NUTRIENT LIMITATION IN A MALAYSIAN ULTRAMAFIC SOIL

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BREARLEY, F. Q. 2005. **Nutrient limitation in a Malaysian ultramafic soil**. To test the hypotheses that low nutrient levels and/or magnesium toxicity prevent the occurrence of *Dryobalanops lanceolata* (Dipterocarpaceae) on tropical ultramafic soils, a nutrient addition experiment was conducted. *Dryobalanops lanceolata* seedlings were planted in soil from Mount Tawai, an ultramafic mountain in central Sabah, Malaysia and subjected to four treatments: +P, +Ca, +NPK and +NPKCa. Addition of +P reduced the leaf mass per area but increased the leaf area ratio and foliar P concentrations. However, it did not increase the biomass or total leaf area of *D. lanceolata*. Additions of +NPK and +NPKCa increased the biomass, total leaf area, foliar P and K concentrations but not foliar N concentration. Calcium additions had no effect on seedling growth, indicating that magnesium toxicity was not important. The occurrence of *D. lanceolata* in this tropical ultramafic soil was limited by both potassium availability and low levels of soil phosphorus.

Key words: Borneo – *Dryobalanops lanceolata* – nutrient fertilization – phosphorus – potassium – seedling growth – serpentine – tropical rain forest

BREARLEY, F. Q. 2005. Pengehadan nutrient dalam tanih ultramafik di Malaysia. Satu kajian penambahan nutrien dijalankan untuk menguji hipotesis bahawa paras nutrien yang rendah dan/atau ketoksikan magnesium menghalang pertumbuhan *Dryobalanops lanceolata* (Dipterocarpaceae) di atas tanih ultramafik tropika. Anak benih *D. lanceolata* ditanam di atas tanih daripada Gunung Tawai iaitu sebuah gunung ultramafik di tengah Sabah, Malaysia. Anak benih *D. lanceolata* didedahkan kepada empat jenis perlakuan iaitu +P, +Ca, +NPK dan +NPKCa. Perlakuan +P mengurangkan jisim daun bagi suatu luas serta menaikkan nisbah luas daun dan kepekatan P daun tetapi tidak menaikkan biojisim atau jumlah luas daun *D. lanceolata*. Biojisim, jumlah luas daun dan kepekatan-kepekatan P daun dan K daun bertambah dengan perlakuan +NPK dan +NPKCa. Namun, kepekatan N daun tidak bertambah. Pertambahan Ca tidak mempengaruhi pertumbuhan anak benih. Ini menunjukkan bahawa ketoksikan Mg tidak penting. Pertumbuhan *D. lanceolata* di tanah ultramafik tropika ini dihadkan oleh kehadiran K dan paras P yang rendah.

Introduction

Ultramafic soils are derived from igneous ultramafic rocks, which have high concentrations of magnesium, iron and other metals such as nickel, chromium and cobalt. They have low silica levels and are often lacking in major plant nutrients such as nitrogen, phosphorus and potassium. These distinctive edaphic factors

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provide unique challenges to the vegetation and a number of non-exclusive hypotheses have been proposed to account for their characteristic vegetation: low soil nutrients, a high magnesium:calcium ratio leading to magnesium toxicity, nickel toxicity and water stress (Proctor & Nagy 1992, Proctor 1999). Forests on ultramafic soils in South-East Asia typically have a lower stature and a different species composition when compared with the surrounding areas and they often have endemic species (Proctor 1992, Proctor & Nagy 1992). However, generalizations about ultramafic sites are difficult as they are very variable, both chemically and physically.

The vegetation of ultramafic areas in South-East Asia is little known (Proctor 1992). In the Malaysian state of Sabah, on the island of Borneo, where they cover 4.6% (3500 km²) of the land area (Repin 1998), work has been carried out on Mount Kinabalu (Kitayama 1992, Aiba & Kitayama 1999, Kitayama & Aiba 2002) and Mount Silam (Proctor *et al.* 1988, 1989, Bruijnzeel *et al.* 1993). Preliminary work has also been carried out on Mount Tawai (Soepadmo *et al.* 1994, Tangah 1998).

