tall (volume of 903 cm³). The soil/sand mixture in the pots was watered daily and was allowed to equilibrate for a week before the experiment started.

Seeds of *L. floribunda* were obtained from the Forest Research Institute Malaysia, Kepong. They were placed on moistened filter paper in Petri dishes and germinated in a phytotron at a temperature of 26–28 °C and photosynthetically active radiation (PAR) of 49.7 μmol m⁻² s⁻¹ or about 4.4% of full daylight irradiance at Pasoh. After two weeks, germinated seeds were transferred to the surface of alluvial soil from Pasoh Forest Reserve in shallow trays and grown at a very high density in a glasshouse transmitting 236 μmol m⁻² s⁻¹ PAR or 21.1% of full irradiance. Seedlings were transplanted singly into each pot. Thirty seedlings were harvested at the same time. Mean total dry mass was 14.7 mg per seedling. Seedlings were allowed to establish in the new environment for 10 days before nutrient solutions were added.

We established a balanced factorial experimental design with two categorical independent fixed variables: soil type with three levels (alluvial, shale and laterised-shale) and nutrient addition treatments, with seven levels (five additions of 37 mM NH₄NO₃, 37 mM Na₂HPO₄, 32 mM KCl, 5 mM CaCl₂·2H₂O, 9 mM MgCl₂·6H₂O,

9 mM Na₂SO₄ and an unfertilized control). This represents 21 treatments, each of them with five replicates. The amount and concentrations of all nutrient solutions used in this experiment followed those used by Denslow *et al.* (1987) and Burslem *et al.* (1994). Nutrient additions (10 ml) were carried out on five occasions at weekly intervals. Pots were arranged in a completely randomized design in the glasshouse and were watered daily. The experiment was harvested after 54 days because most seedlings to which NH₄NO₃ had been added were dead after the fourth nutrient addition. Measurements of the pH of soil in pots of the control, plus N and plus P treatments were made at the end of the experiment using a portable pH meter calibrated to pH 4.

At the final harvest, the number of leaves was recorded for each seedling and the aboveground components were severed from the roots. Leaves were separated from the stem and leaf areas were determined using a leaf area meter. Roots were excavated from the soil and washed. Each plant component was oven-dried at 70 °C to constant mass and its dry mass recorded. Mass ratios (mass of a plant part divided by total mass) were calculated for leaves (LMR), stems (SMR) and roots (RMR). The relative growth rates (RGR) were calculated as follows: $RGR = \log_e W_2 - \log_e W_1 / t_2 - t_1$, where W_2 is dry mass at final harvest, t_2 , and W_1 is the mean dry mass of the 30 seedlings harvested at t_1 .

The results were submitted to analysis of variance using the General Linear Model procedure of MINITAB following transformation of the data where necessary. Untransformed means are presented in figures and tables. Analyses of variance were carried out to determine the main effects and interactions between nutrient addition treatments and soil type. Significant differences between treatments were then identified using Tukey's test for multiple comparisons (Sokal & Rohlf 1995).

RESULTS

Species, soils and chemical characteristics

At the end of the experiment, a total of 19 seedlings had died, out of the original 105 planted (3 soil types × 7 nutrient treatments × 5 replicates). Of these 19 seedlings, eight were from the +N, four from the +K, six from the +Mg and one from the control treatment. These

differences were statistically significant ($\chi^2 = 29.43$, $p < 0.001$). Seedlings from the +N treatment were not included in the following analyses because too few survived in this treatment. Soils receiving NH_4NO_3 had declined in pH by 0.3–0.9 units while soils that received Na_2HPO_4 had increased by 0.13–0.25 pH units compared with the controls (results not shown). Soil type did not have significant effect on seedling mortality ($\chi^2 = 0.40$, $p > 0.05$).

Comparisons of chemical characteristics between soils collected for this experiment and soils in the 50 ha plot (Wan Juliana 2001) suggested that the differences between parent materials were mostly consistent between sites (Table 1). The pH was lower in the laterised-shale soils than the alluvial and shale soils ($p < 0.05$). Total P, total C and N concentrations, CEC and Al concentrations were higher in shale than alluvial soils ($p < 0.05$). Available P was higher in alluvial than the shale soil ($p < 0.05$). The only difference was that the concentrations of

exchangeable K, Ca and Mg in the soils used in the experiment were highest in the laterised-shale soil ($p < 0.05$) (Table 1), whereas there was no significant difference in the concentrations of these elements for the three soil types collected on the 50 ha Pasoh plot, except for K which was significantly higher in the alluvial soils than the laterised-shale soils (Wan Juliana 2001).

