

The responses of secondary forest tree seedlings to soil enrichment in Peninsular Malaysia: an experimental approach

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Abstract: Secondary forests are gaining prominence in tropical landscapes, but in areas adjacent to agricultural land the mix of species found in them is likely to be influenced by high rates of fertilisation and nutrient run-off. We conducted a pot experiment on three secondary forest species, *Glochidion obscurum*, *Lagerstroemia speciosa* and *Vitex pinnata*, to ascertain their response to nutrient addition. We used three treatments, (1) control (no fertilizer addition); (2) addition of 1 g of rock phosphate; and (3) addition of 1 g NPK, and found that *G. obscurum* and *L. speciosa* increased their growth when levels of nitrogen, phosphorus and potassium were increased, indicating evolutionary adaptation to use a high resource strategy. However, *V. pinnata* did not show the same pattern. It is, therefore, possible that on-going fertilization of low-lying secondary forests will produce growing conditions that lead to the reduction of non responsive species such as *V. pinnata* and favour others, such as *G. obscurum* and *L. speciosa*, at least in the early stages of forest succession.

Resumen: Los bosques secundarios están ganando importancia en paisajes tropicales, pero en áreas adyacentes a las tierras agrícolas la mezcla de especies hallada en ellos podría estar influenciada por tasas de fertilización y escorrentía de nutrientes altas. Hicimos un experimento en macetas con tres especies de árboles secundarios, *Glochidion obscurum*, *Lagerstroemia speciosa* y *Vitex pinnata*, con el fin de indagar su respuesta a la adición de nutrientes. Usamos tres tratamientos: (1) control (sin fertilizante), (2) adición de 1 g de fosfato de roca, y (3) adición de 1 g de NPK. Encontramos que el crecimiento de *G. obscurum* y *L. speciosa* aumentó cuando los niveles de nitrógeno, fósforo y potasio se incrementaron, lo que indica que hay una adaptación evolutiva de uso de una estrategia de recursos altos. Sin embargo, *Vitex pinnata* no mostró el mismo patrón. Por lo tanto, es posible que la fertilización que tiene lugar de los bosques secundarios ubicados en posiciones bajas generará unas condiciones de crecimiento tales que podrán causar una reducción de especies incapaces de responder, tales como *V. pinnata*, pero favorecer otras como *G. obscurum* y *L. speciosa*, al menos en las fases tempranas de la sucesión forestal.

Resumo: As florestas secundárias vêm ganhando proeminência na paisagem tropical, mas em áreas adjacentes às áreas agrícolas a mistura de espécies encontradas nelas é possível que estejam influenciadas por altas taxas de fertilização e de saída de nutrientes. Conduzimos um ensaio em vaso em três espécies florestais secundárias, a *Glochidion obscurum*, a *Lagerstroemia speciosa*, e a *Vitex pinnata*, para avaliar a sua resposta à adição de nutrientes. Usámos três tratamentos, (1) controlo (não adição de fertilizantes); (2) adição de 1 g de rocha fosfatada; e (3) adição de 1 g NPK, e encontramos que a *G. obscurum* e a *L. speciosa*, aumentaram o seu crescimento quando os níveis de azoto, fósforo e potássio aumentaram, indicando uma adaptação evolutiva ao uso de uma estratégia de elevados recursos. Contudo, a *Vitex pinnata* não mostrou o mesmo padrão. É por isso possível que a presente fertilização das florestas

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secundárias de baixa altitude produzam condições de crescimento que conduzam à redução de espécies não reactivas como a *V. pinnata* e favorecer outras, como a *G. obscurum* e a *L. speciosa*, pelo menos nos estágios iniciais da sucessão florestal.

Key words: *Glochidion obscurum*, *Lagerstroemia speciosa*, secondary forests, Soil fertilization, *Vitex pinnata*.

