Forest Ecology and Management 139 (2000) 257–278

Forest Ecology and Management

www.elsevier.com/locate/foreco

Nutrient cycling in secondary forests in the Blue Mountains of Jamaica

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Received 21 September 1999; received in revised form 1 March 2000; accepted 13 March 2000

Abstract

Secondary forests in the Blue Mountains of Jamaica, subject to human disturbance as well as hurricanes, are coming under increasing land-use pressure with a rising population density and the remaining primary forest becoming more remote from settlements. The practice of slash-and-burn agriculture is commonly carried out by local communities. This study reports on estimates of how the secondary forests have recovered to, or close to, the functioning of undisturbed forest, in terms of key soil and nutrient cycling variables. Nutrient conservation was assessed by measuring inputs in throughfall and litterfall, which were compared to site nutrient capital and losses in surface runoff and erosion. Litterfall, litter standing crop and the growth of bioassay plants were measured in paired plots of primary and secondary forests. The results were compared with data already published for key nutrient cycling variables in primary forests of the Blue Mountains to determine the extent to which nutrient cycling and soil fertility in the secondary forest has recovered to primary forest levels. Rates of nutrient loss in runoff and eroded sediment in the secondary forest were low, basal area had recovered to 81% of primary forest levels, and rates of litterfall were high. Litterfall nutrient concentrations were high, particularly for P, and nutrient cycling was rapid as judged by the high ratio of litterfall to litter standing crop. Soil fertility had recovered well in the secondary forests as judged both by chemical analyses and the growth of the bioassay plants. The results indicate that, for forests in the middle of steep slopes, following the cessation of agriculture, tight nutrient cycling and soil condition and fertility are effectively restored during ca. 20 years of secondary succession. This results in the re-establishment of a forest with effective nutrient conservation which offers a high degree of protection of catchment soil and water resources, and the potential to sustain another cycle of agricultural production.

Keywords: Secondary forest; Litterfall; Jamaica; Soil fertility; Nutrient cycling; Tropical rain forest; Montane forest

1. Introduction

There has been a long-running exploration of the factors limiting natural forest productivity on tropical mountains and in particular the role of limitation in the availability to trees of particular mineral nutrients (especially N and P) (Tanner et al., 1998). Healey (1989) and Tanner et al. (1990) provided experimental evidence that the growth of these natural montane forests in Jamaica was limited by P and N. However, this work and others (e.g. Tanner, 1977a,b, 1980a,b, 1981, 1985) in Jamaica has been based, almost entirely, on the study of a series of forest types in close proximity in an area on or close to the crest of the main ridge of the Blue Mountains. Bellingham et al. (1995) have shown how great the impact of natural

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0378-1127/00/$ – see front matter
PII: S0378-1127(00)00442-4

hurricane disturbance is on the vegetation dynamics of these forests, but the effects of disturbance and subsequent secondary succession on forest nutrient cycles have not been quantified. Due to growing land-use pressure, the primary forests of the Blue Mountains have suffered increasing encroachment. As elsewhere on tropical mountains, the forests in the middle of the steep hill-slopes are in a buffer zone between the intact forests remaining at higher altitudes above, and agricultural land below. As such they are under increasing pressure from wood harvesting and slash-and-burn agriculture which has created a mosaic of secondary forests of different ages. Secondary forests are increasing in area throughout the tropics and may comprise about 31% of the total closed forest land (Brown and Lugo, 1990). They are usually fast-growing ecosystems that can potentially provide a sustainable supply of valuable commodities to nearby human communities. However, their successful management requires us to know, following the abandonment of agriculture or reduction of harvesting pressure, how well nutrient cycling and soil condition and fertility recover. Is it sufficient to enable either the re-establishment of forest ecosystem with effective nutrient conservation which offers a high degree of protection of catchment soil and water resources and biodiversity; or another cycle of forest harvesting or agricultural production? These concerns are particularly acute for steep hill-slope sites, where the loss of nutrients through down-slope runoff, erosion and leaching during periods of agriculture, and subsequently, may lead to a more serious reduction in soil fertility during the cropping cycle than in other sites.

This paper investigates the extent to which secondary forests in the Blue Mountains of Jamaica, subject to human disturbance as well as a recent hurricane, have recovered to, or close to, the functioning of undisturbed forest, in terms of key soil and nutrient cycling variables. The objectives were to

1. establish how well secondary forest conserves nutrients,
2. determine the extent to which nutrient cycling and soil fertility in the secondary forest have returned to the levels in primary forest.

The approach taken for meeting these objectives was (a) to undertake detailed quantification of components of the nutrient cycle in four intensively studied replicate secondary forest plots; (b) to compare litterfall, litter standing crop and the growth of bioassay plants in three pairs of plots of primary and secondary forests.

2. Methods

2.1. Study area

The Blue Mountains of Jamaica are a geologically recent tropical mountain range, characterised topographically by steep slopes and highly-dissected terrain, with sharp ridges and deep gullies. Natural soil development is poor, owing to a combination of steepness of slope and significant erosion. The natural vegetation is montane tropical rain forest (Shreve, 1914). Grubb and Tanner (1976) classified the montane forests of the Blue Mountains into seven forest types. Some of the forest on slopes (up to about 1600 m) has a long history of clearance, recently for two major land uses — cash crop cultivation by small farmers and coffee plantations (Eyre, 1987), but in places forest clearance for coffee, tea and cinchona plantations, and subsistence agriculture by the workforce, goes back at least 200 years (Barker and McGregor, 1988). Typically, land cleared for cash cropping is cultivated for several years and then abandoned when levels of production fall. The secondary forest consists of shrubs and early-successional forest tree species, often dominated by the introduced Australian tree, *Pittosporum undulatum* (Goodland and Healey, 1995; Healey et al., 1995).

The study area was located on the south-west slopes of the main ridge of the Blue Mountains in the adjacent catchments of the Green and Clyde Rivers, head-water tributaries of the Yallahs River (Fig. 1). The forests of this area corresponds to Dry Slope Forest type (Grubb and Tanner, 1976), with elements of Gully Forest and Wet Slope Forest in the bottoms of gullies, and Mull Ridge Forest on the descending ridges. The elevation is around 1300 m. The Yallahs Basin as a whole has a high natural propensity for erosion (McGregor et al., 1985). The underlying geology is complex, both the 'Blue Mountain Volcanics', which include granodiorite, and 'Blue Mountain Shales', which consist of mudstones, sandstones and