Effects of nutrient addition and soil types on seedling growth

All measures of *L. floribunda* seedling growth showed highly significant differences ($p < 0.001$) in response to nutrient addition treatments (Table 2 and Figure 1). Differences between soil types were also significant ($p < 0.01$) except for leaf number but there were no significant interactions between these two factors on seedling growth (Table 2). These analyses suggest that these two factors acted independently on the growth.

Table 1 Mean (\pm standard error) top soil (0–20 cm) chemical characteristics of alluvial, shale-derived and laterised-shale soils collected from Pasoh Forest Reserve

Soil characteristic	Alluvial (BTU)	Shale (MSG–DRN)	Laterised-shale (PBR–BLN)
pH	4.60 \pm 0.10	4.54 \pm 0.04	4.29 \pm 0.13
Total P (mg g ⁻¹)	32.7 \pm 0.0	155 \pm 6.4	181 \pm 29.0
Available P (mg 100 g ⁻¹)	0.069 \pm 0.010	0.047 \pm 0.010	0.039 \pm 0.010
K (mg 100 g ⁻¹)	7.04 \pm 0.01	2.46 \pm 0.07	8.85 \pm 0.08
Ca (mg 100 g ⁻¹)	1.06 \pm 0.02	1.18 \pm 0.01	1.69 \pm 0.15
Mg (mg 100 g ⁻¹)	0.65 \pm 0.01	0.55 \pm 0.02	1.14 \pm 0.02
Al (mg 100 g ⁻¹)	1.61 \pm 3.12	10.43 \pm 2.22	5.34 \pm 0.30
C %	1.09 \pm 0.07	na	2.23 \pm 0.16
N %	0.04 \pm 0.01	na	0.24 \pm 0.02
CEC (me 100 g ⁻¹)	2.99 \pm 0.09	6.30 \pm 0	9.90 \pm 0.08

na = not available

Table 2 F-values and degree of significance following two-way ANOVA on leaf number, leaf area, total dry mass and relative growth rate to determine the effects of nutrient addition, soil type and the interaction between soil type and nutrient addition on growth of *Lagerstroemia floribunda* seedlings in pots of soil taken from Pasoh Forest Reserve

Source of variation	Leaf number	Leaf area	Total dry mass	Relative growth rate
Nutrient addition	35.52 ***	47.89 ***	49.14 ***	47.89 ***
Soil type	0.30	5.97 **	7.00 **	6.12 **
Nutrient addition \times soil type	0.45	0.64	1.22	0.96