Introduction

Fertilization of soils is taking place on a massive scale in many parts of the world (Chapin 1983; Grime 1977; Joji 2000; Koerner *et al.* 1997; Tiessen 1995; Vitousek *et al.* 1997). One plausible impact of prolonged nutrient enrichment on vegetation is the destabilization of plant assemblages via selective death of sensitive species and changes in competitive relationships (Bazzaz 1996). For example, plants that are efficient users of soil nutrients, i.e., those species adapted to nutrient poor soils, may be out-competed by species adapted to nutrient-rich soils (Vitousek *et al.* 1997).

There is a well-established view that fast-growing plant species are nutrient-demanding (or employ high resource strategies *sensu* Chapin 1983) compared to slower-growing species, which may accumulate nutrient reserves (the luxury consumption strategy *sensu* Chapin 1983) while increasing growth only minimally when soil nutrient levels are increased (Chapin 1983; Grime 1977; Grubb 1989; Lawrence 2001). In tropical areas the majority of secondary forest species are thought to be fast-growing and light-demanding compared to primary forest species because light and nutrient availability in secondary forests is often higher and usually more variable than in primary forests (Bazzaz 1991; Brown & Lugo 1990; Guariguata & Ostertag 2001; Nogueira *et al.* 2004; Rees *et al.* 2001; Whitmore 1984). In many fast-growing species growth rates tend to increase when soils become more fertile, giving them a greater competitive ability (Chapin 1983; Lawrence 2001, 2003). This may mean that both secondary forest species and weedy species, which naturally possess a broad tolerance to high soil nutrient availability, could become dominant over a larger area than at present when widespread soil fertilization takes place (Bazzaz 1996; Lawrence 2003).

Corlett (1994) defines secondary forests as those that regenerate after total clearance and are thus found on sites where there has been a break in site occupation by forest. Regrowth of forest on

such sites depends on propagules arriving from outside of the site as well as from the seedbank and will therefore tend to have a greater proportion of species that are opportunistic and fast-growing than primary forests. It might also be expected that where such sites have been the recipients of artificial fertilisers, either from local runoff or through delivery in flood waters, plant species that employ high resource strategies will be more common.

Secondary forests are gaining prominence in tropical landscapes. Emrich *et al.* (2000) reported that secondary forests now constitute about 30 % of tropical forest areas. If secondary forests eventually become the dominant forest cover in many tropical areas it becomes important to understand how their biodiversity might be affected by eutrophication of soils through artificial fertilization. Many previous studies have concentrated on the factors affecting regeneration of trees and species diversity in primary forests but this research emphasis must change as primary forest is replaced with secondary forest. Identifying how species in secondary forests respond to soil fertilization is therefore of great importance for understanding the regeneration dynamics of these forests and for prioritising conservation efforts. Of particular importance are the secondary forests regenerating naturally in threatened and spatially limited habitats such as floodplains and riverbanks. Floodplain habitats are naturally heterogeneous because they are shaped by disturbance events related to annual flooding patterns and tend therefore to be species diverse (Hughes 1997; Junk 1989) and to make significant contributions to overall tropical forest species diversity (Salo *et al.* 1986). Because they are at the receiving end of physical, biological and human activities taking place in a catchment they are particularly prone to increased nutrient loading via flood events as well as nutrient additions from local runoff associated with agriculture in riparian zones. Although discharge of nutrients from cultivated land into riparian zones is one of the most common phenomena along tropical rivers,

including those in Southeast Asia (Dudgeon 2000), there are very few studies of the effect of nutrient enrichment on floodplain tree species.

We have therefore identified three secondary forest tree species that are commonly found in the riparian or floodplain zones of Peninsular Malaysia to investigate the growth response of their seedlings to increased levels of the important plant nutrients, nitrogen, phosphorus and potassium. Our research hypothesis is that seedlings of these secondary forest species would respond positively to nutrient addition. We used seedlings in our study because this regeneration stage is crucial in ensuring successful plant establishment (Grubb 1977).