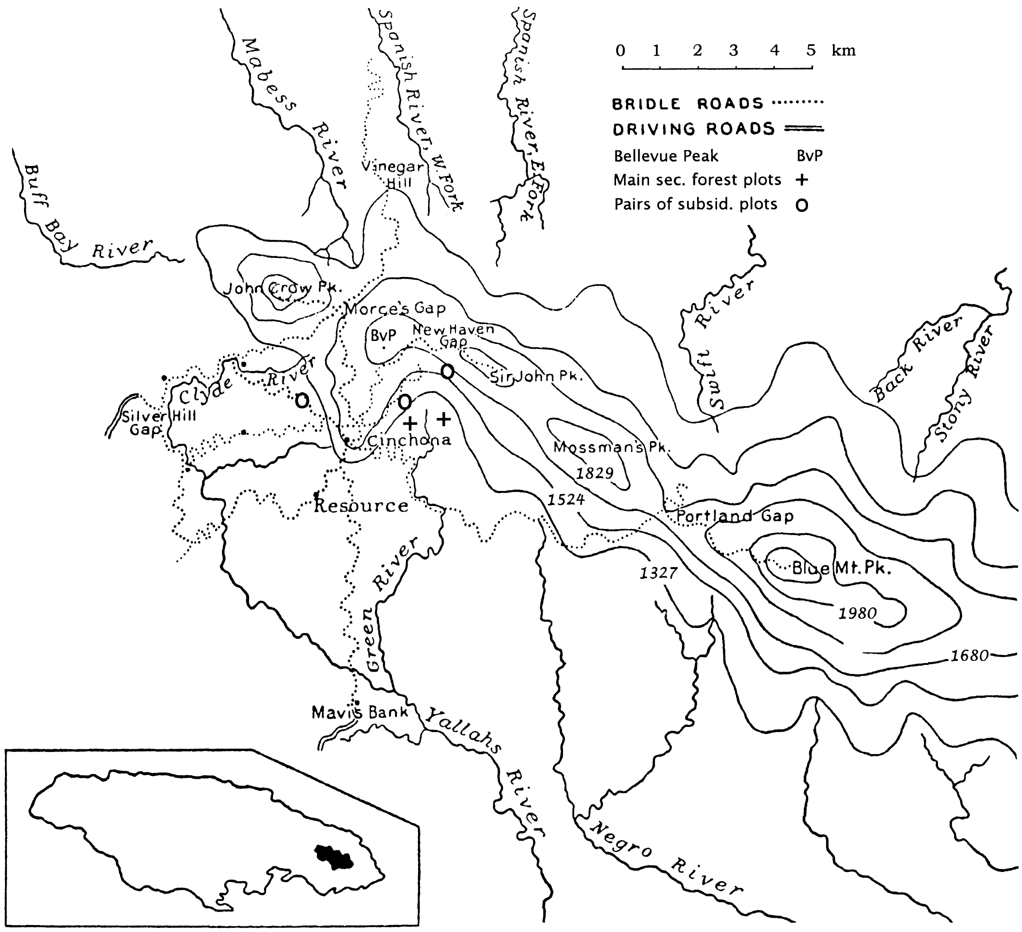

Fig. 1. Map of study area (after Shreve, 1914) showing the positions of the sample plots. Contour heights are given in meters. The Blue Mountains are indicated in black on the inset map of Jamaica.

conglomerates, are present. Soils of the area are reported as eutric and chromic Cambisols (FAO-UNESCO, 1975); we confirmed the presence of these soil types in the study area. At the study sites, soil depth varied depending upon the proximity of bedrock or presence of accumulations of colluvium. Soils were very stony, average stone content in the upper 10 cm was around 65% by mass, often with a substantial quantity of boulders. Soil texture was variable, ranging from sandy loam and silt loam to clay loam, but the soil was freely drained in all situations. Profiles under forest were marked by dark, humic A horizons, but after cultivation the topsoils apparently lose organic matter (OM) and display a noticeable reddish-brown hue.

Mineralogical examination reveals the presence of minerals that could be derived from mafic material (epidotes, chlorites and amphiboles), as well as from shale (quartz and hydrous mica), and in consequence the soil mineralogy is largely consistent with the underlying geology (D.A. Jenkins, personal communication). Cambisols are regarded as comparatively 'young' soils, in that weathering of rocks and minerals is active. However, in addition to minerals associated with fresh, unweathered sources, concentrations of other minerals are more indicative of intensive weathering. Most notably the latter includes resistant iron ore minerals (magnetite and ilmenite) and also a smectitic component to the clay mineralogy. The origins of these minerals may be through incorporation of highly-weathered soil material from an earlier, much more extensive and flatter land surface that has been eroded. Some evidence of this earlier surface remains in the vicinity of the study as small areas of deep, highly-weathered soils (Nitosols) capping some of the lower altitude interfluves. Erosion of this earlier land surface into the present highly-dissected form would inevitably have resulted in a mix of both highly-weathered and fresher material occurring within the Cambisols on the slopes.

Average annual rainfall recorded by Shreve (1914) over 39 years at 1525 m above sea level was 2685 mm; however, the annual total was variable between years ranging from 1510 to 4575 mm. Subsequently, between 1921 and 1950, mean annual rainfall at this Cinchona station was 2230 mm (Tanner, 1980b). In most years, there is a clear but variable seasonality in rainfall with the major wet period usually occurring around October and November (October mean monthly total at Cinchona was 455 mm) and a minor wet period in May (mean monthly total was 271 mm); February and July have the lowest mean monthly rainfalls (102 and 97 mm, respectively) (Shreve, 1914). Shreve (1914) also recorded mean annual rainfall at a station 1705 m above sea level, which was 2890 mm. Monthly mean temperature at 1525 m ranged from 14.6 to 17.6°C; monthly absolute maxima ranged from 21.3 to 24.4°C compared to 18.7–25.3°C at 1705 m. The ranges of monthly minima were 9.6–13.5 and 7.8–12.9°C, respectively.

2.2. *Forest types, plot locations and dimensions*

In June and July 1992, four main plots were established in the Green River Valley between 1250 and 1310 m altitude in areas of secondary forest, cleared for agricultural cultivation most recently in the early 1970s for one cropping cycle (according to members of the local community) and subsequently abandoned because of declines in productivity. Following local practice, a number of the larger trees would have been retained during the period of agriculture, and they are clearly identifiable in the present forest. Before the 1970s, these forests had most probably been subject to at least one cycle of clearance for agriculture but had probably been allowed to regrow since ca. 1900.

The slope angle of the four main plots ranged from 26 to 31° between the plots and was constant within each of the plots (all the plots were in a mid-slope position and none of them occupied or included obvious convex zones of higher than average net erosion, or deposition zones of net sedimentation).

Each main plot was 10 m (across slope)$\times$20 m (down slope), with an inner assessment area of 8 m$\times$15 m. The plots were bounded on the upper border using galvanized steel barriers, and trenched on the lateral borders. All stems $\geq$2 cm diameter at breast height were identified and measured, and the density and basal area of each species calculated.

In the vicinity of the main secondary forest plots there was no remaining primary forest that could be used in a direct comparison. Therefore, in August and September 1992, subsidiary plots were established at three locations where primary and secondary forest did occur in close proximity. These were two locations at higher altitudes in the Green River catchment (mid-slope below Bellevue Peak at 1430 m altitude (the closest to the main plots) and just below the main ridge adjacent to Newhaven Gap and Sir John's Peak at 1590–1680 m altitude); and in one location in the adjacent Clyde River catchment (upper slope between Cinchona and Morce's Gap at 1300 m altitude) (Fig. 1). At each location, one 225 m^2 plot of 15 m$\times$15 m was located in an area of young secondary forest that had been disturbed within the last 30 years, and one in much older secondary or primary forest, which appeared to have suffered no significant disturbance within the last 150 years (hereafter referred to as primary). Each pair of plots was matched in aspect and slope angle, which were within the same range as the main plots. The disturbance histories of the forests concerned were determined by using a combination of local knowledge and observations of forest structure and composition. All stems $\geq$2 cm diameter at breast height were identified and measured, and the density and basal area of each species calculated.

2.3. *Nutrient cycling in secondary forest main plots*

2.3.1. *Rainfall and throughfall*

A data-logging rain gauge was established at each plot to record the amounts and intensities of rainfall over the measurement period. The sampling period commenced in September 1992 and concluded in September 1994.