** $p < 0.01$, *** $p < 0.001$

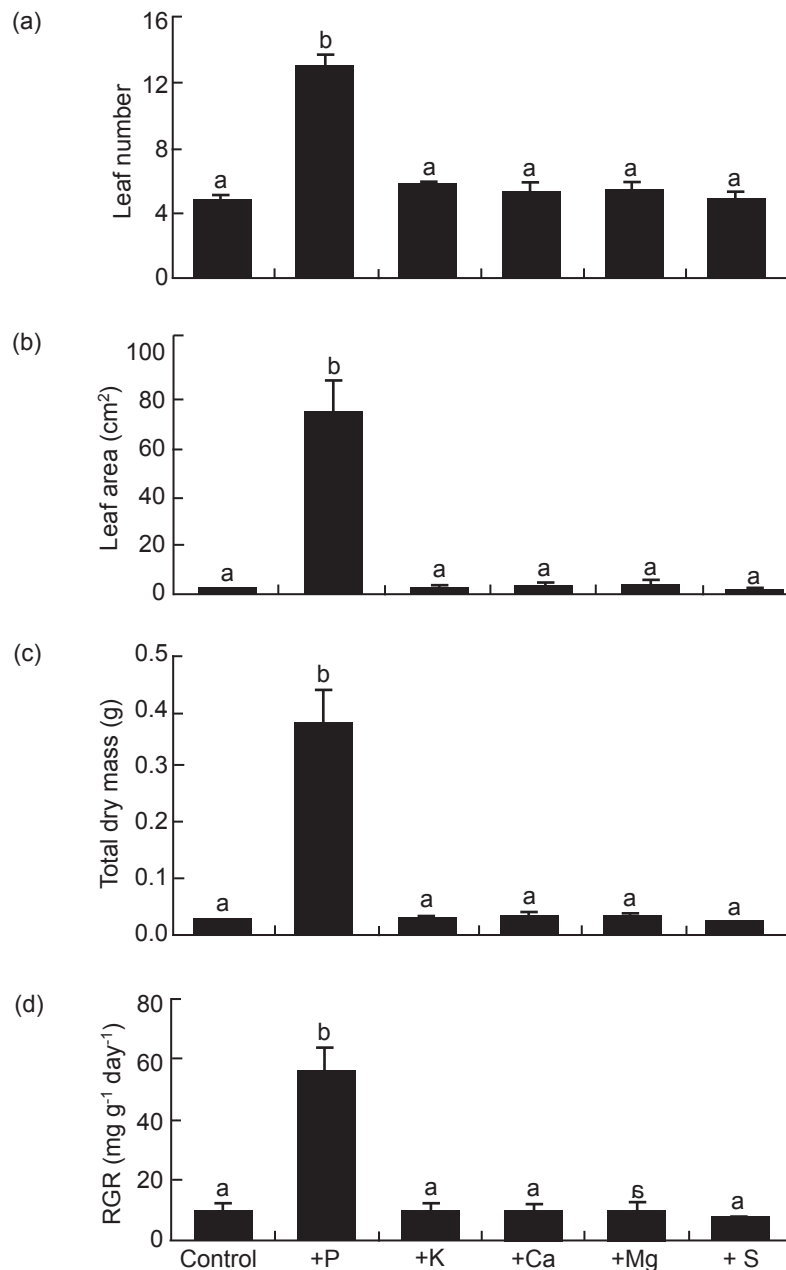


Figure 1 Untransformed mean (\pm SE) leaf number (a), leaf area (b), total dry mass (c) and relative growth rate, RGR (d) of *Lagerstroemia floribunda* seedlings grown for 54 days in three soil types (alluvial, shale and laterised-shale) without nutrients ('control') or with additions of P (+P), K (+K), Ca (+Ca), Mg (+Mg) and S (+S). Significant differences between nutrient treatments are indicated with different letters according to Tukey's test ($p < 0.001$).

All plant growth variables showed very clearly that P was the primary limiting nutrient (Figure 1). Seedlings that received added P showed a 2.7-fold increase in the number of leaves, 30-fold increase in total leaf area, 12.7-fold increase in total dry mass and 5.5-fold increase in relative growth rate over control plants. The other nutrient addition treatments (K, Ca, Mg and S) did not affect the growth of *Lagerstroemia* seedlings.

There was strong evidence ($p < 0.01$) of significant difference in the growth of *Lagerstroemia* seedlings on alluvial, shale and laterised-shale soils for three out of the four growth variables measured. Leaf area, dry mass and relative growth rate were higher in seedlings grown on shale soil than on laterised-shale soil (Figure 2). However, there were no differences in leaf area or total dry mass between seedlings grown on alluvial and shale soils or between