Materials and methods

The experiment was carried out using a replicated randomised block design with three replicates for each treatment in two blocks (Fig. 1). The null hypothesis was no difference between the blocks, i.e. treatment effects were similar for both blocks. Each of the two treatment blocks was placed in the front yard of two home gardens in Negeri Sembilan, Peninsular Malaysia ($102^{\circ} 20.6' E$ and $2^{\circ} 47.7' N$). Fifty-four seedlings of each of three species were used for the experiment making a total of 162 seedlings.

Top soil (depth < 10 cm) was dug up from abandoned paddy fields about 2 km from the experimental site in 2003. The soils were sieved

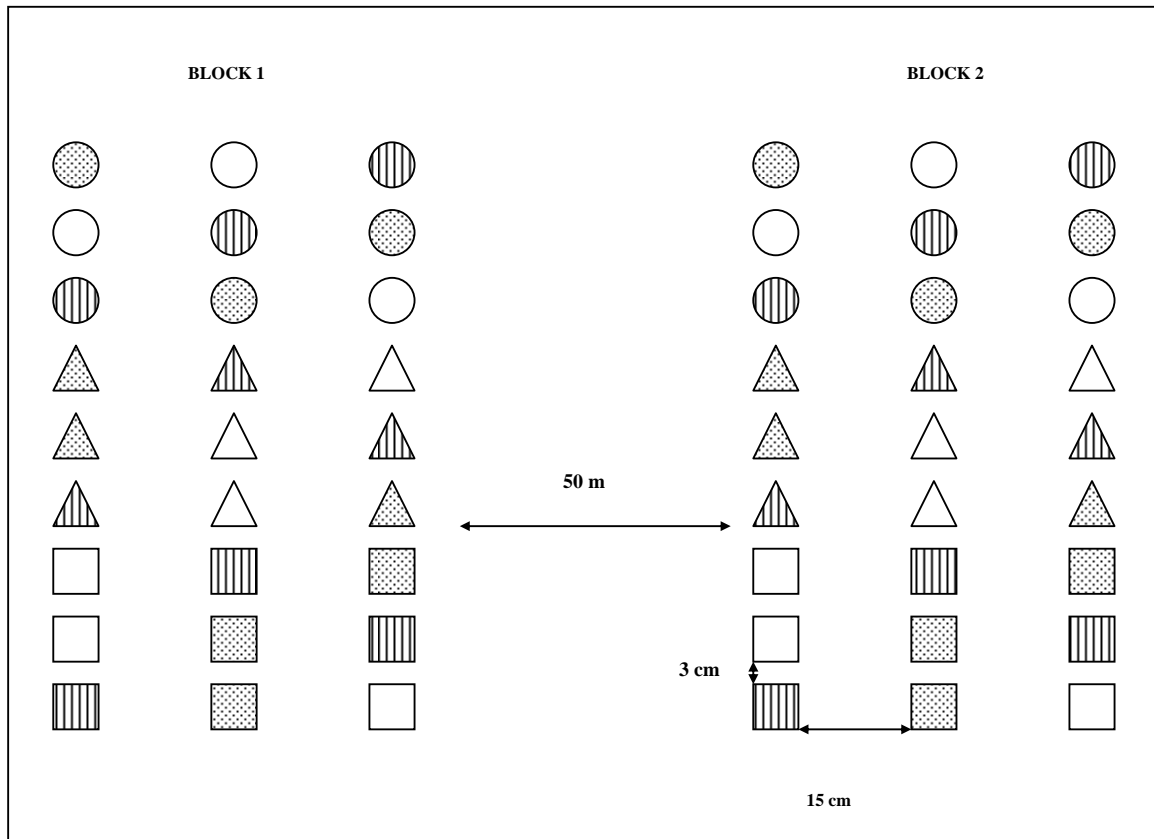


Fig. 1. Schematic representation of the pot experiment layout (Different geometric shapes represent different species; different patterns represent different treatments).

through 2 cm x 2 cm wire mesh, mixed and potted into black polythene bags of diameter 20 cm and height 10 cm (or about 3.1 l per pot) and later stored in the shade for about 4 months. Nutrient concentrations in the paddy soils at the outset of the experiment are given in Table 1.