Collectors to measure throughfall reaching the soil surface were placed in the plots. Five collectors each of 165 cm^2 surface area with sharp edges angled to 30° were located in each plot and were then emptied and randomly relocated on a fortnightly basis. Between September 1992 and September 1994, quantities were recorded and bulked samples collected on a per-plot basis each month for nutrient analysis. Samples were filtered through 0.45 μm filters within 24 h of collection and were stored with a 1% mercuric chloride preservative until analysis. They were analysed for dissolved K and Ca by sequential inductively-coupled optical emission spectrometry. Phosphate-P and total P were analysed using the molybdenum blue colorimetric method on an auto-analyser, in the case of total P after digestion using sulphuric acid and hydrogen peroxide (Allen, 1989). Nitrate-N was determined using automated liquid chromatography (Dionex model 2000). Ammonium-N was determined on an auto-analyser, using the indophenol-blue colorimetric method (Allen, 1989). Total N was calculated as the sum of nitrate-N and reduced forms of N (organic-N plus ammonium-N). The sum of these reduced forms was obtained using a sulphuric acid/hydrogen peroxide digestion followed by indophenol blue colorimetry on an auto-analyser (Allen, 1989). Dissolved organic carbon (DOC) was determined by auto-analyser, using UV-digestion and the phenolphthalein colorimetric method (Skalar Analytical, 1993). Blank samples were also analysed following the same procedure to ensure there was no contamination.

2.3.2. Surface runoff and eroded sediments

Soil sediment and water from runoff were collected with a modified type of Gerlach trough (Morgan, 1979). The collecting gutter was covered with a lid to prevent the direct entry of rainfall, and sediment and runoff were channelled from the gutter into covered collecting buckets. Three of these metre-long troughs were placed at the bottom end of the inner assessment area of each plot during June–July 1992. Samples were collected on a fortnightly basis from September 1992 to September 1994. The total amount of runoff water collected was measured in the field and a subsample removed for chemical analyses carried out as for throughfall (Section 2.3.1). The total mass of sediment eroded was recorded, collected, oven-dried, and the entire sample separated into three fractions: litter was separated by hand, and coarse (>2 mm) and fine (<2 mm) mineral fractions were separated by sieving. All mineral fractions were weighed, the fine mineral and litter fractions retained for analysis, and the gravel fraction (>2 mm) discarded (on the assumption that the elements in this fraction are much less available for plant uptake than those in the other two fractions). The litter fraction was analysed for total N and P using a sulphuric acid/hydrogen peroxide digestion (Allen, 1989).

The <2 mm fraction of eroded sediments was also analysed for total N and P using the same procedure, and also pH, percentage silt, sand and clay, exchangeable Ca, Mg, K and Na, loss-on-ignition and available-P by:

- particle size analysis — hydrometer method (Anderson and Ingram, 1993),
- loss-on ignition (OM content) — ignition at 550°C for 2 h (Allen, 1989),
- pH — in a 1:2.5 weight:volume soil:deionised water suspension after 30 min,
- exchangeable Ca, Mg, K and Na — ammonium acetate extraction at pH 7 (Anderson and Ingram, 1993), but varying the method by shaking the soil/extractant for 1 h on an orbital shaker, rather than using leaching columns,
- available-P — sodium bicarbonate extraction, 0.5 M, pH 8.5 (Anderson and Ingram, 1993).

The analyses of OM, total N and total P were carried out at the Institute of Terrestrial Ecology (ITE) Merlewood Research station and the remaining analyses at the ITE Bangor Research Unit. In both cases, the integrity of results supplied by the laboratories was checked by the analysis of certified reference samples (if available), alongside laboratory reference samples, and in the case of total N and P the Merlewood laboratory also regularly participates in the International Soil Exchange and the International Plant Exchange quarterly inter-laboratory comparison schemes, organised by Wageningen Agricultural University. The results of all the chemical analyses are expressed on an air-dry basis.

2.3.3. Soil physical and chemical characteristics

Three composite soil samples were collected from each plot in June 1992 and October 1993. Surface litter was removed before coring. The samples were composites of five randomly-located individual samples taken to a depth of 10 cm with a soil corer of volume 785 cm^3. Analyses were carried out as for the eroded sediments described in Section 2.3.2, plus:

- moisture content — oven-drying for 24 h at 105°C,
- bulk density — soil cores of known volume collected and bulk density calculated from dry mass/volume,
- exchangeable acidity (Al plus H) — unbuffered potassium chloride extraction (Anderson and Ingram, 1993), but varying the method by shaking the soil/extractant for 1 h on an orbital shaker, rather than using a beaker. Also, the titration step was undertaken on an automatic titrator,
- cation exchange capacity — calculated as the 'effective' CEC, which is the sum of the exchangeable bases (Ca, Mg, K and Na) plus exchangeable acidity,
- base saturation — calculated as the percentage of the CEC occupied by the exchangeable base cations.

The results of all the chemical analyses were expressed on an air-dry weight basis.

2.3.4. N-mineralisation rates

Six soil cores were collected from each plot from the surface 10 cm soil depth in September 1994, using a corer of 10 cm diameter. Half of the cores from each plot were bulked by plot, and 10 g (wet soil) sub-samples extracted for inorganic-N measurement by shaking for 1 h in 100 ml of 1 M potassium chloride, and filtering through potassium chloride pre-washed Whatman No. 44 filter papers. Inorganic-N concentrations were corrected to a per-gram dry-weight basis. The remaining cores were enclosed as intact cores in gas permeable plastic bags and inserted back into the holes from which they were taken. They were then removed after 30 days and extracted individually for inorganic-N measurement. Blank samples of potassium chloride were also analysed after the same procedure to ensure there was no contamination.

Extracts were analysed for nitrate-N and ammonium-N colorimetrically by auto-analyser using methods following Allen (1989). The difference between the final inorganic-N content and the inorganic-N content in the initial bulked sample is net mineralisation. Nitrate-N and ammonium-N contents of both sets of extracts were determined to assess rates of nitrification, as well as mineralisation.

2.3.5. Litterfall

Five litter traps each of 0.15 m^2 were placed randomly in each of the four main secondary forest plots. These were emptied and randomly replaced in the plots on a monthly basis. The contents of fine litter (foliar and reproductive material and woody material <2 cm diameter) were dried and weighed after separating the woody material from the foliar and reproductive material. The samples were bulked by a 3-month increment and analysed for N and P concentrations using a sulphuric acid/hydrogen peroxide digestion (Allen, 1989) and nutrient contents determined by multiplying concentrations and amounts of litterfall. The standing crop of fine litter was determined in September 1993 and September 1994 by harvesting all above-ground fine litter in five randomly-positioned 1 m^2-quadrats in each plot. The contents of fine litter were dried and weighed after separating the woody material from the foliar and reproductive material, and the biomass of both fractions determined.

2.4. Comparison of nutrient cycling in primary and secondary forests

2.4.1. Litterfall

Ten litter traps each of 0.15 m^2 were placed randomly in each of the six subsidiary plots in September 1992 and litterfall was measured over the following 16 months. The traps were emptied and randomly replaced in the plots on four occasions in January, May and October of 1993 and February 1994. The contents of fine litter were dried and weighed after separating the woody material from the foliar and reproductive material. The standing crop of fine litter was determined in February 1994, by harvesting all above-ground fine litter in five randomly-positioned 0.25 m^2-quadrats in each plot. This was oven-dried, and the fine woody material was separated from the foliar and reproductive material and biomass determined.