It has been hypothesized that phosphorus is the major limiting nutrient in tropical rain forest soils (Vitousek 1984, Vitousek & Sanford 1986), but there is still considerable debate as to the exact nature of nutrient limitation. This is because in bioassay experiments, different species have shown responses to different nutrients under different experimental conditions (Sundralingham 1983, Denslow *et al.* 1987, Burslem *et al.* 1994, 1995, Gunatilleke *et al.* 1997, Webb *et al.* 1997, Yap *et al.* 2000, Brearley 2003). Previous fertilization experiments on temperate ultramafic sites have shown a response to the major plant nutrients (Spence & Millar 1963, Ferreira & Wormell 1971, Proctor 1971, Carter *et al.* 1988, Hobbs *et al.* 1988, Looney & Proctor 1989, Huenneke *et al.* 1990, Nagy & Proctor 1997, Chiarucci *et al.* 1998, 1999), most notably to phosphorus (Spence & Millar 1963, Koide & Mooney 1987, Carter *et al.* 1988, Nagy & Proctor 1997) but also occasionally to nitrogen (Turitzin 1982, Looney & Proctor 1989, Huenneke *et al.* 1990).

Dryobalanops lanceolata (Dipterocarpaceae) is a common species in the lowland evergreen rain forests of Sabah. It grows to a very large size and produces a medium hardwood which is commonly used for timber (Meijer & Wood 1964) but it is absent from ultramafic soils (Meijer 1964, J. Tangah, pers. comm.). This study explored the broad ecological question of what factors affect species distribution in the very diverse rain forests of South-East Asia. It tested the hypotheses that *D. lanceolata* was absent from ultramafic soils due to low soil nutrient concentrations and /or a high magnesium:calcium ratio leading to magnesium toxicity, by carrying out a bioassay in which major nutrients were added to the soil in the presence or absence of additional calcium (to ameliorate magnesium toxicity). I hypothesized that the species will respond most to the addition of phosphorus and also to the addition of calcium if magnesium is at toxic concentrations in the soil.

Materials and methods

Study site

Mount Tawai is an ultramafic mountain (1273 m) situated in central Sabah (5° 32' 45" N, 117° 4' 30" E), around 20 km south of Telupid. The geology of the area is based on serpentinite and has been described by Tongkul (1997). The vegetation on the mountain is lowland evergreen rain forest grading into lower montane rain forest with scrub vegetation at the summit (Tangah 1998).

Methodology

Soil was taken from a depth of up to 20 cm from the lowland evergreen rain forest in Mount Tawai Forest Reserve (180 m asl), mixed in a 3:2 ratio with ultramafic soil from a track adjacent to the reserve and sieved to 5 mm. Eight samples of the mixed soil were analysed for pH (H_2O) and pH (0.01 M KCl) mixed in a 1:2.5 ratio with distilled water. Loss on ignition was determined after heating the soils to 550 °C for four hours. Total N and P were analysed with a flow injection analyser (Burkard SFA-2) after a semi micro-Kjeldahl digestion for N and a nitric acid/ perchloric acid digestion for P. Phosphorus was extracted from 2 g of soil with 20 ml of 0.03 M ammonium fluoride plus 0.1 M hydrochloric acid by shaking for 1 min in a test tube (Bray II method). The solutions were filtered and analysed on a spectrophotometer (Hitachi U-2000) using the molybdenum blue colour development method (Anderson & Ingram 1993). Exchangeable K, Ca, Mg and Na were analysed by atomic absorption spectrophotometry (GBC 932AA) after extraction with 1 M ammonium acetate and Ni was analysed by atomic absorption spectrophotometry (Perkin-Elmer 2100) after separate extractions with 0.5 M acetic acid and 1 M ammonium acetate. All results are expressed on an oven-dry (105 °C for 24 hours) basis.