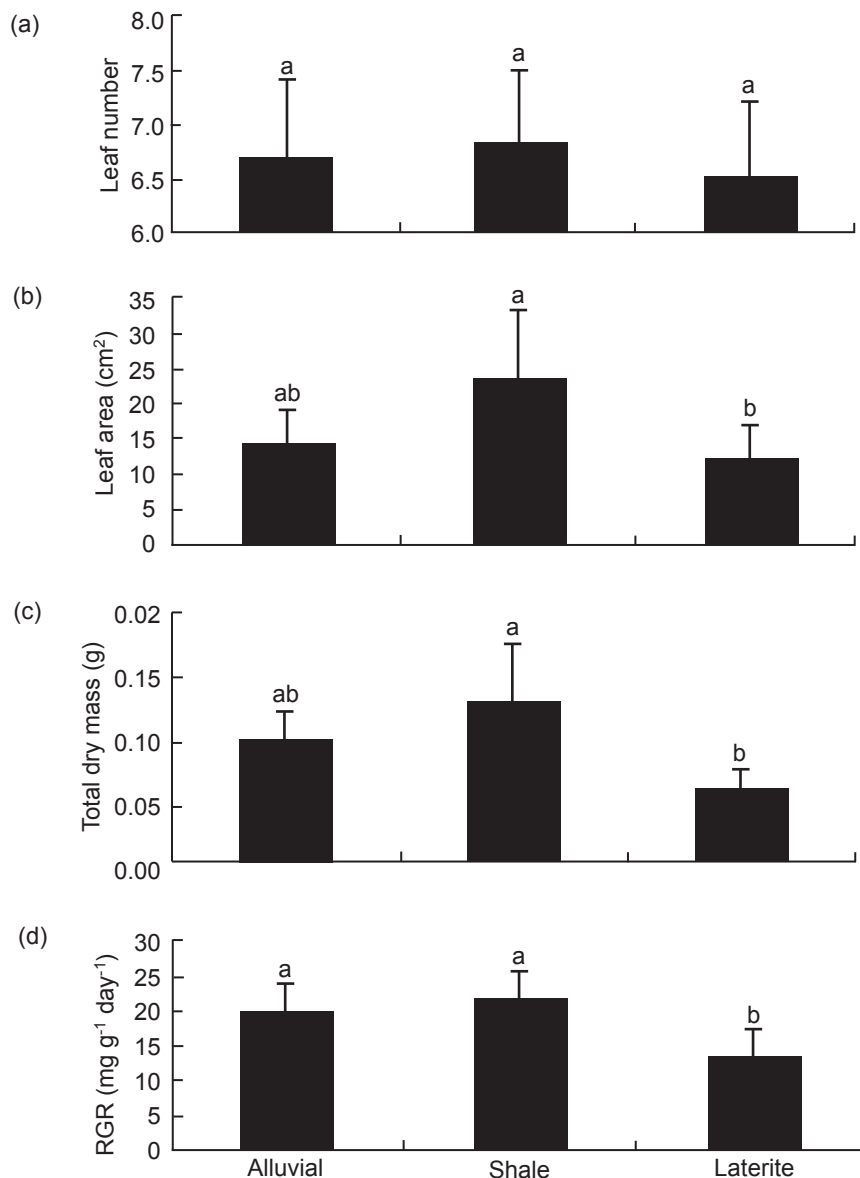


Figure 2 Untransformed mean (\pm SE) leaf number (a), leaf area (b), total dry mass (c) and relative growth rate, RGR (d) of *Lagerstroemia floribunda* seedlings grown for 54 days in three soil types at Pasoh Forest Reserve, Peninsular Malaysia. Significant differences between soil type treatments are indicated with different letters according to Tukey's test ($p < 0.01$).

those grown on alluvial and laterised-shale soils. Relative growth rates were higher for seedlings grown on shale ($21.5 \text{ mg g}^{-1} \text{ day}^{-1}$) and alluvial ($19.8 \text{ mg g}^{-1} \text{ day}^{-1}$) soils than on laterised-shale soil ($13.6 \text{ mg g}^{-1} \text{ day}^{-1}$).

Effects of nutrient addition and soil types on the distribution of dry mass

All four biomass allocation variables differed significantly between nutrient addition treatments (Table 3). Only the +P treatment resulted in a significantly higher specific leaf area and shift in

dry mass allocation compared with the control (Figure 3). In the +P treatment, dry mass was concentrated in the leaves (59%) rather than roots (28%) or stems (13%). In the control treatment, a greater proportion of dry mass was allocated to the roots (42%) than the leaves (39%) or the stems (19%). Therefore, the addition of P significantly increased specific leaf area and leaf mass ratio (LMR) and decreased stem mass ratio (SMR) and root mass ratio (RMR) compared with the control.