Table 1. Nutrient concentrations in soils from the abandoned paddy fields used in the pot experiment (from Hashim 2006).

Sampling depth (cm)	pH in H ₂ O	N (%)	Total P ($\mu\text{g g}^{-1}$)	K (cmol kg^{-1})	Total C (%)
10	4.7	0.15	123	0.22	1.59

Seedlings were germinated from fallen and mature seeds of parent trees growing on abandoned paddy fields. After approximately 3.5 months in the nursery, seedlings were transplanted into pots and transferred to a shaded area for acclimation to the pot environment. Approximately 2 weeks later, the plants were transferred to the experimental blocks for a period of 2 months, i.e. a short enough period to prevent pot effects (Gunatilleke *et al.* 1997). The seedlings received about 50 % full sunlight, which was higher than in many previous studies (Table 2) but likely to be representative of the light environment of the secondary forest understorey (cf. Denslow *et al.* 1987). During this period plants were watered daily with tap water, and all seedlings were equally exposed to rain. Pot position was changed weekly and in a random way to reduce edge and neighbour effects.

The three experimental treatments used in this study were:

1. No fertilizer addition;
2. Addition of 1 g rock phosphate (Christmas Island Rock Phosphate, CIRP); and
3. Addition of 1 g NPK (45) fertilizer (N15: P₂O₅15: K₂O15).

The choice of fertilisers was based on the NPK values of fertilisers supplied to local farmers for different crops. Rock phosphate was used to investigate whether seedlings would respond to phosphorus alone, although in general farmers did not apply any phosphates to the paddy fields. However, phosphates could be delivered in flood waters where there is upstream habitation. Rock phosphate (CIRP) provides plant-available phosphate under acidic soil conditions (Hedley *et al.* 1995) and was available in the field area. As the soils used in the experiment were taken from

abandoned riparian paddy fields and had pH values measured at around 4.7 (Hashim 2006), CIRP was considered an interesting treatment to use in the experiment. The amount of fertilizer used in the experimental treatments was based on the amounts used by other studies and on the amounts used by farmers on their fields. For example, Turner (1991) used 0.952 g NPK fertilizer per pot, which is a similar amount to that used in this study (Table 1). However, based on our interviews with farmers the fertilizer application rate in local paddy fields ranged from 148.2 kg ha⁻¹ for urea to 197.6 kg ha⁻¹ for NPK fertilizer. These values translate approximately to 0.0006 and 0.0008 g cm⁻², for urea and NPK fertilizer, respectively. Since the experimental pots measured 20 cm in diameter, this means that each pot should receive 0.25 and 0.18 g, respectively, considerably less than the amount applied. In the event, 1 g was chosen as a compromise between insufficient fertiliser application to see any treatment effects, and fertiliser application levels that have been demonstrated to yield differences in plant responses. Treated seedlings were fertilised twice for a cumulative application of 1 g fertilizer over the course of the experiment.

Plant height was measured using a ruler accurate to 0.1 cm. Plant stem diameter was measured at 2 cm above ground level using electronic callipers accurate to 0.1 mm before first fertilization and again at harvest. In order to harvest the plants, all individual plants were clipped at ground level, and the soils were soaked in water so as to separate the roots easily. The cleaned plant samples were dried at room temperature for a week (about 27 °C). An oven was not used because no ovens were available in the field area. The dried plant materials were weighed using an electronic balance accurate to 0.01 g.