Two-year-old seedlings of *D. lanceolata* Burck (kapur paji) were obtained from the INFAPRO nursery, Danum Valley, Sabah. They were planted in 2 litres of ultramafic soil in black polybags and placed under neutral-density shade cloth, allowing transmission of 20% of full sunlight (up to 8.1 mol m^{-2} d^{-1}; as measured in Brearley 2003), on four shade tables in the nursery of the Forest Research Centre, Sepilok, Sandakan, at a density of 27 cm × 25 cm per seedling. All seedlings were ectomycorrhizal at planting. Initial measurements of mean height and leaf number were recorded as 46.8 ± 0.82 (SE) cm and 6.5 ± 0.25 leaves. There were no differences between the heights or leaf number of the seedlings in the different treatments at the beginning of the experiment (p > 0.75 in both cases).

Five treatments were applied every two weeks to 16 replicates per treatment, with four replicates per shade table:

(1) Control: 100 ml of water (all water used was rain water)
(2) +P: 100 ml of 0.0224 M NaH_2PO_4
(3) +Ca: 100 ml of 0.0133 M $CaCO_3$

(4) +NPK: 100 ml of 0.0191 M NH_4NO_3, 0.0224 M NaH_2PO_4 and 0.0136 M KCl

(5) +NPKCa: 100 ml of 0.0191 M NH_4NO_3, 0.0224 M NaH_2PO_4, 0.0136 M KCl and 0.0133 M $CaCO_3$

The seedlings were randomized with respect to their position within the tables and re-randomized every month. After six months, height and leaf number were re-measured. The seedlings were harvested, divided into leaf, main stem and branch as well as tap root and fine root (< 2 mm diameter) fractions, dried at 60 °C for 96 hours and weighed. Relative height growth rates (RGR) and relative leaf production rates (RPR) were calculated according to Hunt (1990) as:

RGR or RPR = $(\log_e M_6 - \log_e M_0)/6$ months

where M_0 and M_6 are the measurements at the beginning and end of the experiment respectively. To determine the proportion of the seedling's biomass allocated to each fraction, mass ratios were calculated as:

Mass ratio = biomass of fraction/total biomass of seedling

A sample was taken from each of the three youngest, fully expanded leaves per seedling and these were bulked before digestion in a salicylic/sulphuric acid mix (33 g l^{-1}) with a lithium sulphate/copper sulphate (10:1 ratio) catalyst. The digests were analysed for N and P using a flow injection analyser (Tecator 5042 Detector and 5012 Analyser) and for K, Ca, Mg and Ni using atomic absorption spectrophotometry (Perkin-Elmer 2100). Leaf mass per area was recorded for the youngest of these three leaves by tracing the leaf area of the fresh leaf and measuring the tracing on a leaf area meter. The leaf was then dried as above and weighed. The total leaf area of the dry leaves of all seedlings was measured on the leaf area meter and the difference between fresh and dry leaf areas was corrected for by increasing the values by 12% (F. Q. Brearley, unpublished data). The leaf area ratio was then calculated as:

Leaf area ratio = total leaf area/total biomass of seedling

One-way ANOVAs were used to analyse the data and each of the treatment means were compared with the control mean using Dunnett's test. Data was subjected to Box-Cox transformations where necessary. Analyses were performed using Minitab 13.20 (Minitab Inc., State College, Pennsylvania, USA).

Results

The soils used in the experiment had a pH (in H_2O) of 5.3, low levels of the major plant nutrients (especially low in the case of extractable P), high levels of Mg and Ni, and a Mg:Ca ratio of 1.6 (Table 1). They were similar to other tropical ultramafic soils but were more acidic, had less exchangeable/extractable P, Ca, Mg and Ni and the Mg:Ca ratio was fairly low. There were no extreme values as observed at other sites (Table 1).