Biomass allocation within a plant differed significantly between soil types, but specific leaf

Table 3 F-values and degree of significance following two-way analysis of variance on specific leaf area, leaf mass ratio, stem mass ratio and root mass ratio to determine the effects of nutrient addition, soil type and the interaction between soil type and nutrient addition on biomass allocation of *Lagerstroemia floribunda* seedlings grown in pots of soil taken from Pasoh Forest Reserve, Peninsular Malaysia

Source of variation	Specific leaf area	Leaf mass ratio	Stem mass ratio	Root mass ratio
Nutrient addition	19.28 ***	14.92 ***	6.61 ***	7.85 ***
Soil type	0.34	6.73 **	11.85 ***	10.73 ***
Nutrient addition × soil type	2.93 **	1.44	1.65	0.62

** p < 0.01 *** p < 0.001

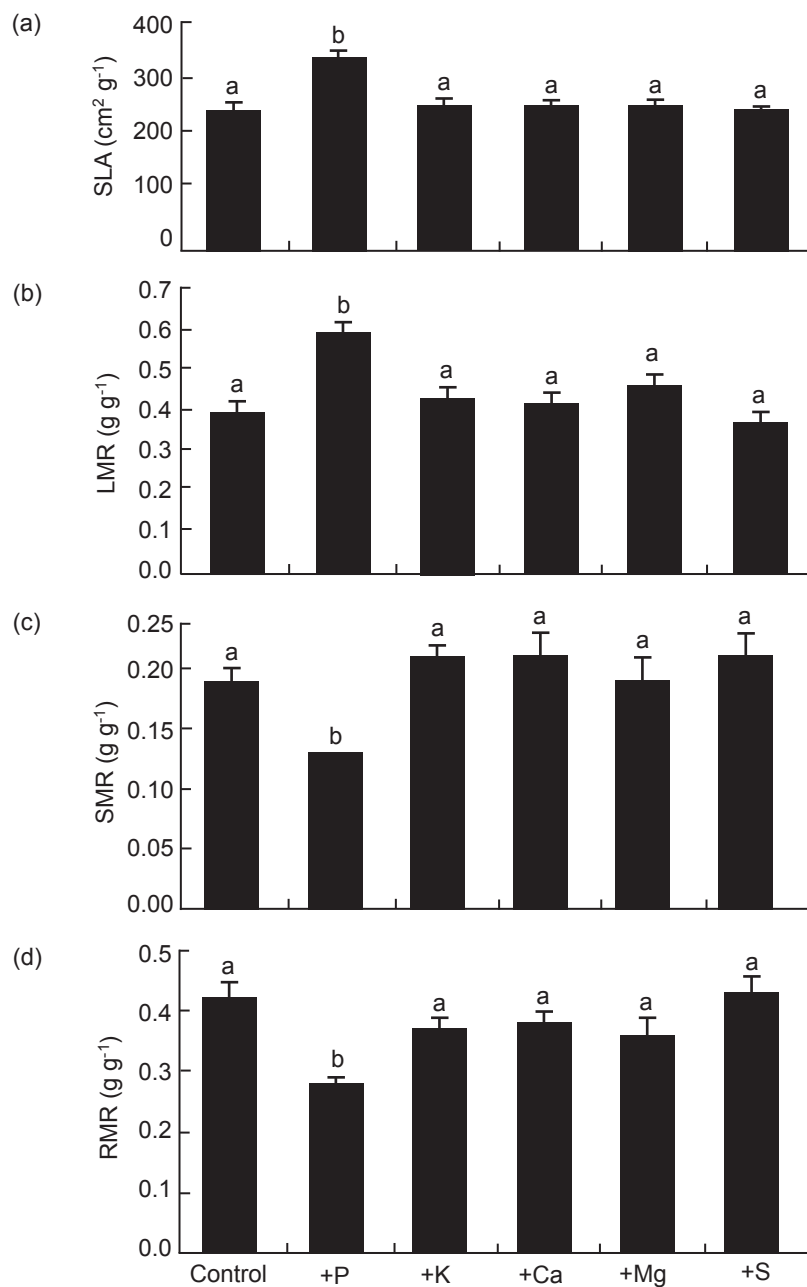


Figure 3 Effects of nutrient additions and an unmanipulated control on specific leaf area (SLA), mean leaf mass ratio (LMR), stem mass ratio (SMR) and root mass ratio (RMR) for *Lagerstroemia floribunda* seedlings grown for 54 days in pots of three Pasoh soil types. The significance of the difference between nutrient treatments is indicated with different letters according to Tukey's test (p < 0.001).

area did not (Table 3). On alluvial soils, the greatest proportion of dry mass was allocated to roots (43%), but seedlings grown on shale and laterised-shale soils allocated more dry mass to leaves (48 and 44% respectively) than to other plant parts (Figure 4). Leaf mass ratio was higher for seedlings grown on shale than alluvial soil; SMR was higher for seedlings grown on laterised-shale soil than either alluvial or shale soil and RMR was higher for seedlings grown on alluvial

soil than either of the two other soil types (Figure 4). There was no evidence of interaction between nutrient addition and soil type on dry mass allocation in *Lagerstroemia* seedlings growing in Pasoh forest soils (Table 3). However, for specific leaf area, the increase in response to the addition of P was very much greater for seedlings growing in laterised-shale soil than in either of the two other soil types (Figure 5).

