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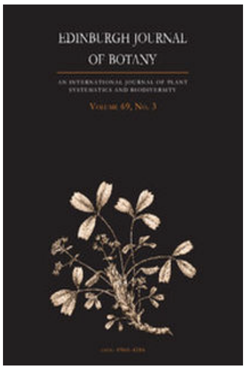
published in
Edinburgh Jounal of Botany
2000

DOI (link to publisher)
10.1017/s0960428600000081

document version
Publisher's PDF, also known as Version of record

citation for published version (APA)
Proctor, J., Baker, A. J. M., van Balgooy, M. M. J., Bruijnzeel, L. A., Jones, S. H., & Madulid, D. A. (2000). Mount Bloomfield, Palawan, Philippines: Forests on greywacke and serpentinized peridotite. *Edinburgh Jounal of Botany*, *57*(2000), 121-139. https://doi.org/10.1017/s0960428600000081



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Edinburgh Journal of Botany / Volume 57 / Issue 01 / March 2000, pp 121 - 139
DOI: null, Published online: 04 December 2000

Link to this article: http://journals.cambridge.org/abstract_S0960428600000081

How to cite this article:
J. PROCTOR, A. J. M. BAKER, M. M. J. VAN BALGOOY, L. A. BRUIJNZEEL, S. H. JONES and D. A. MADULID (2000). MOUNT BLOOMFIELD, PALAWAN, PHILIPPINES: FORESTS ON GREYWACKE AND SERPENTINIZED PERIDOTITE. Edinburgh Journal of Botany, 57, pp 121-139

MOUNT BLOOMFIELD, PALAWAN, PHILIPPINES: FORESTS ON GREYWACKE AND SERPENTINIZED PERIDOTITE

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The forest across a sharp boundary between greywacke and serpentinized peridotite is described from a site with seasonal rainfall on Palawan, Philippines. The forest on greywacke was of much larger stature (trees up to 26m) than that on the serpentinized peridotite (trees up to 18m). The tree (>10cm dbh) species richness was the same on both substrata with 38 species in one 0.16ha plot on each side of the boundary. There were many more individuals in the greywacke plot (149) than on the serpentinized peridotite (114). Floristically the plots were very different, with only one tree species, an unidentified *Madhuca*, occurring on both sides of the boundary. The soil over the greywacke was notably more acid, had lower Mg/Ca quotients, and much lower nickel concentrations than the soil over serpentinized peridotite.

Keywords. Rain forests, serpentines, species diversity, ultrabasic, ultramafic.

INTRODUCTION

The vegetation of ultramafic rocks (frequently called ultrabasics or serpentines) is often sparse or stunted and has rare or endemic species. Until recently, outside New Caledonia (Jaffré, 1980), it was little studied in the tropical Far East. Several accounts are now available e.g. for: Mount Silam in Sabah, Malaysia (Proctor *et al.*, 1988, 1989; Bruijnzeel *et al.*, 1993), Mount Piapi in the Talaud Islands, Indonesia (Proctor *et al.*, 1994), Mount Giting-Giting on Sibuyan Island, Philippines (Proctor *et al.*, 1998), and Mount Kinabalu in Sabah (Aiba & Kitayama, 1999); and there are many papers relating to more recent work in New Caledonia (e.g. Jaffré & Veillon, 1995). An overview for the whole region was given by Proctor (1992). Few generalizations can be made about this ultramafic vegetation except that it varies greatly in its physiognomy and in the composition and endemism of its flora. The island of Palawan, Philippines, has several areas of ultramafic rocks which have been little documented botanically apart from the report by Podzorski (1985). In 1986, we visited the largely ultramafic Mount Bloomfield (10°12′N, 118°52′E) on the west coast of Palawan at the southern margin of St Paul's National Park near the village of Sabang (Fig. 1). In 1988 the forests described in this paper were damaged by charcoal-burners and we are not aware of their present condition.

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Detailed vegetation and soil comparisons across geological boundaries are rare in Malesia and those involving ultramafic rocks have not previously been made in the Philippines. The present paper aims to describe the physical environment of Mount Bloomfield and to describe the soils and several features of the forests on each side of a sharp geological boundary at about 50m asl, between greywacke and serpentinized peridotite, on the eastern footslopes of the mountain. The scrub and *Gymnostoma*-woodland at higher altitude on Mount Bloomfield have been described by Proctor *et al.* (1997).

PHYSICAL ENVIRONMENT

Climate

The climate of Palawan is monsoonal (Am to Aw according to the Köppen, 1930, system), with rain-bearing south-westerlies blowing from May until December and drier north-easterlies from January until April. As a result of its mountainous character, the west coast of Palawan is distinctly wetter than the east. There are no long-term rainfall observations in northwest central Palawan, but the climate station on Coron Island (off the northern tip of Palawan) is probably representative for the study area. From 1951–1980 the mean annual rainfall was 2615mm (range 1979–3175mm), distributed over 133 rain days which occurred mainly from May to October (PAGASA, 1987). According to Bruijnzeel (1990), annual evapotranspiration totals for lowland rain forests which are not short of water are usually 80–90% of Eo (open water evaporation calculated using the equation of Penman (1956) modified for tropical conditions by Kijne, 1974). They have been calculated for Coron and when combined with the rainfall data they show that, depending on soil water retention capacity, severe water deficits might occur between January and April, particularly when the previous December was dry (<60mm), which happens once every 2–5 years (Bureau of Soils, 1980). For instance, the total rainfall from 1 January to 30 April 1987 at the base (c.20m asl) of Bloomfield was less than 10mm.