2.4.2. Bioassay of nutrient availability

In April 1993, one bulked soil sample was collected as a composite of five randomly-located individual samples taken to a depth of 10 cm with a soil corer of volume 785 cm^3 from each of the six subsidiary plots. This was passed through a 2 mm sieve and transported to Cinchona Botanic Garden at 1525 m altitude and 2 km south of the plots. Soils were mixed with acid-washed sand in the ratio 2:1 soil:sand to improve drainage; 500 ml pots were filled with the mixture. Wildings of three tree species (*Acacia mearnsii*, *Pittosporum undulatum* and *Clethra occidentalis*) were collected from hill-slopes around Cinchona. These plants were selected for uniformity of health and vigour and were approximately 10 cm in height. One plant of each species was planted into each of 10 pots filled with soil from each site, and the height and root collar diameter of each plant was recorded (using 0.1 mm-accuracy callipers). The pots were placed randomly on benches under 50% shade cloth, and regularly watered until the end of the monitoring period 90 days after planting. At this time, height and root collar diameter were recorded and their increments over the 90-day period calculated.

2.5. Statistical analysis

The data sets from the primary/secondary comparisons were subjected to one-way analysis of variance using the statistical package SPSS/PC+V.2 (1988). Data were $\log_{10}$-transformed and significant differences expressed to $P<0.05$.

3. Results

3.1. Forest type

As expected from their southern-slope location, our 10 sample plots correspond most closely to the Dry Slope Forest type of Grubb and Tanner (1976), though they also contained elements of the moister Wet Slope Forest and Gully Forest types. This was indicated by their species composition which was clearly dominated by between five and 11 species classified as having a Dry Slope Forest or broad-ranging distribution by Grubb and Tanner (1976) (Table 1). Confirmation was obtained by P. Bellingham (personal communication) who carried out a DECORANA detrended correspondence analysis ordination and TWINSPAN two-way indicator species analysis classification of our 10 plots together with 23 other existing forest sample plots established in this area of the Blue Mountains by P. Bellingham, E. Tanner and J. Healey. No major difference was found in the regeneration types of the species present between our secondary forest plots (Table 1) and the primary forest plots of Tanner (1977a) and Goodland et al. (1998). This is expected because the high frequency of natural hurricane and landslide disturbance in the area maintains a high abundance of light-demanding species in the primary forests (Dalling, 1994; Bellingham et al., 1995). Nonetheless, our main secondary forest plots contained a lower proportion of shade-tolerant species than the flora reported for Dry Slope Forests as a whole (Grubb and Tanner, 1976; Goodland et al., 1998).

The mean density of stems $\geq$2 cm dbh in the four main secondary forest plots was 7813 stems ha^{-1} but was much lower in the three subsidiary secondary forest plots (3808 stems ha^{-1}) and lower still in the three subsidiary primary forest plots (2800 stems ha^{-1}) (Table 1). There was a corresponding increase in tree basal area with successional age from a mean of 30 m^2 ha^{-1} in the main secondary forest plots to 32.5 m^2 ha^{-1} in the subsidiary secondary forest plots (and 37.1 m^2 ha^{-1} in the subsidiary primary forest plots) (Table 1). Thus, the tree basal area of the main secondary forest plots has already recovered to 81% of that in the subsidiary primary plots, though this could largely be attributed to the abundance of the exotic invasive tree species *P. undulatum* (Table 1) which is, in itself, an important indicator of their secondary status. This species is known to competitively exclude some native pioneer species, and cast a dense shade which would favour shade-tolerant species over more light-demanding competitors (Healey et al., 1995), a factor that may accelerate the successional development of the forest's species composition (whilst limiting total species richness).

3.2. Nutrient cycling in the secondary forest main plots

3.2.1. Soil physical and chemical characteristics

The soil had no distinct surface humus layer, and pH (5.25 (Year 1), 4.93 (Year 2)), base saturation and

Table 1
Species composition, basal area ($m^2\ ha^{-1}$) and density (stems ha^{-1}) of stems >2 cm diameter at breast height in the main and subsidiary plots[a]

Species	Distribution (Grubb and Tanner, 1976)	Regeneration type (Goodland et al., 1998)	Main secondary forest plots		Subsidiary secondary forest plots		Subsidiary primary forest plots	
			Basal area	Density	Basal area	Density	Basal area	Density
Acalypha virgata L. var. *Virgata*	NR	SGB	0	0	0.4	44	1.2	74
Alchornea latifolia Sw.	DS	NP	1.7	250	0	0	0	0
Bocconia frutescens L.	DS	P	0.1	146	0	0	0	0
Boehmeria caudata Sw.	G	P-NP	0.2	396	0	0	0	0
Brunellia comocladiifolia Humb. & Bonpl.	DS	P	0	0	0	0	0.3	15
Cestrum hirtum Sw.	WS/G	Unknown	0.2	63	0	0	0.2	74
Cinchona officinalis L.	NR	P-GB	1.3	708	0	0	0	0
Citharexylum caudatum L.	NR	SGB	0.6	250	0	15	0.1	30
Clethra alexandri Griseb.	HA	NP	0	0	0	0	5.2	207
Clethra occidentalis (L.) Kuntze	DS	NP	3.8	771	3.9	444	4.2	356
Clusia havetioides (Griseb.) Planch. & Triana	DS	ST	0.1	42	0	15	0	0
Critonia parviflora DC. 'montane'	DS	NP-SGB	0	0	0.2	30	0.1	89
Cyathea spp.	WD	Various	0	0	1.1	237	7.2	578
Cyrilla racemiflora L.	DS	SGP	2.6	333	2.0	44	0.5	30
Dendropanax arboreus (L.) Decne & Planch.	WS	GB	0	0	0.2	74	0.3	44
Eugenia marchiana Griseb.	WD	ST	0	0	0.1	30	0	0
Eugenia monticola (Sw.) DC var. *Monticola*	WD	ST	2.7	1313	2.0	148	1.0	148
Eugenia virgultosa (Sw.)	WD	ST	0.1	146	1.4	252	0.4	119
Gordonia heamatoxylon Swartz.	WD	SGB-GB	0	0	0.1	15	0.6	74
Guarea glabra Vahl	WD	ST	0	0	0	0	0.6	59
Hedyosmum arborescens Sw.	WD	SGB	0	0	0	0	0.1	30
Ilex macfadyenii (Walp.) Rehder	DS	SGB	5.8	1083	2.6	385	1.1	148
Juniperus lucayana Britton	DS	NP	0.2	21	5.6	15	0	0
Lyonia jamaicensis (Sw.) D. Don	DS	SGP	0.1	42	0.4	44	0	0
Maytenus jamaicensis Krug & Urban	MR/WS	ST	0	0	0.1	44	1.2	59
Miconia quadrangularis (Sw.) Naud. var. *Quadrangularis*	DS	NP	0.1	63	0	0	0	0