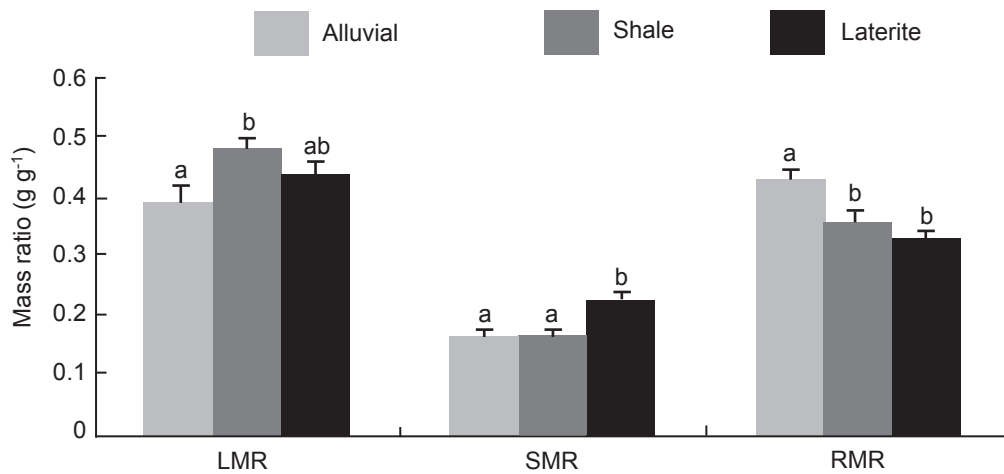


Figure 4 Effects of soil type on mean leaf mass ratio (LMR), stem mass ratio (SMR) and root mass ratio (RMR) for *Lagerstroemia floribunda* seedlings grown in pots of soil from Pasoh Forest Reserve, Peninsular Malaysia. The significance of differences between soil types is indicated with different letters according to Tukey’s test ($p < 0.01$).

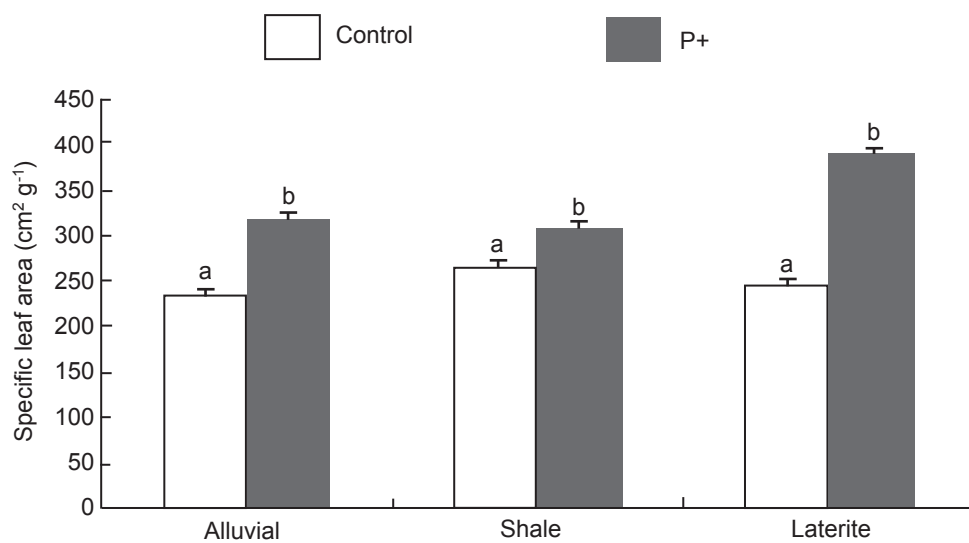


Figure 5 Effects of nutrient addition and soil type on specific leaf area of *Lagerstroemia floribunda* seedlings grown for 54 days in pots of soil taken from Pasoh Forest Reserve. The significance of differences between treatments is indicated with different letters according to Tukey’s test ($p < 0.05$).