Table 1 Chemical characteristics of ultramafic soil from Mount Tawai, Sabah, Malaysia used in the bioassay experiment (mean ± SE) and comparison with other South-East Asian ultramafic sites

Parameter	Mount Tawai, Sabah, Malaysia	Mount Silam, Sabah, Malaysia	Mount Piapi, Talaud Islands, Indonesia	Mount Giting-Giting, Sibuyan, The Philippines	Mount Bloomfield, Palawan, The Philippines
	This study	Proctor *et al.* 1988	Proctor *et al.* 1994 (Plots 5 & 6)	Proctor *et al.* 1998 (Plots 1A & 1B)	Proctor *et al.* 1999 (Plots 9–12)
Altitude (m)	180	280	200	325 & 385	50
pH (H_2O)	5.3 ± 0.06	5.7	6.1	5.5	6.8
pH (KCl)	4.9 ± 0.07	–	–	–	–
Loss-on-ignition (%)	12.6 ± 0.30	–	13.3	12.9	12.6
P total ($\mu g\ g^{-1}$)	201 ± 9.4	–	–	–	–
P extr. ($\mu g\ g^{-1}$)	0.34 ± 0.05[a]	4.1[b]	2.5[c]	0.49[c]	1.02[c]
N total (%)	0.18 ± 0.01	–	–	–	–
Ca exch. (m-eq 100 g^{-1})	0.86 ± 0.04	7.7	4.6	1.16	4.27
Mg exch. (m-eq 100 g^{-1})	1.38 ± 0.04	24.6	15.6	2.51	18.1
Mg:Ca	1.60 ± 0.04	3.12	4.5	2.39	4.9
K exch. (m-eq 100 g^{-1})	0.17 ± 0.01	0.14	0.30	0.09	0.32
Na exch. (m-eq 100 g^{-1})	0.09 ± 0.01	0.10	0.61	–	–
Ni exch. ($\mu g\ g^{-1}$)	2.39 ± 0.08	13	32.3	18.1	46
Ni extr. ($\mu g\ g^{-1}$)[b]	10.80 ± 0.36	25*	–	–	360
Ni total ($\mu g\ g^{-1}$)	2980 ± 70	1200*	–	–	6900
Co total ($\mu g\ g^{-1}$)	123 ± 3.0	–	–	–	1400
Cr total ($\mu g\ g^{-1}$)	9620 ± 310	–	–	–	10000

[a] = Bray II extractant, [b] = Acetic acid extractant, [c] = Olsen's extractant, * = S. Nortcliff (unpublished, in Proctor & Baker 1994)

Addition of +P or +Ca did not improve the growth of *D. lanceolata* but addition of +NPK and +NPKCa caused a significant increase in the seedlings' biomass by around 60% ($F_{4,75}$ = 8.48, p < 0.001; Figure 1a) and a significant increase in the seedlings' leaf area by around 100% ($F_{4,75}$ = 13.41, p < 0.001; Figure 1b). The relative height growth rate and leaf production rate showed a similar pattern but the differences were not statistically significant (RGR height: $F_{4,75}$ = 2.37, p = 0.060; Figure 1c. RPR leaf: $F_{4,75}$ = 2.05, p = 0.096; Figure 1d).