Miconia spp.	DS	Various	0	0	0	0	0	15
Myrsine coriacea (Sw.) R. Br. ex Roem. & Schult.	DS	SGB	0	0	0.1	59	0.1	15
Ocotea patens (Sw.) Nees	WS	GB-ST	0	0	0.5	89	0.4	44
Palicourea alpina (Sw.) DC.	DS	NP	0.5	63	0	0	0.5	59
Pittosporum undulatum Vent.	NR	SGB-GB	8.3	1542	2.0	1215	0.2	104
Podocarpus urbanii Pilger	DS	GB	0	0	1.1	30	0	0
Psychotria corymbosa Sw.	DS	SGB	0.2	146	0.1	74	0	15
Psychotria sloanei Urban	MR/WS	GB	0	0	0.1	15	0	0
Schefflera sciadophyllum (Sw.) Harms	WD	HE	0	0	1.2	89	0	0
Turpinia occidentalis (Sw.) G. Don	WD	SGB	0	0	5.4	89	5.5	89
Unknown			0	0	0	0	1.6	15
Vaccinium meridionale (Sw.)	DS	SGP	1.0	208	1.9	267	4.4	252
Viburnum spp.	DS	NP-GB	0	21	0.1	30	0	15
Wallenia calyptrata Urban	DS	ST	0.4	208	0	15	0.2	44
Total			29.9	7813	32.5	3808	37.1	2800
Between-plot standard errors			5.8	1023	5.5	738	7.9	413

[a] DS: Present in Dry Slope Forest (other species were not recorded as present in Dry Slope Forest); WD: wide distribution (in at least three other forest types); MR/WS: Mull Ridge and Wet Slope Forests; WS/G: Wet Slope and Gully Forests; WS: Wet Slope Forest; G: Gully Forest; HA: High Altitude Forests; NR: not recorded; P: pioneer; SGP: slow-growing pioneer; NP: near-pioneer; SGB: strongly gap-benefiting; GB: gap-benefiting; ST: shade-tolerant; HE: hemi-epiphyte.

Table 2
Soil, 0–10 cm depth, in the main secondary forest plots (n=4)

	Year 1			Year 2	
	Mean	S.E.		Mean	S.E.
Chemical and physical characteristics					
pH	5.25	0.08		4.93	0.09
Exchangeable-Ca (cmol kg^{-1})	11.78	1.10		11.63	0.35
Exchangeable Mg (cmol kg^{-1})	3.22	1.33		2.16	0.33
Exchan'geable-K (cmol kg^{-1})	0.80	0.13		0.67	0.16
Exchangeable Na (cmol kg^{-1})	0.38	0.01		0.17	0.02
Total OM[a] (g kg^{-1})	210.83	18.48		228.46	16.96
Total P (g kg^{-1})	1.53	0.42		1.43	0.19
Available-P (g kg^{-1})	0.11	0.02		0.10	0.01
Total N (g kg^{-1})	6.83	0.61		6.46	0.59
Nitrate-N increase (g kg^{-1} 30 per day)	0.016	0.004	(1994 only)		
Total N mineralised (g kg^{-1} 30 per day)	0.014	0.006	(1994 only)		
Exchangeable acidity (cmol kg^{-1})	0.41	0.08	(1992 only)		
Cation exchange capacity (cmol kg^{-1})	16.89	2.23	(1992 only)		
Base saturation (%)	97.57	0.30	(1992 only)		
Moisture content (%)	19.94	4.15		12.47	2.38
Bulk density (Mg m^{-3})	0.85	0.09		0.80	0.03
% sand (>60 μm)	42.30	12.95	(1992 only)		
% silt (2–60 μm)	31.63	6.85	(1992 only)		
% clay (<2 μm)	26.07	6.75	(1992 only)		
Nutrient content (kg ha^{-1}) and N-mineralisation rate (kg ha^{-1} 30 per day)					
Exchangeable Ca	4027.4	573.9		3585.1	133.8
Exchangeable Mg	617.2	197.5		422.1	68.8
Exchangeable K	278.8	67.2		208.0	45.6
Exchangeable Na	73.1	7.0		30.9	2.0
Total OM[a]	177233.3	17794.3		182669.4	11766.2
Total P	1403.0	481.5		1143.8	153.9
Available P	92.7	17.9		84.6	11.9
Total N	5924.7	1061.2		5187.0	493.8
Nitrate-N increase (30 days)	12.4	3.5	(1994 only)		
Total N mineralised (30 days)	11.5	4.5	(1994 only)		

[a] Organic matter.

exchangeable-Ca concentrations (Table 2) were all much higher than in the soils studied by Tanner (1977a), as expected for forests growing on more calcareous substrate and at a lower altitude. Total OM concentration, CEC and moisture content were lower than for Tanner's soils. Values for all the other comparable variables (total N and exchangeable Mg, K and Na) lay within the range of Tanner's four forest types. Dalling and Tanner (1995) measured soil bicarbonate extractable-P concentration in soil of 0–10 cm depth from five slope forests (four primary and one secondary) between 1460 and 1700 m altitude in the Blue Mountains as 21.4($\pm$4.0) μg g^{-1} in the forests and 4.8($\pm$2.1) μg g^{-1} on adjacent landslides. Our results fall in the middle of this range at 10.9 and 10.0($\pm$2.1 and 1.4) μg g^{-1}). In a less precise determination of soil characteristics from a wider sampling area in the Blue Mountains, Grubb and Tanner (1976) reported that the younger 'lithosols' of the slope forests had a pH range of mostly 4.0–5.5, a range that encompasses the pH values we obtained.

3.2.2. *Rainfall and throughfall*

Total annual rainfall was very similar between the 2 years of the study (2548 mm, 14 September 1992–13 September 1993 versus 2530 mm, 14 September 1993–13 September 1994), lying very close to the centre of the range of past values from the nearby

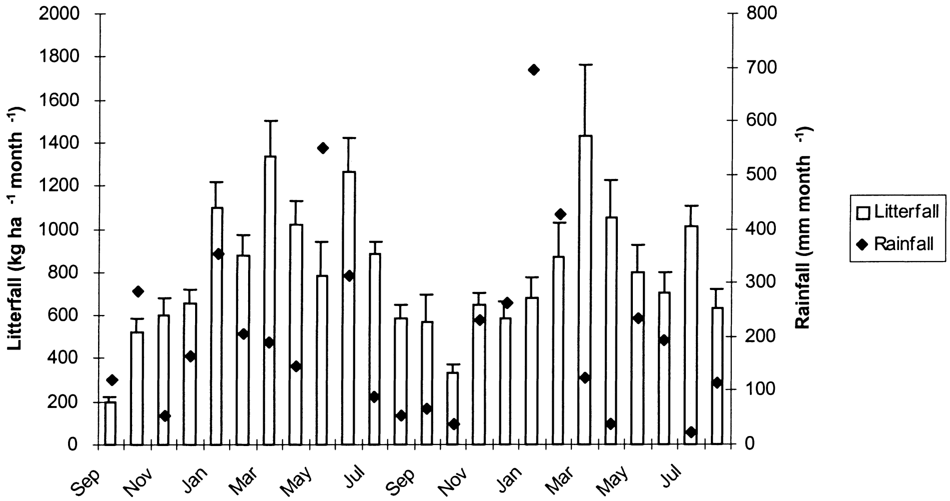

Fig. 2. Seasonal distribution of rainfall and litterfall (means and standard errors, n=4) in the main secondary forest plots from September 1992 to August 1994.

Cinchona meteorological station (Shreve, 1914; Tanner, 1980b). There were, however, notable differences between the years in the seasonal pattern of rainfall. In the first year, the wettest month was May (with 22% of annual rainfall), then January, June and October had distinctly higher than average monthly rainfall, whereas in the second year, January was the wettest month (with 27% of annual rainfall) and February was the only other month with a distinctly high rainfall (Fig. 2). Conversely, in the first year, the highest intensity of rainfall of 190 mm h^{-1} was recorded on 26th January 1993, whereas the highest intensity of rainfall in the second year (330 mm h^{-1}) was recorded on 20th May 1994. During the 2 years, 7 months had less than 100 mm of rainfall; three of these were isolated single months, but there was one pronounced dry period of four consecutive months (the middle July–October). Only the month of July had less than 100 mm of rainfall in both years.