Geology, topography and soils

Mount Bloomfield is part of the Ulugan Bay ultramafic complex, which consists largely of various kinds of peridotite, mainly harzburgite with numerous bands of chromite-rich dunite. The complex is of Palaeocene to Lower Eocene age and is bounded in the east by a thrust plane along which serpentinization has occurred. This so-called 'Sabang thrust' marks the boundary with the Babuyan River Turbidites formation, which is presumably of Upper Eocene age. The latter formation consists of turbiditic sandstones (greywackes) interbedded with thin layers of black shales that have been altered to very low-grade phyllites by contact metamorphism close to the thrust plane (UNDP, 1985). The two geological formations cover extensive parts of Central and South Palawan (Raschka *et al.*, 1985; UNDP, 1985).

The area underlain by the sedimentary rocks typically exhibits gradients of 5–10°,

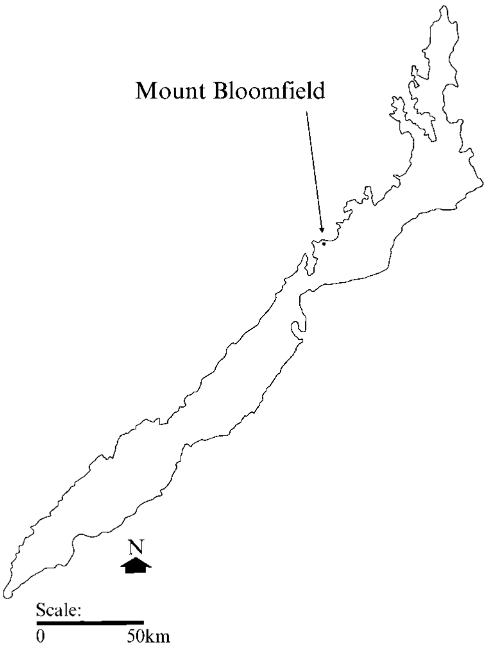

FIG. 1. Location of Mount Bloomfield on Palawan.

whereas slopes on the ultramafic section of the mountain below 200m are generally about 20°. The soil on the greywacke is a Dystric Planosol (FAO/UNESCO, 1989); that on the serpentinized peridotite at 50m is a Eutric Cambisol. Profile descriptions of the soils from one pit on the greywacke and one pit on the serpentinized peridotite are given in Tables 1 and 2.

MATERIALS AND METHODS

The study plots

An 80 × 60m grid of twelve 20 × 20m plots was set up across the boundary between the greywacke and the serpentinized peridotite. There were four 20 × 20m plots (1–4) on greywacke, four plots (5–8) straddled the geological boundary, and four plots (9–12) were on serpentinized peridotite. Work on plots 5–8 was restricted to a floristic description (because of their mixture of soil types) and the data are given in Appendix 1.

Soils

Two soil pits were dug at each of the greywacke (pits a and b) and serpentinized peridotite (pits c and d) ends of the grid and their profiles were described. Duplicate soil samples were collected for analysis from each horizon of each pit. The samples were air-dried, stored in sealed polythene bags, and ground and sieved through a 2mm mesh. pH was measured in a mixture of 10g soil with 25ml deionized water. Loss-on-ignition was measured after burning 5g soil at 375°C for 16h. Metal elements were extracted from 1g subsamples by shaking with 50ml of 2.5% acetic acid. Additionally, in the case of nickel, 2.5g subsamples were extracted with 1M ammonium acetate solution adjusted to pH 7. Total chromium, cobalt, and nickel were extracted by refluxing 0.5g soil with concentrated nitric acid for 1h. The cation concentrations were determined by atomic absorption spectrophotometry using a nitrous oxide/acetylene flame for calcium and magnesium and an air/acetylene flame for the other elements. Particle-size analysis was made on the samples using a hydrometer technique.

Forest structure and floristics

All trees ($>$10cm dbh) were enumerated. The diameters were measured at breast height (1.4m) and herbarium specimens were collected for each individual. The specimens were studied for identification by M.M.J. van B. and a full set of vouchers is stored in the Herbarium of the National Museum, Manila, Philippines (PNH). Identification to species, however, was often impossible because most of the specimens were sterile although they could always be separated into taxa. Shannon-Wiener's index ($\Sigma p_i \ln p_i$) and Simpson's index (1-h, where $h = \Sigma_{pi}{}^2$) were calculated (following Huston, 1994). For each tree the following were recorded: the presence of buttresses ($>$50cm high); the number of lianas (in a range of size classes) gaining support from it; vascular epiphytes (up to 5m up the bole); and the percentage of the bark (at a point 2m up the bole) covered by bryophytes. For each of plots 1–4 and 9–12, two randomly located 4 × 4m quadrats were sampled for trees $<$6m tall (in several size-classes), pandans (*Pandanus* sp.), rattans (climbing palms), and herbaceous angiosperms.