DISCUSSION

Nutrient limitation of tropical tree seedling growth

The results suggest clearly that P was the primary limiting nutrient for the growth of *L. floribunda* seedlings in Pasoh forest soils (Figure 1). According to Chapin (1980), the degree of nutrient limitation can be recognized by the magnitude of the growth responses when the limiting nutrient is added. The substantial increases in relative growth rate, total dry mass, leaf area and leaf number when P was added suggest that P plays a vital role in controlling growth of this species in Pasoh forest soil. In addition, according to Chapin (1980), in order to observe a significant effect of nutrient addition on leaf number, the magnitude of nutrient limitation must be substantial. Since the results showed that a significant effect of nutrient addition on leaf number was only found when P was added (Figure 1), they support the hypothesis that P is the main limiting nutrient for this species when grown in pots. Moreover, relative growth rate of seedlings in the absence of nutrient addition was faster on alluvial soil than on laterised-shale (Figure 2), which parallels the difference in available P between the two soils and contrasts with the difference in total N concentrations (Wan Juliana 2001).

Nevertheless, seedlings that had received additions of N had high mortality in this experiment and a role for N in plant growth cannot be discounted. One possible reason for the high seedling mortality when NH_4NO_3 was added is that the uptake of ammonium ions by the plants was associated with a release of H^+ ions into soil solution that lowered soil pH (results not shown). Lower soil pH decreases the availability of other nutrients to the plant (Binkley 1986), thereby creating nutrient deficiency conditions unsuitable for growth. Lower pH may also increase Al availability and induce direct toxicity to the plants (Brady & Weil 1996). A study in Guyana has also shown that addition of N has a lethal effect on non-legume saplings (Raaimakers 1995).

It is well established that in pot experiments, effects of nutrient addition on growth may result indirectly from changes in soil processes such as N mineralisation rate. Consequently one may see increased growth when P is added, not only because P limits growth but also because P

addition increases N mineralisation rates and therefore N availability in the soil. On the other hand, Chapin (1980) reported that improved plant N status causes up to 10-fold increase in root absorption capacity for phosphate and vice versa. According to this hypothesis if N had been the main limiting nutrient, *Lagerstroemia* seedling growth should have increased when N was added because the plant would take up increased amounts of both N and P. These observations provide further evidence that P and not N is the major limiting nutrient, at least for this test species, in Pasoh forest soil.

Many studies have examined the relationship between forest composition and edaphic factors using indirect methods and have suggested that P is the most limiting nutrient for tropical tree distribution (Baillie *et al.* 1987, Ashton & Hall 1992, Sollins 1998) and forest growth and productivity (Vitousek 1984). However, variable results have been obtained from nutrient limitation experiments. Although few in number, experiments have shown P to be the main limiting nutrient for growth of non-mycorrhizal woody plant seedlings in pots (Burslem *et al.* 1994) and in the field (Raaimakers 1995) and for growth of pioneer species in a field fertilization experiment in Puerto Rico (Fetcher *et al.* 1996). Nevertheless, P limitation is rarely found among mycorrhizal tropical tree species, except when the species lacks mycorrhizas during the experiment (Burslem *et al.* 1995). The probable absence of mycorrhizas on seedlings of the test species may be another factor contributing to P limitation in this experiment.

Amir (1989) suggested that soil fertility at Pasoh was governed by parent material and that the main limiting nutrients were possibly $\text{K} > \text{N} > \text{P}$. He based this assertion on soil chemical analysis, the relationship between nutrient concentrations in soil and leaves, and the basal area of selected tree species including dipterocarps. However, standing basal area is not a measure of plant growth, and correlations between soil chemistry and standing basal area cannot be used to determine cause and effect relationships. We found no significant limitation by K concentration in this experiment (Figure 1).

Although the experiment is limited in its applicability to nutrient limitation in the field, it provides some additional evidence in support of the hypothesis that P is the main limiting nutrient in Pasoh Forest Reserve soils (Wan Juliana 2001). In order to resolve the importance

of P in controlling tree growth of Pasoh forest in its natural habitat, a field experiment should be conducted.