Addition of three or more nutrients led to a significant increase in the leaf:mass ratio ($F_{4,75}$ = 3.99, p = 0.005; Table 2) and a significant decrease in the stem:mass ratio ($F_{4,75}$ = 3.58, p = 0.010; Table 2). Although there were significant differences between treatments with regard to root:mass ratio ($F_{4,75}$ = 2.99, p = 0.024; Table 2), none of the treatments were different from the control. All nutrient addition treatments led to an increase of at least 10% in the fine root:mass ratio although the increases were not statistically significant ($F_{4,75}$ = 2.08, p = 0.092; Table 2). All treatments in which P was added (i.e. +P, +NPK and +NPKCa) increased the leaf area ratio ($F_{4,75}$ = 6.02, p < 0.001; Table 2) and reduced the leaf mass per area (except +NPKCa) ($F_{4,75}$ = 5.31, p = 0.001; Table 2).
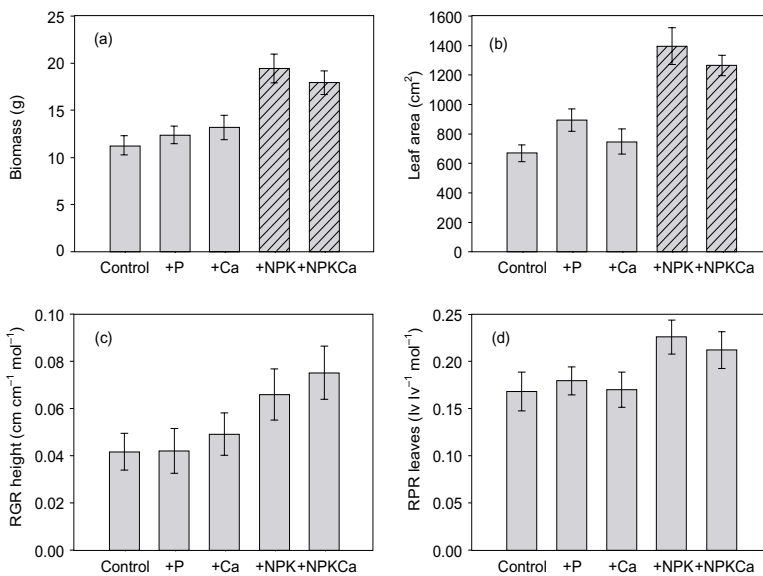

Figure 1   Growth of *Dryobalanops lanceolata* planted in a Malaysian ultramafic soil and subjected to six months of nutrient additions (mean ± SE). Treatments which are significantly different from the control are shown as hatched bars.

Table 2 Biomass allocation patterns of *Dryobalanops lanceolata* planted in a Malaysian ultramafic soil and subjected to six months of nutrient additions (mean ± SE)

	Control	+P	+Ca	+NPK	+NPKCa
Leaf:mass ratio	0.28 ± 0.01	0.31 ± 0.02	0.28 ± 0.02	**0.35 ± 0.02**	**0.35 ± 0.01**
Stem:mass ratio	0.48 ± 0.01	0.46 ± 0.01	0.46 ± 0.01	**0.43 ± 0.01**	**0.43 ± 0.01**
Root:mass ratio	0.24 ± 0.01	0.22 ± 0.01	0.26 ± 0.01	0.21 ± 0.02	0.21 ± 0.01
Fine root:mass ratio	0.055 ± 0.003	0.062 ± 0.006	0.073 ± 0.005	0.064 ± 0.004	0.067 ± 0.005
Leaf area ratio	59.8 ± 2.8	**71.7 ± 2.9**	55.5 ± 4.2	**71.4 ± 3.3**	**72.0 ± 2.5**
Leaf mass per area (g m^{-2})	60.5 ± 1.3	**52.9 ± 1.5**	61.7 ± 2.3	**53.4 ± 2.0**	54.5 ± 1.9

Treatments which are significantly different from the control are shown in bold.