Tree leaves

Mean leaf area, as ⅔ lamina length (to the base of the drip tip) × breadth, was calculated from measurements made on ten typical mature leaves for all enumerated trees. Leaves were then classified into the size classes of Raunkiaer (1934) as modified by Webb (1959). The mean specific leaf area was calculated from a sample of three typical leaves for 32 tree species occurring in plots 1–4 and 27 species in plots 9–12. Area measurements were made on air-dried leaves using a Hipad Digitizing Tablet (Houston Instruments Division, model DTII). Leaves were oven-dried at 60°C for 24h before weighing. For 26 tree species in plots 1–4 and 29 species in plots 9–12, both upper and lower epidermal surfaces of ten leaves were examined for stomatal and hair density and for guard cell and stomatal length using a scanning electron microscope. Densities were obtained from an average of ten 5540μm^2 viewing fields for each leaf and mean length measurements were calculated from ten observations per viewing field. Leaf anatomical studies were made on 15 species from plots 1–4 and 17 species from plots 9–12. In the field, 2–3cm leaf sections were cut through the mid-rib and immediately fixed in formalin acetic alcohol (FAA) prior to sectioning and examination. Using a histokinette, leaf sections were dehydrated in a series of alcohols and bathed in wax. The leaf tissue was subsequently set in wax blocks and 10μm transverse sections were cut using a rotary microtome. The tissue was stained with safranin and light green and mounted for light microscopy. Measurements were made of the total lamina thickness, the thickness of palisade and non-palisade mesophyll tissue, and the thickness of both the upper outer epidermal wall and cuticle combined, and that of the lower outer epidermal wall and cuticle combined. Measurements were made at a magnification of × 1000 under immersion oil on parts of the lamina (between the mid-rib and edge). The presence of hairs, a pluristratified upper epidermis, hypodermis, vascular bundle sclerenchyma, non-vascular bundle sclerenchyma, transcurrent sclerenchyma, secretory structures, and crystals were noted. Crystals and sclerenchyma were observed using polarized light.

RESULTS

Soils

Soil profile descriptions for one pit (a) on greywacke and one on serpentinized peridotite (c) are given in Tables 1 and 2. Apart from horizon depths these were similar to the other pits on the same sites and the profile descriptions for pits b and d are not given here. The chemical analytical data for all four pits is given however in Tables 3 and 4. The soils on greywacke were mildly acid with relatively low concentrations of dilute acetic-acid extractable potassium, calcium, and magnesium. The Mg/Ca quotient always exceeded unity. The soils had substantial amounts of clay and were finer textured than those on the serpentinized peridotite. There were certain clear trends with increasing soil depth, notably decreasing loss-on-ignition, extractable calcium, and sand; and increasing Mg/Ca quotients and clay. The soils on the serpentinized peridotite were around neutral pH and had much higher metal concentrations and Mg/Ca quotients and were more coarsely textured than those on the greywacke. They were also notably higher in chromium, cobalt, and nickel. The serpentinized peridotite pits had similar trends with increasing depth to those on the greywacke.

Forest structure and floristics

A forest-profile diagram showing the forest changes across the geological boundary between greywacke and serpentinized peridotite has been published by Proctor & Nagy (1992). On the greywacke the forest was moderately large, with trees up to 26m, dense (93 individuals per 0.1ha), and had a high basal area (5.22m^2 per 0.1ha) with trees up to 82.2cm diameter (Tables 5 and 6). On the serpentinized peridotite, the trees were smaller (up to 18m), less dense (71 individuals per 0.1ha) and had a smaller basal area (1.91m^2 per 0.1ha) with the largest measured tree, 46.2cm diameter. There was a higher proportion of trees with buttresses on greywacke (28.2%)

TABLE 1. A profile description for a representative soil pit (a) for a forest at 50m altitude on greywacke on Mount Bloomfield. Pit situated on upper part of a 10° slope in plot 1; northerly aspect; parent material greywacke (rich in quartz and plagioclase, with some potassium feldspar, sericite and accessory chlorite) interbedded with low-grade phyllites (rich in sericite and quartz, with accessory chlorite and tourmaline); micro-relief showing small steps of 5–10cm, caused by large tree roots forming local erosion bases; on lower parts of slopes litter had been washed away by saturation overland flow at the height of the rainy season, rest of slope covered by leaf litter; lower part of profile poorly drained