Relative growth rates for all species were calculated based on height increments and on stem diameter increments (Hunt 1982, 1990). Statistical analyses to test for the main effects of treatments or blocks, and the treatment by block interaction were done using General Linear Models (Underwood 1997). Post hoc tests using Bonferroni pairwise comparisons were carried out for all significant treatment effects. All tests were conducted in SYSTAT (SYSTAT 2002).

All three species can be classified as light demanding because they are usually found in open, often degraded areas. They were the most prominent species found on former paddy fields in a parallel field study by Hashim (2006).

Table 2. Growth responses of selected plants from published tropical plant fertilization experiments.

Species	Types of nutrients	% full sun	No. of seedlings	Soil type	Period	Positive or negative growth responses	Location	Reference
all <i>Shorea</i> spp. (T)	P, Mg (1, 0.6 or 0.34 g rock phosphate)	50	100	0-30 cm top soil	24 months	+height (+P) in all spp. -dry mass (+Mg) in six spp.	Sri Lanka	Gunatilleke <i>et al.</i> 1997
<i>Melastoma malabathricum</i> (S)	N, P, K, Mg, Ca, micro	11.2	10	top soil	44 days	+height (+P) +dry mass (+P)	Singapore	Burslem <i>et al.</i> 1994
<i>Dillenia suffruticosa</i> (S)	"	"	13	top soil	8 weeks	+dry mass (+P; +NP)	"	"
<i>Garcinia scortechini</i> (T), <i>Antidesma cuspidatum</i> (T), <i>Dipterocarpus kuntleri</i> (T)	N, P, K, Ca, Mg	3	12	0-20 cm top soil	28 weeks	+dry mass (+all) in only <i>Antidesma</i>	"	Burslem <i>et al.</i> 1995
<i>Dipterocarpus kuntleri</i> (T)	"	1.3	12	0-20 cm top soil	10 months	No response for dry mass (+NPK)	"	"
<i>Shorea macroptera</i> (T)	N, P, K	shaded	40	top soil	6 months	No response for dry mass (+NPK)	Malaysia	Turner <i>et al.</i> 1983
<i>M. malabathricum</i> and <i>Trema tomentosa</i> (T)	N, P, K (0.952 g fertilizer)	60	10	forest soil	2 months	+dry mass (+NPK); +height increment (+NPK)	"	Turner 1991
<i>Phytolacca rivinoides</i> , <i>Piper</i> spp. and <i>Miconia</i> spp. (shrub and herbaceous spp.)	N, P, K, Mg, S, Ca, micro	20	na	top soil and river sand	16-29 and river weeks	+dry mass (+P; +NP) in <i>Phytolacca</i> ; +RGR1 (+NP) in <i>Phytolacca</i> , certain <i>Piper</i> and <i>Miconia</i>	Costa Rica	Denslow <i>et al.</i> 1987
<i>Melicope glabra</i> (T), <i>Macaranga gigantea</i> (T), <i>Persea romosa</i> (T), <i>Peronema canescens</i> (T)	N, P, K	18	10-11	15-20 cm top soil	18 weeks	+relative biomass (+NP) in <i>Macaranga</i> and <i>Persea</i> ; <i>Peronema</i> and <i>Melicope</i> stored additional N,P	Borneo	Lawrence 2001
<i>Glochidion obscurum</i> (T), <i>Vitex pinnata</i> (T), <i>Lagerstroemia speciosa</i> (T)	N, P, K	50	3	0-10 cm top soil	1 and ½ months	+RGR2, +dry mass (+NPK) in <i>Glochidion</i> ; +RGR1 in <i>Lagerstroemia</i>	Malaysia	This study

na = not available.

Glochidion obscurum Blume (Euphorbiaceae) is a small tree with a maximum height around 18 m and geographical distribution from Indo-China to New Guinea. This species is common in open and abandoned mining areas in Peninsular Malaysia (Corner 1988).