Foliar N concentrations were increased by around 10% in all treatments but these increases were not statistically significant ($F_{4,75} = 1.98$, p = 0.106; Figure 2a). Foliar P concentrations were increased significantly in all treatments ($F_{4,75} = 34.22$, p < 0.001; Figure 2b) and were more than doubled in the treatments in which P was added in solution, from around 0.4 mg g^{-1} to around 0.9 mg g^{-1}. Foliar K concentrations were significantly increased in the treatments in which K was added in solution, from around 8 mg g^{-1} to around 11 mg g^{-1} ($F_{4,75} = 12.17$, p < 0.001; Figure 2c). Foliar Ca was only increased significantly in the +NPKCa treatment ($F_{4,75} = 4.31$, p = 0.003; Figure 2d) as was the reduction in the foliar Mg:Ca ratio ($F_{4,75} = 3.00$, p = 0.024; Figure 2f). Foliar Mg was unaffected by nutrient additions ($F_{4,75} = 0.41$, p = 0.802; Figure 2e). Foliar Ni was below 0.01 mg g^{-1} in all seedlings (data not shown).
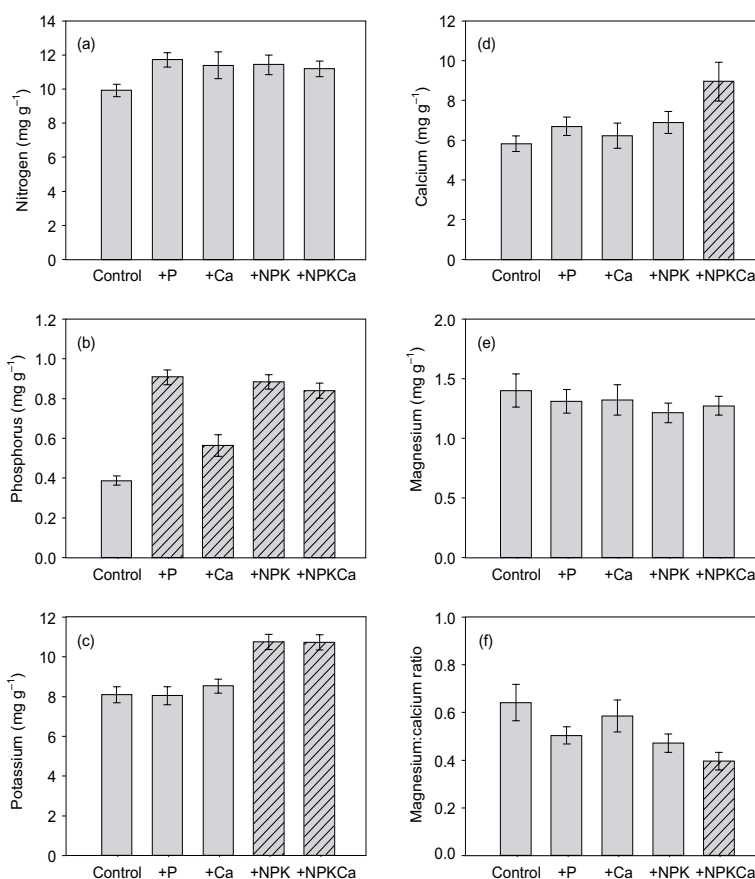

Figure 2   Foliar nutrient concentrations of *Dryobalanops lanceolata* planted in a Malaysian ultramafic soil and subjected to six months of nutrient additions (mean ± SE). Treatments which are significantly different from the control are shown as hatched bars.

Discussion

A reduction in leaf mass per area and an increase in leaf area ratio and foliar P was found with +P addition but this did not lead to increases in seedling growth. Increases in growth were only possible with further additions of N and K. Foliar K increased with additions of K in solution whereas foliar N did not increase with additions of N in solution, suggesting that K was the more limiting of the two nutrients.

The lack of an increase in foliar N in N-fertilized seedlings may be due to the high Mg concentrations in the ultramafic soil which can facilitate N uptake. Seedlings may therefore have become saturated with N and did not respond to further N addition. Miller and Cumming (2000) found that N uptake was doubled in *Pinus virginiana* seedlings exposed to a Mg:Ca ratio of 5 when compared with a ratio of 0.5. They suggested that elevated Mg availability facilitates N transport to foliage in excess of functional need. However, it is possible that some of the additional N was incorporated into new growth rather than increasing in concentration within the leaves.