Ah	0–2/6cm; dark brown (10YR 3/4) to dull yellowish brown (10YR 5/4) loamy very fine sand; fine to medium crumb; many (very) fine pores; friable; non-sticky; abundant (very) fine roots, frequent medium to coarse roots; abrupt and smooth boundary to Eg.
Eg	2/6–22/29cm; bright yellowish brown (10YR 7/6) very fine sandy clay loam; few medium faint light grey mottles with orange brown rim; moderate to strong fine angular blocky; common fine to medium pores; friable, non-sticky; frequent (very) fine roots, common medium to coarse roots; gradual and slightly wavy boundary to Bgt.
Bgt	22/29–56cm; bright yellowish brown (10YR 6/6) clay loam; many medium sharp distinct white mottles associated with very fine roots; common fine pores; strong (very) coarse angular blocky, more massive with depth; firm to very firm, slightly sticky; few roots (all dimensions), with frequency decreasing with depth; gradual and smooth boundary to BCg.
BCg	56–100+cm; bright reddish brown (2.5YR 5/8) to light yellow (2.5YR 7/3) mottled clay loam; fine mottles becoming more distinct with depth; very coarse angular blocky, becoming more massive with depth; few very fine pores but common fine pores; firm to very firm, sticky; few roots (all dimensions); frequent angular rock fragments (gravel-sized unweathered quartz to strongly weathered shale).

TABLE 2. A profile description for a representative soil pit (c) for a forest at 50m altitude on serpentinized peridotite on Mount Bloomfield. Pit situated on a 20° slope; easterly aspect; parent material serpentinitic colluvium (rock consisting of 99% serpentine, with accessory chromite, secondary magnetite and chlorite); surface very stony with ubiquitous signs of erosion by (saturation) overland flow; profile well drained

Ah	0–8/17cm; dark brown (7.5YR 3/3) fine sandy loam; moderate fine to medium granular; many (very) fine pores; slightly firm, slightly sticky; frequent very fine, common fine to medium, and few coarse roots; few gravel-size angular weathered rock fragments; abrupt and wavy boundary to B.
B	8/17–22/25cm; dark brown (5YR 3/3) sandy (clay) loam; strong fine to medium angular blocky; many fine pores; slightly firm to firm, slightly sticky; common (very) fine to medium, few coarse roots; few gravel-size angular weathered rock fragments; gradual and wavy boundary to BC.
BC	22/25–48/58cm; dark reddish brown (5YR 3/4) gravelly (clay) loam; moderate to strong very fine to fine angular blocky; many fine to medium pores; firm, slightly sticky; common to frequent very fine to medium roots, very few coarse roots; very frequent angular gravel-to stone-sized strongly weathered rock fragments.

TABLE 3. The pH, loss-on-ignition, acetic-acid extractable potassium, calcium, magnesium, the Mg/Ca quotient and the percentage of clay, sand and silt for each horizon of soil pits (a) and (b) on greywacke and of soils pits (c) and (d) on serpentinized peridotite

	Horizon and depth (cm)	pH (log units)	LOI (%)	K	Ca (m-equivs 100g^{-1})	Mg	Mg/Ca	Clay (%)	Sand (%)	Silt (%)
(a)	A_h 0–2/6	5.3	17.0	0.21	0.32	0.55	1.67	16.0	42.3	41.7
	E_g 2/6–22/29	4.9	5.7	0.10	0.13	0.49	3.72	27.8	40.0	32.3
	B_{gt} 22/29–56	5.0	4.0	0.12	0.14	0.48	3.62	29.0	35.2	35.8
	BC_g 56–100 +	5.0	5.0	0.15	0.08	0.62	8.85	41.6	30.7	27.7
(b)	A_h 0–4/5	5.1	8.0	0.26	0.95	1.76	1.98	24.1	46.7	29.1
	E_g4/5–22	5.2	4.5	0.23	0.20	1.84	9.64	24.1	38.5	37.4
	B_{gt} 22–39	5.3	3.5	0.31	0.34	2.04	7.45	31.3	31.8	36.9
	BC_g39–140	5.3	4.3	0.25	0.27	1.84	7.57	33.0	34.5	32.6
(c)	A_h 0–8/17	6.7	11.6	0.38	2.79	15.9	5.72	14.1	45.6	40.3
	B 8/17/–22/25	6.5	8.5	0.29	1.00	19.3	21.4	27.2	27.2	45.7
	BC 22/25–48/58	6.8	7.0	0.22	0.61	25.4	41.4	36.6	33.9	29.5
(d)	A_h 0–6/10	6.6	12.9	0.23	1.96	16.2	8.3	1.4	67.7	30.9
	B 6/10–22/28	6.8	6.5	0.21	0.49	13.7	28.1	18.4	39.2	42.4
	BC 22/28–60/80	7.2	8.0	0.27	0.33	23.8	79.9	29.3	33.9	29.5

TABLE 4. The concentrations (μg g^{-1}) of acetic-acid extractable and total chromium, cobalt and nickel and ammonium-acetate exchangeable nickel for each horizon of soil pits (a) and (b) on greywacke, and (c) and (d) on serpentinized peridotite