Lagerstroemia speciosa (L.) Pers. (Lythraceae) is a medium-sized tree, which can reach a height of 17 m in the open but may grow up to 30 m in forests. This species can be found in China, Indo-China, Peninsular Malaysia, Sumatra, Borneo, India and Sri Lanka, and is a well-known riverine species (Corner 1988; MacKinnon *et al.* 1996).

Vitex pinnata L. (Verbenaceae) is an evergreen tree of maximum 24 m in height, and is common in secondary forests and in open degraded areas (Burkill 1935; Corner 1988; Keng 1969). This species is distributed all over Southeast Asia (Corner 1988).

Results

In this experiment we obtained the following results, presented for individual species separately:

Glochidion obscurum

The treatment effects for stem diameter increments were statistically significant ($P < 0.05$). Diameter relative growth rate showed higher mean response to the addition of full fertilizer (NPK), as compared with phosphorus addition and the no-fertiliser control. Bonferroni post hoc tests

showed that only the response to full fertilizer addition was significantly different from the control (Table 3). On the other hand, relative growth rates based on height increments were not statistically significant for either treatment or block effects, or for interactions between treatments and blocks ($P > 0.05$; Table 3).

The treatment effects for total dry weight were also statistically significant ($P < 0.05$). The mean total dry weight in response to addition of full fertilizer (NPK) was higher than the no fertilizer control, followed by the phosphorus addition. As in the case of diameter relative growth rate, Bonferroni post hoc tests showed that only the response to full fertilizer addition was significantly different from the no fertiliser control (Table 3). In fact, mean total dry weight in response to only P addition was slightly lower than the control, although this was not statistically significant. The root to shoot (R/S) ratios for all treatments were similar for *G. obscurum* and were approximately twice the R/S ratio of the other two experimental species (Table 3).

Lagerstroemia speciosa

The relative growth rates based on height increments between treatments and blocks were statistically significant ($P = 0.03$ and $P = 0.04$, respectively). For the treatment effects, the mean height relative growth rate in response to addition of full fertilizer (NPK) was the highest followed by the response to only phosphorus addition, and then

Table 3. Results of the analysis of growth responses of the three experimental species to three different nutrient treatments, using Generalised Linear Models.

Treatment	RGR1 cm cm ⁻¹ d ⁻¹	RGR2 mm mm ⁻¹ d ⁻¹	Total weight g	Root to shoot ratio
G	3.03 (0.07)	1.61 (0.59) ^a	9.74 (1.14) ^a	0.68 (0.04)
G+NPK	3.26 (0.76)	1.87 (0.30) ^b	16.73 (1.89) ^b	0.64 (0.07)
G+P	3.05 (0.64)	1.62 (0.04) ^a	9.10 (0.77) ^a	0.63 (0.05)
L	4.02 (0.42) ^{ab}	1.94 (0.03)	16.89 (1.26)	0.35 (0.01)
L+NPK	4.18 (0.06) ^c	2.00 (0.04)	21.27 (2.20)	0.31 (0.02)
L+P	4.10 (0.02) ^{bc}	1.88 (0.03)	15.39 (0.93)	0.30 (0.03)
V	3.28 (0.11)	1.50 (0.09)	6.80 (1.11)	0.38 (0.02)
V+NPK	3.34 (0.08)	1.50 (0.06)	7.39 (0.63)	0.34 (0.04)
V+P	3.37 (0.04)	1.47 (0.05)	6.06 (0.60)	0.38 (0.03)

G = *Glochidion obscurum*, L = *Lagerstroemia speciosa*, V = *Vitex pinnata*. +NPK = with full fertilizer addition, +P = with phosphorus addition. RGR1 = relative growth rates based on height increments, RGR2 = relative growth rates based on stem diameter increments. Values are mean \pm standard error in parentheses; n = 6. Values in bold are statistically significant at $P < 0.05$. Superscripts represent results of post-hoc tests using Bonferroni pairwise comparisons where different letters denote significance at $P < 0.05$.

the control. Post hoc tests showed that height relative growth rate in response to only P addition was not significantly different from the other two treatments, but that the full fertiliser treatment was significantly different from the control treatment (Table 3).