There was a strong correlation between the total amounts of rainfall and throughfall for each sampling period (r^2=0.92) (Fig. 3). Over the 2 years, rates of canopy interception of rainfall remained close to 50% (y=0.491x+2.864). The percentage interception did not decrease with increasing precipitation, probably because during major rainfall events (which would have dominated the higher fortnightly rainfall values) at first there was canopy storage and then stemflow continuously increased as a proportion of precipitation. We noted very high stem flow rates on trees in these forests during large rainfall events. Nutrient contents in throughfall differed between the years (Table 3). DOC was 135% greater in the second than the first year, and nitrate-N was 90% greater but all other throughfall nutrient contents were between 10 and 57% greater in the first year than the second.

3.2.3. Surface runoff and eroded sediments

When expressed as a proportion of rainfall the amount of surface runoff of water was very low (Table 4), suggesting that high water storage capacity

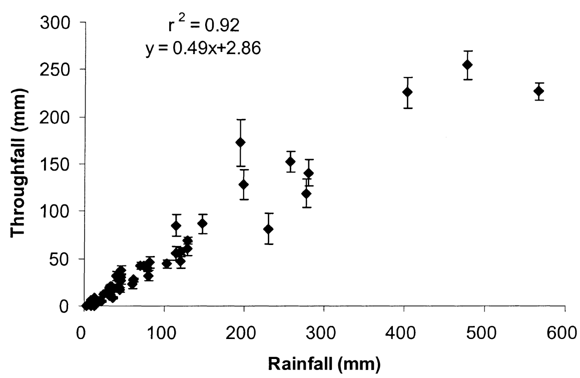

Fig. 3. The relationship between the total amount of rainfall and throughfall in the main secondary forest plots (mean values, n=4, plus or minus standard error) for each fortnightly sampling period between September 1992 and September 1994.

Table 3
Nutrient contents (kg ha^{-1} per year) in throughfall in the main secondary forest plots (n=4)

	Year 1		Year 2	
	Mean	S.E.	Mean	S.E.
Ca	22.72	1.05	20.38	3.19
K	72.86	6.48	62.37	2.70
DOC[a]	150.91	9.68	356.11	15.07
Total P	4.75	0.64	3.68	0.20
Phosphate-P	3.57	0.58	2.84	0.16
Total N	11.52	0.72	10.47	0.58
Nitrate-N	1.56	0.17	2.98	0.27
Ammonium-N	5.87	0.35	3.74	0.17

[a] Dissolved organic carbon.

Table 5
Nutrient content of runoff water (kg ha^{-1} per year) from the main secondary forest plots (n=4)

	Year 1		Year 2	
	Mean	S.E.	Mean	S.E.
Ca	0.37	0.09	0.33	0.07
K	1.04	0.21	0.65	0.14
DOC[a]	0.82	0.18	1.24	0.23
Total P	0.03	0.01	0.03	0.01
Phosphate-P	0.04	0.01	0.03	0.01
Total N	0.18	0.03	0.12	0.03
Nitrate-N	0.02	0.01	0.02	0.01
Ammonium-N	0.10	0.02	0.05	0.01

[a] Dissolved organic carbon.

of the forest and excellent drainage would buffer the system against peaks in rainfall amount and intensity.

Due to the small amounts of surface runoff, nutrient losses in runoff water were low (Table 5), especially when considered as a proportion of nutrient inputs and recycling in throughfall (inputs from atmospheric deposition and recycling by foliar leaching) (Table 3). The highest was loss of K in runoff, which was a little over 1% of the amount in throughfall in Year 1. Losses of nutrients in eroded sediments (particles <2 mm) were also low for the same reasons (Table 6). The eroded sediments were dominated by mineral particles >2 mm and by litter (Table 4). Similarly, the analysed mineral fraction (<2 mm) was dominated by the largest sized particles — the sand fraction (>60 μm).

Over the 2 years, rates of loss of total P and N in the eroded sediment (<2 mm) were just 35% higher than those dissolved in runoff water, whereas losses of Ca and especially K were much lower in the eroded sediment than the runoff water. Relative to the nutrient content of the top 10 cm of soil (Table 2), nutrient losses in runoff and eroded sediment were very small. For total P 0.018% was lost per year, whereas there was twice the rate of loss of total N (0.038%). Losses of cations were not measured in the litter fraction of the eroded sediment, however, losses in runoff and the <2 mm mineral fraction of the eroded sediment were just 0.013% of the nutrient capital in the top 10 cm of soil for exchangeable Ca, but higher for the more soluble exchangeable-K (0.36%).

Table 4
Quantity of surface runoff from 120 m^2 in the main secondary forest plots (n=4)

	Year 1		Year 2	
	Mean	S.E.	Mean	S.E.
Runoff (mm)	3.08	0.58	2.72	0.56
Runoff (% of rainfall)	0.12	0.02	0.11	0.02

3.2.4. N-mineralisation rates

Net mineralisation of total N over 30 days in the top 10 cm of soil was 11.53 kg ha^{-1} (Table 2). This is equivalent to 173% of the amount of N in fine litterfall over the same period (Table 8) and is equivalent to just 0.21% of the standing stock of total N in the top 10 cm of soil. The rate of conversion to nitrate-N over 30 days (12.44 kg ha^{-1}) was very similar to that of total N.

3.2.5. Litterfall inputs

Total annual inputs of fine litter were nearly the same in the 2 years (9530 and 9107 kg ha^{-1} per year, respectively (Table 7)) as was the proportion composed of small woody material (10%). The seasonal distribution of fine litterfall showed the highest rates during the period January–July (Year 1) and March–July (Year 2), with low rates in August–December (both years) (Fig. 2). There was no obvious correlation between each month's fine litterfall and rainfall. However, the highest rates of litterfall did occur during and following the second half of the driest period of the year.

The standing crop of fine litter (mean of 5348 kg ha^{-1}) showed little variation between the

Table 6
Eroded sediments (litter, and <2 mm and >2 mm mineral fractions) from the main secondary forest plots (n=4)

	Year 1		Year 2	
	Mean	S.E.	Mean	S.E.
Dry mass of each fraction (kg ha^{-1} per year)				
Litter	235.55	41.19	204.25	42.17
Mineral soil <2 mm	44.09	15.99	21.94	15.94
Mineral soil >2 mm	328.43	182.14	247.74	140.75
N and P concentration and content of the litter fraction				
Total P (g kg^{-1})	0.94	0.23	0.88	0.21
Total N (g kg^{-1})	8.23	0.62	8.43	0.44
Total P (kg ha^{-1} per year)	0.18	0.04	0.14	0.02
Total N (kg ha^{-1} per year)	1.88	0.51	1.64	0.51
Chemical and physical characteristics of the <2 mm mineral fraction				
Exchangeable-Ca (cmol kg^{-1})	13.14	1.92	9.59	0, n=1
Exchangeable Mg (cmol kg^{-1})	2.86	0.66	2.00	0, n=1
Exchangeable-K (cmol kg^{-1})	1.87	0.46	1.90	0, n=1
Exchangeable Na (cmol kg^{-1})	0.95	0.32	0.30	0, n=1
Total OM[a] (g kg^{-1})	272.50	59.22	210.00	0, n=1
Total P (g kg^{-1})	1.10	0.17	0.90	0, n=1
Available-P (g kg^{-1})	0.19	0.03	0.10	0, n=1
Total N (g kg^{-1})	6.58	1.21	4.10	0, n=1
% sand (>60 μm)	67.50	4.24	68.00	0, n=1
% silt (2–60 μm)	20.25	3.89	20.00	0, n=1
% clay (<2 μm)	12.25	0.35	12.00	0, n=1
Nutrient content (kg ha^{-1} per year) of the <2 mm mineral fraction				
Exchangeable Ca	0.24	0.01	0.08	0, n=1
Exchangeable Mg	0.04	0	0.01	0, n=1
Exchangeable K	0.03	0	0.01	0, n=1
Exchangeable Na	0.01	0	0	0, n=1
Total OM[a]	12.01	0.95	4.61	0, n=1
Total P	0.06	0	0.02	0, n=1
Available-P	0	0	0	0, n=1
Total N	0.32	0.02	0.09	0, n=1

[a] Organic matter.