	Horizon and depth (cm)	$Cr_{(extr)}$	$Co_{(extr)}$	$Ni_{(extr)}$	$Cr_{(tot)}$	$Co_{(tot)}$	$Ni_{(tot)}$	$Ni_{(exch)}$
(a)	A_h	1	1	0.8	200	200	550	0.4
	E_g	1	0	0.5	200	100	300	0.3
	B_{gt}	0	1	0.6	100	200	350	0.8
	BC_g	0	1	0.6	100	200	350	0.8
(b)	A_h	1	4	9.6	600	200	500	1.4
	E_g	2	2	7.0	550	200	600	2.2
	B_{gt}	2	2	7.3	450	200	650	2.2
	Bc_g	1	3	10.3	230	200	830	4.8
(c)	A_h	4	18	381	12000	1600	7400	72.1
	B	6	13	320	11000	1400	7900	83.1
	BC	9	9	301	6500	1100	8400	66.1
(d)	A_h	3	25	319	15000	1200	5400	44.1
	B	2	7	196	15000	1200	5600	34.2
	BC	3	5	124	6000	80	6500	25.1

TABLE 5. The percentages of trees (⩾10cm dbh) in a range of diameter-classes in 0.16ha sites on (a) greywacke and (b) serpentinized peridotite on Mount Bloomfield.

	Diameter class (cm)							
	10–19.9	20–29.9	30–39.9	40–49.9	50–59.9	60–69.9	70–79.9	80–89.9
(a)	61.1	16.7	12.7	2.0	3.4	2.0	1.4	0.7
(b)	74.3	19.5	4.4	1.8	0	0	0	0

TABLE 6. The tree (≥10cm dbh) density, basal area, number of species, number of species per individual, Shannon-Wiener's and Simpson's indices and the percentages of trees with buttresses, supporting lianas (>1cm dbh), with bryophyte cover exceeding 10% at a bole height of 2m, with vascular epiphytes in the lower 5m of the tree, and trees with microphylls (230–2000mm^2) or smaller leaves, on 0.16ha sites on greywacke and serpentinized peridotite on Mount Bloomfield, Palawan

	Greywacke	Serpentinized peridotite
Tree (≥10cm dbh) density (100m^{-2})	9.3	7.1
Basal area (m^2 100m^{-2})	0.52	0.19
No. of species	38	38
No. of species per individual	0.26	0.34
Shannon-Wiener's index	2.91	3.16
Simpson's index	0.92	0.93
Buttressed (≥50cm) (%)	28.2	6.2
Trees with lianas (>1cm dbh) (%)	9.3	35.4
Trees with >10% bryophyte cover (%)	0.0	41.0
Trees with vascular epiphytes (%)	0.8	11.5
Trees with microphylls or smaller leaves (%)	13	47

compared with those on the serpentinized peridotite (6.2%). Small tree (<3m tall) density was much greater in plots 9–12 but for trees >5cm dbh the greater density was in plots 1–4 (Table 7). The trees on the greywacke had fewer lianas and much less bole bryophyte cover than those on the serpentized peridotite (Table 6). However pandans and ferns were found only on the greywacke and those areas had more rattans and cyperaceous herbs but fewer bamboos and other angiosperm herbs than on the serpentinized peridotite (Table 7).

The tree species richness of the two substrata were identical with 38 species per

TABLE 7. The densities (100m^{-2})±95% CLs of a range of plant synusiae in eight 4×4m subplots located in stratified random design within 0.16ha sites on greywacke (plots 1–4) and a similar area on serpentinized peridotite (plots 9–12)

Synusia	Greywacke	Serpentinized peridotite
Trees <1m	157±35	353±299
1–<3m	8.9±1.9	180±40
>3m tall <5cm dbh	51±20	66±21
5–<10cm dbh	15±5	9±4
Pandanaceae	28.9±17.8	0
Arecaceae (rattans)	83.6±35	7.8±7.2
Poaceae (bamboo)	17.2±25.4	77.3±62.6
Ferns (filmy)	43.8±72.1	0
(non-filmy)	1200±1200	0
Cyperaceae	96.9±28.9	3.1±5.6
Other herbs	14.9±14.5	85±169

each 0.16ha. The indices of diversity (Table 6) were similar but there were more species per individual tree on the serpentinized peridotite. Only one species, an unidentified *Madhuca* (*Sapotaceae*), occurred in plots on both sides and there were considerable differences in the family composition on crossing the geological boundary. The families (Table 8) which accounted for at least 5% of the individuals on the greywacke but were not recorded from the serpentinized peridotite were the

TABLE 8. The percentage contribution of each family to tree ($\geqslant$10cm dbh) density, and basal area in 0.16ha sites on greywacke and serpentinized peridotite on Mount Bloomfield