Mechanistic basis of tree seedling growth response to P addition

An increase in the ratio of leaf area to leaf dry mass (SLA) and the shift in biomass allocation from roots to shoots contributed to the growth response to the addition of P in this experiment. P addition resulted in a 1.4-fold increase in SLA relative to the control treatment and more than half of plant dry mass was allocated to the leaves in the +P treatment compared with 39% in the control treatment (Figure 3). Lambers and Poorter (1992) showed that SLA and RGR correlated positively across a large sample of plant species. These correlations arise because the increase in leaf area per unit leaf mass and plant mass enhances the rate of carbon gain per unit plant mass.

Effects of soil type on seedling growth

Comparisons between the three soil groups used in the experiment (Table 1) showed that variation in nutrient availability paralleled the differences found in the 50 ha Pasoh plot soils (Wan Juliana 2001). In both cases, alluvial soil possessed the lowest Al concentrations, and the highest available P concentrations and pH, and laterised-shale soils possessed the lowest pH and available P concentrations.

Seedling relative growth rate was greater in shale and alluvial soils than in laterised-shale soils, which supports the hypothesis that P is the primary limiting nutrient in Pasoh forest soils (Figure 2). The mechanism involved in promoting seedling growth on shale soils is potentially the same as that determining the growth response to nutrient addition, where seedlings allocated an increased proportion of dry mass to the leaves in response to increased nutrient supply. However, a different mechanism was found when seedlings were grown on alluvial soil because although slightly more dry mass was allocated to the roots (43%) than the leaves (39%) on this soil type, growth was as fast as on shale soils where the proportional allocation of dry mass to leaves was much greater (48%). Although increased RMR values could increase the proportion of daily fixed carbon that is respired by the roots (Atkin &

Lambers 1998), it is possible that this leads to an increase in the efficiency of the accumulated mass of the plant to produce more mass (Chapin 1980). On the laterised-shale soil, although seedlings allocated more of their dry mass to the leaves (44%), growth was lower than on shale or alluvial soils. Therefore, despite having the advantage of higher LMR when grown on laterised-shale soils, *Lagerstroemia* seedlings were not able to assimilate nutrients from laterised-shale soils to support faster growth.

There are other potential explanations for the growth and dry mass allocation data presented. Firstly, in the wild, *Lagerstroemia* is found on riverbanks that are presumably nutrient-rich, and the species grows well in limestone, quartzite and shale soil habitats (Everett & Whitmore 1983). Therefore, although shale soil does not provide optimum soil conditions for crop growth (Wan Juliana 2001), *Lagerstroemia* could have become well adapted to this soil type. Secondly, plants originating from nutrient-rich soil show greater plasticity in dry mass distribution in response to variation in nutrient supply than do species from nutrient-poor environments (Huante *et al.* 1995, Chapin 1980). Therefore, as it is a species that is associated with nutrient-rich soil, *L. floribunda* might be able to modify its form and physiology to sustain growth in the variable nutrient availability conditions of Pasoh soils. Thirdly, the high Al saturation and bulk density of the laterised-shale soils may inhibit nutrient uptake, particularly of N and P, and thereby indirectly limit growth rate of seedlings growing in that soil (Stuhrmann *et al.* 1994). Finally, toxicity of Fe and Al ions, both of which are present at high concentrations in the laterised-shale soil, may also be explanations for the low growth rate of *L. floribunda* seedlings on laterised-shale soil. Similar results were obtained by ter Steege (1994) who found that seedlings of a non-pioneer tropical tree species in Guyana grew more slowly on a laterised-shale soil than sandy soil.

CONCLUSIONS

This study provides new evidence that growth of *L. floribunda* seedlings in Pasoh soils was limited by P availability, and suggests that available P is the most important nutrient controlling tree spatial distribution and tree species growth at Pasoh.

Additionally, the absence of significant differences in seedling mortality and SLA

in response to soil types indicates that the differences in nutrient availability in Pasoh soils are not great enough to affect seedling survival, although they did affect growth rate. We conclude that *L. floribunda* might show higher growth rates on alluvial and shale-derived soils as a result of its high morphological plasticity in response to soil conditions. Its low growth rates on laterised-shale soil might also result from poor tolerance to high Al concentrations. Experimental tests of these hypotheses are required.

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