Soil phosphorus concentrations were low when compared with other tropical non-ultramafic soils [e.g. Barito Ulu, Central Kalimantan: 1.3 µg g^{-1} (Mirmanto *et al.* 1999); Bukit Belalong, Brunei: 1.5 µg g^{-1} (Pendry & Proctor 1997); Kabili–Sepilok, Sabah: 0.7 µg g^{-1} (Brearley 2003)]. This is especially notable, as the Bray II extractant used in this study is stronger than the other extractants used for the soils above and those in Table 1. The decrease in leaf mass per area with +P, +NPK and +NPKCa in this study showed that there was a change in leaf structure with the addition of nutrients. However, there was no increase in growth with +P alone indicating that there were no major changes in physiological processes and growth was further limited by another nutrient or a toxic substance. Burslem *et al.* (1995) found that foliar P was increased in all four species from a lowland evergreen rain forest in Singapore when fertilized with P but there was an increase in growth in only one of the species, *Antidesma cuspidatum.* A number of bioassays of nutrient limitation in temperate ultramafic soils also showed that P was limiting to plant growth (Spence & Millar 1963, Koide & Mooney 1987, Carter *et al.* 1988, Nagy & Proctor 1997).

Although soil K was not particularly low when compared with other tropical ultramafic (Table 1) or non-ultramafic soils [e.g. Bukit Belalong, Brunei: 0.23 m-eq 100 g^{-1} (Pendry & Proctor 1997); Mount Mulu, Sarawak: 0.16–0.25 m-eq 100 g^{-1} (Proctor *et al.* 1983); Kabili–Sepilok, Sabah: 0.29 m-eq 100 g^{-1} (Brearley 2003)] there was still a response to its addition. The low levels of foliar K in trees on Mount Silam, mostly less that 5 mg g^{-1} (Proctor *et al.* 1988), were considered distinctive by Proctor (1992) and indicate that this nutrient is poorly supplied to the vegetation on this mountain in eastern Sabah. It is also noteworthy that Proctor *et al.* (1999) compared soil K in ultramafic soils and sandstone greywacke soils on Mount Bloomfield, Palawan, the Philippines, and found that the ultramafic soil had higher levels of all nutrients except for K. Looney and Proctor (1989) also found low

foliar K (< 5 mg g^{-1}) in plants from Rhum, Scotland. In a companion experiment (F. Q. Brearley, unpublished data), it was found that there was little difference in the growth of *D. lanceolata* when grown in ultramafic or non-ultramafic soils but foliar K concentrations were significantly lower when grown in ultramafic soils supporting the hypothesis of K limitation in this soil type.

The lack of a growth response to Ca addition is most likely because the Mg:Ca ratio was not very extreme when compared with some other ultramafic sites, e.g. Meikle Kilrannoch, Scotland, with a ratio of 12.3 (Nagy & Proctor 1997) or Mount Piapi, Indonesia, with a ratio of up to 29.8 (Proctor *et al.* 1994). This indicates that Mg toxicity is not important in preventing the growth of *D. lanceolata* in this soil. However, foliar Ca was increased and the Mg:Ca ratio was reduced in the treatment with +NPKCa. The addition of CaCO$_3$ may improve seedling growth by a liming effect but these soils are around 1 pH unit less acidic than typical ultisols under lowland evergreen rain forest in other parts of Borneo. Therefore, this effect is unlikely to be important.

It is possible that there was a slight effect of Ni toxicity in the soil which was alleviated by nutrient addition. In a bioassay carried out in the Philippines, Proctor *et al.* (1999) showed that all nutrient addition treatments reduced foliar Ni in *Zea mays.* This may have been a physiological effect or it may have been due to a reduction in available soil Ni. Alteration of K uptake is a toxic effect of excess Ni in *Triticum aestivum.* Addition of Ni (40 mM) led to increased root leakage of K and subsequent reductions in foliar K and tissue water content (Pandolfini *et al.* 1992). Loss of water from the tissues following Ni addition may be one of the reasons for the susceptibility to drought of ultramafic species where there is a high soil Ni concentration.