	Greywacke		Serpentinized peridotite	
Family	Density	Basal area	Density	Basal area
Anacardiaceae	2.7	12.2	2.7	4.1
Aquifoliaceae	0.7	0.2	1.8	1.1
Bignoniaceae			0.9	0.4
Burseraceae			6.3	7.2
Chryosobalanaceae			7.2	11.7
Clusiaceae	6.8	2.9	1.8	0.9
Combretaceae			2.7	1.9
Dipterocarpaceae	14.3	8.7		
Ebenaceae			6.3	4.1
Elaeocarpaceae	0.7	6.5		
Erythroxylaceae			1.8	2.3
Euphorbiaceae	2.0	0.4	2.7	1.5
Fabaceae	0.7	0.1		
Fagaceae	0.7	0.6		
Flacourtiaceae			0.9	0.9
Lauraceae			10.8	11.2
Loganiaceae	6.7	2.3		
Melastomataceae	0.7	0.4	0.9	0.8
Meliaceae	0.7	0.2	4.5	10.7
Myrtaceae	17.0	16.7	25.2	23.6
Ochnaceae	0.7	0.1	5.4	6.7
Oleaceae	1.4	0.4		
Podocarpaceae			0.9	0.5
Polygalaceae	0.7	0.4		
Rhizophoraceae			5.4	4.3
Rubiaceae	2.0	0.5	1.8	1.0
Rutaceae	0.7	0.1		
Sapotaceae	8.2	8.6	1.8	1.7
Saxifragaceae	0.7	0.1		
Symplocaceae	17.0	12.8		
Theaceae	2.0	0.9		
Thymeleaceae	12.2	24.7		
Ulmaceae			2.7	1.3
Verbenaceae	0.7	0.2	3.6	1.5
Unidentified			1.8	0.6

TABLE 9. The means (with range in parentheses) of some anatomical features of leaves of 15 species (32 for lamina thickness) on greywacke and 17 species (27 for lamina thickness) on serpentinized peridotite on Mount Bloomfield

	Greywacke	Serpentinized peridotite
Lamina thickness (μm)	296 (191–434)	302 (157–482)
Specific leaf area ($cm^2\ g^{-1}$)	84.0 (51.9–128.8)	76.4 (37.6–129.7)
Upper epidermis cell wall and cuticle thickness (μm)	8 (4–20)	9 (4–13)
Species with 1, 2, ⩾3 palisade mesophyll layers (%)	1, 53; 2, 40; 3, 7	1, 35; 2, 47; 3, 18
Species with a hypodermis (%)	13	6
Non-vascular – bundle sclerenchyma (%)	13	6
Transcurrent sclerenchyma (%)	20	6
Crystals (%)	100	100
Pluristratified epidermis (%)	0	24
Mean stomatal density (mm^{-2})	268 (95–813)	343 (70–661)
Mean stomatal length (μm)	10.0 (2.5–16.5)	9.2 (3.2–30.6)
Species with lower epidermal hairs (%)	8	14

Dipterocarpaceae, *Loganiaceae*, *Symplocaceae*, and *Thymeleaceae*. The families which accounted for at least 5% of the individuals on the ultramafic side of the boundary but were not recorded on the greywacke were the *Burseraceae*, *Chrysobalanaceae*, *Ebenaceae*, *Lauraceae*, and *Rhizophoraceae*.

Tree leaves

The greywacke trees had many fewer microphyllous and many more mesophyllous individuals than those on the serpentinized peridotite (Table 6). Of the results of the other foliar investigations only the greater occurrence of species with a pluristratified epidermis (24% on the serpentinized peridotite versus 0% on the greywacke) was statistically significant between the forest types (Table 9).

DISCUSSION

Soils

The use of acetic acid as an extractant for cations was shown by Proctor & Craig (1978) for Zimbabwean ultramafic soils to give results which were very similar to those for ammonium acetate extractions, except for chromium, cobalt, and nickel. Data for acetic acid and ammonium acetate extractable nickel are given in Table 4.

The greywacke soil was unusual for a non-ultramafic in having a relatively high concentration of magnesium and had Mg/Ca quotients which exceeded unity near the surface and reached up to 8.85 in the deepest horizons. The soil on the serpentinized peridotite was relatively calcareous in its surface layers but nevertheless, because of its high concentrations of magnesium, the upper horizons had high (but not exceptionally so) Mg/Ca quotients similar to those of medium to large stature rain forest on other Malesian ultramafic soils (Proctor *et al.*, 1988; Proctor, 1992; Proctor *et al.*, 1994, 1998) but which exceeded those of the soils under scrub vegetation at higher altitudes on Mount Bloomfield (Proctor *et al.*, 1997). It had very high Mg/Ca quotients, which reached 79.9 in the deepest horizons. Greywacke nickel concentrations were a little higher than is normally found for non-ultramafic soils (Proctor & Woodell, 1975) and those on the serpentinized peridotite were very high and exceeded those reported for relatively large stature rain forest in Sabah (Proctor *et al.*, 1988) and in the Philippines (Proctor *et al.*, 1998) but were fairly similar to those for scrub vegetation on Mount Piapi, Talaud Islands (Indonesia) (Proctor *et al.*, 1994) and at higher altitudes on Mount Bloomfield (Proctor *et al.*, 1997).