Table 7
Fine litterfall mass (kg ha^{-1} per year)

	Year 1		Year 2	
	Mean	S.E.	Mean	S.E.
Main secondary forest plots (n=4)				
Leaves	8553.2	760.8	8213.5	855.5
Wood	977.0	235.5	893.8	475.0
Subsidiary primary forest plots (n=3)				
Leaves	7422.2	851.6		
Wood	2031.6	736.2		
Subsidiary secondary forest plots (n=3)				
Leaves	6017.1	701.0		
Wood	1200.6	377.2		

years (Table 9). The annual amount of fine litterfall (Table 7) was equivalent to 174% of the standing crop, whereas the loss of litter down-slope by erosion (Table 6) was equivalent to just 4% of the standing crop.

The amounts and concentrations of N and P in the fine litterfall were very constant between the 2 years (Table 8). Relative to the contents in the top 10 cm of soil (Table 2) the amount of N in the fine litterfall per hectare per annum was 1.4% in Year 1 and 1.5% in Year 2, and the amount of P was 8.2% of the available-P in Year 1 and 9.3% in Year 2 (0.5 and 0.7% of total soil P, respectively). Relative to the total loss of N and P in eroded sediment and dissolved in runoff

Table 8
Nutrient concentrations and contents in fine litterfall (foliar and reproductive material and woody material <2 cm diameter) in the main secondary forest plots (n=4)

	Year 1		Year 2	
	Mean	S.E.	Mean	S.E.
N (g kg^{-1})	9.30	1.44	9.57	0.99
P (g kg^{-1})	0.89	0.24	0.94	0.24
N (kg ha^{-1} per year)	81.90	11.65	79.75	9.84
P (kg ha^{-1} per year)	7.61	1.18	7.84	1.22

Table 9
Standing crop of fine litter (kg ha^{-1})

	Year 1		Year 2	
	Mean	S.E.	Mean	S.E.
Main secondary forest plots (n=4)				
Leaves	4180.7	446.7	4047.6	558.3
Wood	1264.7	94.3	1203.7	157.7
Subsidiary primary forest plots (n=3)				
Leaves	3455.8	113.4		
Wood	867.8	277.3		
Subsidiary secondary forest plots (n=3)				
Leaves	2194.4	81.7		
Wood	538.6	157.2		

(Tables 5 and 6), recycling of N in the fine litterfall was 3441% in Year 1 and 4311% in Year 2 and recycling of P was 2819 and 4126%, respectively.

3.3. Comparison of nutrient cycling in the subsidiary primary and secondary forest plots

3.3.1. Litterfall

The amounts of both the leaf and wood components of fine litterfall were consistently higher in the subsidiary primary forest plots than in the subsidiary secondary forest plots over the course of the year (Fig. 4). Mean annual totals of fine litterfall were 9500 kg ha^{-1} in the primary forest plots and 7000 kg ha^{-1} in the secondary forest plots; the leaf litterfall components of these were 7400 kg ha^{-1} (78%) and 6000 kg ha^{-1} (86%), respectively. The total fine litterfall from the subsidiary primary forest plots was very similar to that obtained in the main secondary forest plots, which were at a lower altitude (Table 7). Litterfall in the subsidiary secondary forest plots were less than those in the main plots. There was no evidence of any association between the seasonal distribution of litterfall in the subsidiary plots and rainfall (Fig. 4).

The difference in litterfall amounts between the primary and secondary forest plots was reflected in the standing crop of fine litter. Both the leaf and small woody components were 60% higher in the primary forest (Table 9). Litter standing crop in the subsidiary primary forest plots was slightly less than that in the

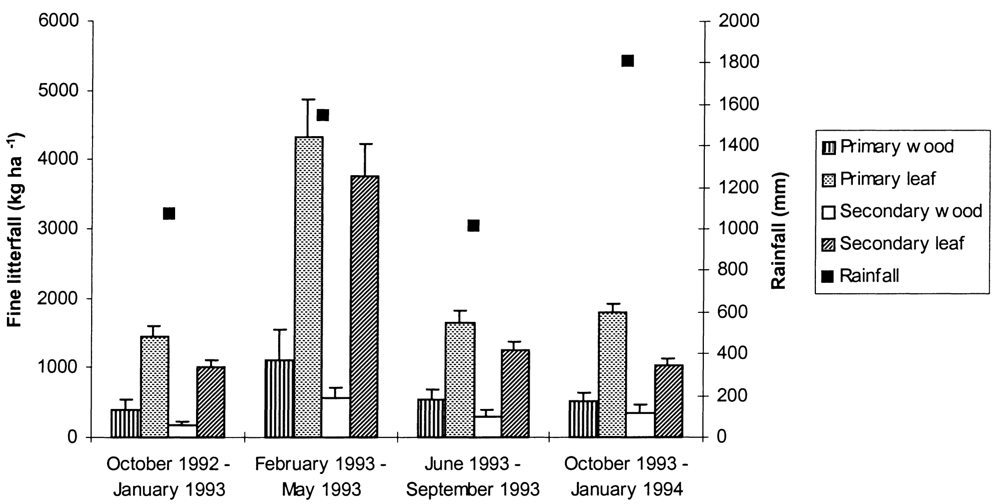

Fig. 4. Fine litterfall (foliar and reproductive material (indicated as 'leaf') and woody material <2 cm diameter (indicated as 'wood')) in the subsidiary primary and secondary forest plots (means and standard errors, n=3) in 4-month periods and total rainfall during the same periods.

Table 10
Root collar diameter (mm) and height (mm) increment over 90 days of bioassay plants of three tree species growing in soil from the subsidiary primary and secondary forest plots (means and standard errors, n=3)

	Height increment		Root collar diameter increment	
	Mean	S.E.	Mean	S.E.
Primary forest				
Clethra occidentalis	54.06	7.43	1.07	0.18
Acacia mearnsii	118.70	11.32	1.36	0.13
Pittosporum undulatum	46.23	7.92	0.89	0.13
Secondary forest				
Clethra occidentalis	49.70	13.52	0.82	0.17
Acacia mearnsii	125.00	14.04	1.67	0.16
Pittosporum undulatum	33.15	8.18	0.84	0.16

main secondary forest plots (values for leaf litter were closer than for small wood).

3.3.2. Bioassay of nutrient availability

There were no significant differences (P<0.05) in either root collar diameter or height increment for any of the three test species between the plants grown in soil from the subsidiary primary and from the secondary forest plots (Table 10). There were, however, differences between species, with *A. mearnsii* having much greater increments of both height and root collar diameter than either *P. undulatum* or *C. occidentalis* (P<0.05).