Vitex pinnata

In this species, no statistically significant results were found when comparing either the treatment or block effects or the interactions between these two for all three growth variables (Table 3). The R/S ratios of this species, under all treatments, were similar to those of *L. speciosa*, but approximately half the R/S ratios of *G. obscurum*.

Discussion

The positive growth responses to nutrient additions displayed by *G. obscurum* and *L. speciosa* are consistent with our hypothesis, as well as with the findings of other studies on fast-growing, light-demanding species (Lawrence 2001). The lack of growth response demonstrated by *V. pinnata* is also consistent with findings from other studies, which suggest that a small proportion of light-demanding species do not respond to nutrient additions (Lawrence 2001, 2003). However, we did not analyse foliar nutrient concentrations in this study to ascertain if the species was employing the luxury consumption strategy (*sensu* Chapin 1983), i.e., sequestering additional nutrients without an increase the growth variables that we measured. Moreover, as no previous nutrient bioassays have been carried out using the same species, direct comparisons cannot be made.

A vegetation survey of secondary forests growing on former fertilised paddy fields in the floodplains of Negeri Sembilan (Hashim 2006), found that of the three study species, *G. obscurum* had the highest number of individuals (per 1200 m²) with a dbh \geq 5 cm and appeared more advanced in terms of successional stage as there were many more older individuals than younger individuals of this species (Fig. 2). In comparison, *V. pinnata* and *L. speciosa*, had the most individuals in the smallest size class (< 1 cm dbh and taller than 10 cm). *V. pinnata*, in particular, has the greatest number of individuals in the smallest class size (175 per 1200 m²) and was the slowest of the three study species to regenerate. In fact, *V. pinnata* has a long germination period (43-168 days) compared with *G. obscurum* (12-49 days) (Ng 1992; Hashim 2006).

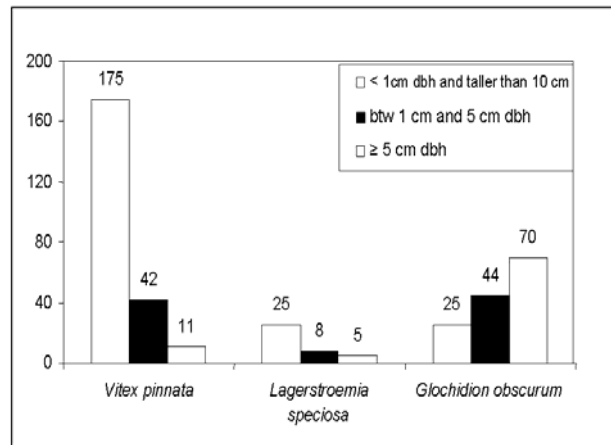


Fig. 2. The number of individuals (per 1200 m²) in different size classes of the three experimental species surveyed in abandoned paddy fields (Hashim 2006).

These field results suggest that *G. obscurum* is a fast-growing species on open sites that have previously been cultivated and fertilized. In our pot experiment *G. obscurum* responded positively to the NPK fertilizer additions. This species also had high R/S ratios under all treatments, approximately twice the R/S ratio found in the other two experimental species. This may be due to inherent differences in R/S ratios among the species. Alternatively, it may indicate that *G. obscurum* responds differently to soil conditions experienced in the experimental pots. The highest R/S ratio was found in the pots with *G. obscurum* receiving the NPK treatment and may reflect a response by this species to rapid growth under soil conditions that were on average drier than would be found in a floodplain. The soil that was used in the experiment was sandy (65 % sand) and during hot or dry days (40 % of days) the seedlings of all species experienced periodic dry soil conditions. This is unlike conditions found in abandoned paddy fields in the floodplains, which have high soil moisture values (Hashim 2006). As *G. obscurum* appears to be particularly well able to grow rapidly on abandoned paddy fields and to take up nutrients, allocation of biomass to roots may have taken place to compensate for the soil desiccation during the pot experiment (see Dias-Filho 1995).