Forest structure and floristics

The tree stature was greater on the greywacke, with a basal area of $5.2\text{m}^2\ 0.1\text{ha}^{-1}$ compared with that of $1.9\text{m}^2\ 0.1\text{ha}^{-1}$ on the serpentinized peridotite. A basal area of $3.65\text{m}^2\ 0.1\text{ha}^{-1}$ is a pantropical average for rain forests generally (Dawkins, 1958, 1959). Small-stature forests are not an invariable feature of ultramafics however. Fox & Tan (1971) described a large stature forest on ultramafics in Sabah, and Proctor *et al.* (1988) described forests from the ultramafic Mount Silam in Sabah where two plots at 280m and 330m had a basal area of $3.82\text{m}^2\ 0.1\text{ha}^{-1}$ and $4.62\text{m}^2\ 0.1\text{ha}^{-1}$ respectively and emergent trees up to about 48m high. Jaffré & Veillon (1995) found a basal area of $4.95\text{m}^2\ 0.1\text{ha}^{-1}$ for an ultramafic forest in New Caledonia compared with $5.55\text{m}^2\ 0.1\text{ha}^{-1}$ for a forest on schist.

The similarity of species richness and diversity between the greywacke and serpentinized peridotite plots is remarkable (Table 6) but must be coincidental because of the different numbers of individual trees. This differing numbers of individuals must be taken into account in comparisons of species richness. The tree species richness on Mount Silam was 38 from 82 individuals for a 0.16ha part of the plot at 280m, and 49 from 101 individuals for a 0.16ha part of the plot at 330m. Plots of the same dimensions on the Bloomfield greywacke had 149 individuals and on the serpentinized peridotite 114 individuals. Jaffré & Veillon (1995) found 58 species (trees >10cm dbh) from 314 individuals in a 0.25ha plot on schist and 69 species from 383 individuals in a similar-sized ultramafic plot in New Caledonia. The almost total floristic difference across the geological boundary on Mount Bloomfield contrasted greatly with trans-boundary studies in rain forests in New Caledonia which showed a roughly 30% species change (Jaffré, 1980). With the exception of the *Saxifragaceae*, all the greywacke families which did not occur in the ultramafic plots on Mount Bloomfield have been recorded on ultramafic soils elsewhere in south-east Asia. The absence of dipterocarps from the Bloomfield ultramafics is surprising in view of their importance on Mount Silam where Proctor *et al.* (1989) recorded a nickel-accumulating dipterocarp species. It is possible that the much higher soil nickel concentrations on Mount Bloomfield exclude the dipterocarps because the family is also important on the less nickel-rich soils of Mount Sibuyan in Romblon Province in the Philippines (Proctor *et al.*, 1998).

Among the smaller synusiae, the density of small trees (<3m high) (Table 7) is lower than that recorded by Proctor *et al.* (1988) for lowland (280m and 330m) ultramafic forests in Sabah (mean 9.3m^{-2}) but for trees (>3m high) the densities exceed those of the Sabah forests (mean 3.2m^{-2} for trees >3m high and <5cm dbh; and 6.0m^{-2} for trees $\geqslant 5$cm–<10cm dbh). The *Pandanaceae* were absent from the lower plots on Mount Silam as they are from plots 9–12 but they did occur at higher altitude (480–870m) on Silam and a pandan species is widespread on the ultramafic scrub on Gunung Piapi in the Talaud islands of northern Sulawesi (Lam, 1927; Proctor *et al.*, 1994). The absence of ferns from plots 9–12 is very surprising in view of the abundance of the 'other' herbs. Ferns occurred at a mean density of 1.2m^{-2} in the lower plots on Mount Silam.

Tree leaves

The high proportion of microphyllous leaves among the trees on the serpentinized peridotite (47% of the individuals) (Table 6) is not a general feature of ultramafic forests and on Mount Silam even the summit cloud forest had a lower proportion (29.6%) of microphylls (Proctor *et al.*, 1988). Although many leaf features of the serpentinized peridotite trees are not significantly different from those of the greywacke the differences which occur (e.g. lower specific leaf area, higher mean stomatal density) are largely in the direction of increasing scleromorphy (Table 9). Overall, apart from the high proportion of microphylly on the serpentinized peridotite, leaves from both sides of the geological boundary showed no exceptional morphological or anatomical features compared with lowland evergreen rain forests elsewhere (e.g. Roth, 1984, for Venezuela). The leaves of the trees on serpentinized peridotite had none of the extreme scleromorphic features associated with heath forest leaves for which Peace & MacDonald (1981) found, for ten species in Sarawak, a mean lamina thickness of 457μm (range 335–612μm), and 50% of species with a hypodermis. Similarly, Sobrado & Medina (1980) found for ten species in a 'bana' forest on white sands in Venezuela a mean lamina thickness of 457μm (range 229–761μm) and 60% of the leaves with a hypodermis. Leaf anatomy of the Bloomfield scrub and *Gymnostoma*-woodland at 180m asl and above, and foliar chemistry for all the Bloomfield vegetation types are discussed in Proctor *et al.* (1997, 2000).

CONCLUDING REMARKS

The adjacent forests on the greywacke and the serpentinized peridotite show many floristic and structural contrasts which might be caused by differences in the soil chemistry. However, differences in water supply and fire frequency, or both, might be important determinants of the vegetation and this is discussed more fully by Proctor *et al.* (1999) in the light of additional information on hydrology and a consideration of the other vegetation types on the mountain (Proctor *et al.*, 1997).