It is notable that much of the increase in growth of *D. lanceolata* was related to an increase in the allocation of resources to leaf tissue and it appeared that there was no increase in photosynthesis (as there was no increase in foliar N). Brearley (2003) found an increase in the growth of *Shorea leprosula* with the addition of P and K which was due to an increase in leaf allocation. However, there was no increase in the maximum rate of photosynthesis.

The only comparable bioassay of a tropical soil is that of Proctor *et al.* (1999) who grew *Z. mays* in soil from Mount Bloomfield. In this experiment, there was a clear growth response to the addition of N, P and K together. There was a smaller response to Ca addition. Foliar N was only increased with +NPKCaCO$_3$ (but not +NPKCaSO$_4$), and foliar P actually decreased with P additions. Foliar K increased in all treatments in which K was added. There are also a number of studies in which *D. lanceolata* has been planted in 'normal' tropical soils and subjected to fertilization treatments. Sundralingham (1983), Nussbaum *et al.* (1995) as well as Yap and Moura-Costa (1996) all showed increases in the growth of *Dryobalanops* species when given additional nutrients. Bungard *et al.* (2002) did not see a growth response when N, P and K were added to *D. lanceolata* in the forest understorey but there was change in photosynthetic physiology, with an increased rate of photosynthetic induction. Yap *et al.* (2000), providing a range of concentrations of

N, P and K under nursery conditions, saw marked responses, most notably to N which agreed with the suggestion of Bungard *et al.* (2002) that neither P nor K limited the growth of *D. lanceolata*. This contrasts with the results presented here which shows that N is probably not limiting the growth of *D. lanceolata* in an ultramafic soil.

These results can also be compared with other fertilization experiments on temperate ultramafic soils. Carter *et al.* (1988) showed that P addition increased the cover of grass species on the Keen of Hamar ultramafic debris site in Scotland, which initially had a very low vegetation cover. In their experiment, any treatment which added P increased vegetation cover. Ferreira and Wormell (1971) added N, P and K and later Ca to a single, unreplicated plot on Rhum, Scotland. There was a clear response to the nutrients but it was impossible to tell which nutrient was having the over-riding effect due to a lack of foliar analyses. Chiarucci *et al.* (1999) fertilized quadrats in an Italian ultramafic garigue. They found that single nutrients added alone increased the total biomass, but none significantly; only if nutrients were added in combination did biomass increase significantly. Nagy and Proctor (1997) found that the addition of N, P and K led to large increases in plant cover at Meikle Kilrannoch, Scotland, an area with very toxic soil; of these three, P was considered to be the main limiting nutrient. They also found an increase in plant cover with Ca addition but this effect was much smaller.

Meijer (1964) stated that *D. lanceolata* trees strictly avoid the ultrabasic and J. Tangah (pers. comm.) has not recorded *D. lanceolata* on ultramafic soil at Mount Tawai. From the results presented here, it appears that, whilst *D. lanceolata* can grow on ultramafic soil, it may be prevented from occurring on ultramafic soils by competitive exclusion from other species which are better adapted to the edaphic conditions. *Dryobalanops lanceolata* may also be more susceptible to drought; this drought susceptibility will be exacerbated by low soil K (Pandolfini *et al.* 1992).

Conclusions

This study showed that the addition of the major plant nutrients, N, P and K improved the growth of *D. lanceolata*, a hardwood of the Dipterocarpaceae, on a tropical ultramafic soil. Of these three, K and P were both considered to be limiting nutrients. Calcium addition did not improve the growth of *D. lanceolata,* leading to the conclusion that Mg toxicity was not important. This conclusion is reinforced by the presence of a low Mg:Ca ratio when compared with other ultramafic sites. The role played by Ni remains equivocal and would be a fruitful avenue for further research.

Acknowledgements

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