Lagerstroemia speciosa showed the highest relative growth rates (Table 2), absolute growth rate (see Fig. 3) and had the greatest total weight at the end of the experiment but was the least

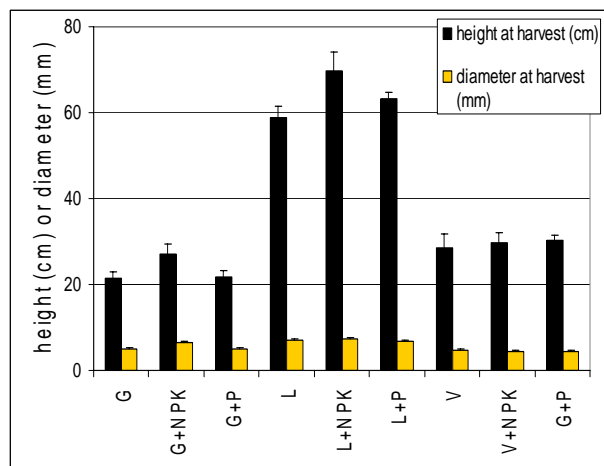


Fig. 3. Height and basal diameter of the three experimental species under different experimental treatments, at the time of harvest.

common of the three species in the former paddy fields in all size classes (Fig. 2). Of the three study species it is the one that is capable of growing the tallest and it is also the most specialist riparian species. Rapid growth rates tend to be associated with both these characteristics. Its lack of presence in the former paddy fields is difficult to account for but may reflect its response to other factors such as light levels or its mechanism of dispersal (*L. speciosa* is dispersed by wind compared to the other two experimental species, which are both dispersed by animals (Corner 1988). *Vitex pinnata* was the most common in the former paddy fields with large numbers of individuals in the smallest size class but few in larger size classes. It was the slowest growing in terms of stem diameter increment and total weight, though not in terms of absolute growth rate (Fig. 3) of the three study species and did not respond to fertilizer treatments. This would suggest that it is not very nutrient responsive and is better placed in the luxury consumption category (*sensu* Chapin 1983). It might also suggest that *V. pinnata* is effective at dispersal and germination but not necessarily at establishment and longer-term survival in the former paddy field environment.

According to Hashim (2006), both recently abandoned paddy fields and older established riparian forest strips were found to be at risk of fertilizer enrichment from neighbouring agricultural plots in the floodplains as well as from homegardens, townships, and single-crop plantations at higher elevations. The common types of fertilizer being supplied to farmers in the study area by

government agencies include NPK (12.5: 15:16.3) for rubber, and urea (46 % N) and NPK (17.5:15.5:10) for rice cultivation.

The fact that the floodplain secondary forests in this study area have been exposed to prolonged agricultural use, and indeed that most parts of the floodplains continue to be used for agriculture today, should be a cause for concern for the conservation of secondary forest species that do not show a growth response to high fertilizer loading.

In conclusion, the results of this pot experiment showed that two common secondary forest species in Peninsular Malaysia, *G. obscurum* and *L. speciosa*, supported the research hypothesis that secondary forest species increase their growth when levels of chosen nutrients were increased. This suggests a possible adaptation towards a high resource growth strategy to ensure their survival in the wild. However, *V. pinnata* did not show the same patterns, perhaps because it responds more directly to other environmental variables such as light levels. It is suggested that on-going fertilization of the floodplain soils could lead to nutrient-responsive species like *G. obscurum* and *L. speciosa* out-competing species like *V. pinnata* whose growth did not respond to fertilizer treatments. However, it is likely that growth responses are not entirely driven by nutrient levels and that other environmental factors should be studied in order to understand the regeneration dynamics in these secondary forests.

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