ACKNOWLEDGEMENTS

We thank the Government of the Republic of the Philippines for permission to carry out research there, and the staff, especially Mr E. Reynoso, of the Herbarium of the National Museum, Manila, for their help.

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Received 29 April 1998; accepted with revision 18 March 1999

APPENDIX 1

The tree species recorded from (a) a 0.16ha site on greywacke, (b) a 0.16ha site on serpentinized peridotite, and (a)/(b) the 0.16ha transitional site between the two, on Mount Bloomfield. *Initially all assigned to same species but greywacke specimens lost and conspecificity unconfirmed

Family and species	(a)	(a)/(b)	(b)
ANACARDIACEAE			
Buchanania insignis Bl.			+
B. microphylla Engl.			+
Swintonia acuta Engl.	+		
AQUIFOLIACEAE			
Ilex sp. A	+		
Ilex B			+
BIGNONIACEAE			
Radermachera gigantea (Bl.) Miq.			+
BURSERACEAE			
Canarium asperum Benth. ssp. *asperum*		+	+
Protium connarifolium Merr.			+
CHRYSOBALANACEAE			
Atuna racemosa Rafin. ssp. *racemosa*			+
Licania palawanensis Prance		+	+
L. splendens (Korth.) Prance		+	+
CLUSIACEAE			
Calophyllum? *obliquinervium* Merr.	+		
C. soulattri Brum. f.	+		
Garcinia sp. 1	+		
Garcinia sp. 2*	+		+
Garcinia sp. 3			+
Unidentified	+		
COMBRETACEAE			
Terminalia sp.	+		
Terminalia cf. *nitens* Presl		+	+
DILLENIACEAE			
Dillenia sp.		+	
DIPTEROCARPACEAE			
Vatica maritima Sloot.	+	+	
Dipterocarpus? *hasseltii* Bl.	+	+	
EBENACEAE			
Diospyros ferrea (Willd.) Bakh.			+
Diospyros sp.		+	+
ELAEOCARPACEAE			
Elaeocarpus floribundus Bl.	+		

Family and species	(a)	(a)/(b)	(b)
ERYTHROXYLACEAE			
Erythroxylon ecarinatum Burck		+	+
EUPHORBIACEAE			
Austrobuxus nitidus Miq.	+		
Croton sp A	+	+	
Croton sp B			+
Euphorbiaceae sp.		+	
Suregada glomerulata (Bl.) Baill.		+	+
FABACEAE			
Intsia bijuga (Coleb.) O.K.		+	
Intsia palembanica Miq.	+		
FAGACEAE			
Castanopsis psilophylla Soepadmo	+		
FLACOURTIACEAE			
Scolopia luzoniensis Planck.			+
LAURACEAE			
Dehaasia sp.			+
Litsea sp. 1			+
Unidentified		+	
LOGANIACEAE			
Fagraea racemosa Wall.	+	+	
MELASTOMATACEAE			
Memecylon sp. A	+		+
MELIACEAE			
Aglaia sp.			+
?*Dysoxylum* sp.	+	+	
MYRTACEAE			
Syzygium alcinae (Merr.) Merr. & Perr.	+	+	
Syzygium leucoxylon Korth.	+	+	
Syzygium? *palawanensis* (C.B.Rob.) Merr. & Perr.	+	+	
Syzygium? *parvum* Merr.		+	
S. punctilimbum Merr.		+	+
Syzygium sp. 1	+	+	
Syzygium sp. 2		+	+
Syzygium sp. 3		+	
Syzygium sp. 4			+
Syzygium sp. 5			+
Syzygium sp. 7		+	
Syzygium sp. 8			+
?*Tristaniopsis*			+
OCHNACEAE			
Brackenridgea palustris Bartell. ssp. *foxworthyi* (Elm.) Kanis		+	+
Gomphia serrata (Gaertn.) Kanis	+		

Family and species	(a)	(a)/(b)	(b)
OLEACEAE			
Olea borneensis Boerl.	+		
PODOCARPACEAE			
Podocarpus polystachyus R. Br. ex Endl.			+
POLYGALACEAE			
Xanthophyllum sp.	+	+	
RHIZOPHORACEAE			
Carallia borneensis Oliv.		+	+
RUBIACEAE			
Canthium sp.*	+	+	+
Rubiaceae sp.*	+	+	+
Timonius sp.	+		
RUTACEAE			
?*Tetractomia* sp.	+		
SAPOTACEAE			
Madhuca sp.	+	+	+
Palaquium stenophyllum H.J. Lam	+		
Planchonella linggensis (Burck) Pierre	+		
SAXIFRAGACEAE			
?*Polyosma* sp.	+		
STERCULIACEAE			
Sterculia sp.		+	
SYMPLOCACEAE			
Symplocos polyandra (Blco.) Brand	+		
THEACEAE			
Camellia lanceolata (Bl.) Keng	+		
Ternstroemia sp.	+		
THYMELEACEAE			
Gonystylus sp.	+	+	
VERBENACEAE			
Premna sp.	+		+
ULMACEAE			
Celtis sp.			+
UNIDENTIFIED			
Unidentified 1		+	
Unidentified 2			+
Unidentified 3			+