4. Discussion

4.1. Nutrient conservation by secondary forests

Rates of canopy rainfall interception were very high compared to other studies — throughfall was only 50%, whereas values for montane forests usually average 81% of incident rainfall (Bruijnzeel, 1990). However, recent rainfall interception studies in tropical montane cloud forests have produced lower throughfall values than this average (62–65%), even with significant cloud water inputs (Cavelier et al., 1996, 1997; Clark et al., 1998). Furthermore, Hafkenscheid et al. (1998) and Hafkenscheid (2000) observed throughfall levels of 59.5–73% in ridge top forest at 1825 m in the Blue Mountains. They also encountered a very high ratio of stem flow to precipitation (13–18.3%) which they attributed to a high proportion of leaning and multi-stemmed trees. Most montane forest tree species lack drip tips on their leaves, and many have a dominance of upwardly-growing (orthotropic) rather than horizontal (plagiotropic) branches in their canopies (in contrast to many lowland forest tree species); both factors are likely to contribute to a higher ratio of stemflow to throughfall in montane than in lowland forests. However, the high epiphyte loads of tropical montane trees (e.g. species of Bromeliaceae in Jamaica) are also likely to lead to high rates of retention of precipitation in the canopy. Whether interception is due to retention of water above ground on the leaf surfaces, bark and epiphytes (followed by its evaporation) or due to stemflow (taking water that has flowed over a long length of plant surface to one point on the ground) may have major implications for nutrient conservation as the latter has a far greater potential to cause nutrient losses through leaching, runoff (and associated erosion). There is no direct evidence of the mechanism leading to the high levels of interception found in the secondary forests of our study. However, these forests were on steep hill-slopes and contained a high proportion of multi-stemmed trees, and we observed high rates of stem flow. Therefore this is likely to have been a major mechanism.

Nutrient contents in throughfall water (Table 3) were generally in the range reported in three studies of tropical montane forests reviewed by Parker (1983) and Vitousek and Sanford (1986), e.g. 8–30 kg ha^{-1} per year for N, 7–21 kg ha^{-1}per year for Ca and 70–74 kg ha^{-1}per year for K, though our values for total P (3.68 and 4.75 kg ha^{-1}per year) were above the values in the two previous studies (1.4 and 2.5 kg ha^{-1}per year). These annual throughfall nutrient amounts were generally high in comparison with the standing-stock of nutrients measured in the live leaves of well-developed Mull Ridge forest at 1530 m altitude in the Blue Mountains by Tanner (1985): 113% for K; 100% for total P; 37% for Ca; 12% for total N.

Nutrient losses in runoff and erosion were, however, very low (less than 0.04% of the stocks in the top 10 cm of soil for all measured nutrients except for K, which was 0.4%). Nutrient contents in throughfall water (Table 3) were much greater than those in runoff water (Table 5), ranging from 24,610% for DOC, to 14,050% for total P, 8002% for K, 7330% for total N (11,350% for nitrate-N and 6407% for ammonium-N) and 6157% for Ca. There is no information about what proportion of throughfall nutrients were absorbed in the soil or leached through the soil into ground water. The coarse texture of the soils means that there was the potential for significant leaching of nutrients down through the soil profile, but, even so, it is unlikely on these long hill-slopes that (averaging out zones of deposition due to topographic variation) total nutrient losses from secondary forests down-slope exceed inputs from up-slope. Furthermore, high leaching rates cannot be assumed because the high concentration of polyphenolic compounds in the leaf litter of montane forests is likely to lead to strong binding and low leaching losses of many mobile nutrients (Bruijnzeel et al., 1993). At this stage, no firm conclusions can be drawn about the significance of throughfall nutrient contents for overall nutrient conservation by these secondary forests. However, overall, there are strong indications that they have a high net conservation of nutrients and may well, in fact, be experiencing a net increase in total nutrient stocks, which is the expectation for secondary forests (Vitousek and Reiners, 1975).

Where low rates of soil erosion occur in secondary or plantation forests it is not possible, with certainty, to determine whether this is due to good conservation of the soil by the forest, or due to the loss of a high proportion of the erodible material during the period following the initial clearance of the forest when the soil surface was left exposed. Thus, Richardson (1982) attributed the seven-times lower rates of erosion that she recorded in a Jamaican pine plantation versus in adjacent lowland rainforest, of the type cleared to establish the plantation, to the cover of the soil surface by pine needles. However, an equally likely explanation is that significant erosion of the more erodible material occurred prior to the establishment of the plantation trees. Nonetheless, the soils of the secondary forests in our study contained a high proportion of fine erodible material (e.g. 26% clay, Table 2) and the annual rates of erosion recorded (e.g. 33 kg ha^{-1}per year of particles <2 mm, Table 6) represented a tiny proportion of the amount of potentially erodible material present in the surface soil (e.g. less than 0.2% of that present in the top 1 cm of soil). Therefore, despite the steep slopes and high rates of rainfall, these secondary forests are providing high levels of conservation of soil resources.

4.2. Comparison of nutrient cycling and soil fertility between secondary and primary forests

A wide range of tree stem basal areas have been reported from southern-slope forests in the Blue Mountains, from 56.2(±7.4) m^2 ha^{-1} (in Bellingham and Tanner (2000) plots in essentially primary forest just 250 m down from the main ridge crest) to 15.8(±0.8)m^2 ha^{-1} (in Goodland and Healey (1995) plots further down the slopes in secondary forest extensively invaded by the exotic tree species, *P. undulatum*). The basal area of all three sets of our plots lay towards the middle of this range, but there was a clear difference from the younger main secondary forest plots, 29.9(±5.8) m^2 ha^{-1}, to the subsidiary primary forest plots, 37.1(±7.9) m^2 ha^{-1}. Tanner (1977a) found that basal area was ca. 40% higher in ridge-top forests of more upper-montane character than slope and gully forests with more lower-montane affinities. However, Bellingham and Tanner (2000) found evidence that relative basal area increment between 1990 and 1994 was higher in five southern-slope forest plots (0.028(±0.004)) than in six ridge-top forest plots (0.022(±0.003)). Secondary sub-tropical forests in Puerto Rico recovering from cultivation showed a basal area of 7.2 m^2 ha^{-1} after 6 years, increasing to 28.5 m^2 ha^{-1} after 20 years and 22.8 m^2 ha^{-1} after 50 years (Lugo, 1992). Thus, the secondary forests of our study in Jamaica have shown a greater rate of recovery of basal area than these, and there is no evidence of any limitation to their eventual recovery back up to primary forest levels.

The mean litterfall production from our main secondary forest plots (9319 kg ha^{-1} per year) is very similar to that of 34 published studies of secondary forest litterfall (whose mean is 9200 kg ha^{-1}per year, Table 11). Brown and Lugo (1990) found that in secondary forests high rates of litter production are established relatively quickly: mean annual litterfall increased from 1-year-old to 7-year-old forests, and then showed no further increase up to at least 21 years (Table 11). Our values from ca. 20-year-old secondary forest fall in the lower half of Brown and Lugo (1990) range; and slightly below the average for mountain secondary forests (9800 kg ha^{-1}per year, Table 11). In mountain environments this mean litterfall rate of studies of secondary forests is, surprisingly, higher than that of apparently primary forests (7900 kg ha^{-1}per year); the same result has also been obtained in direct comparisons within the same study area (Table 11, Proctor, 1983; Vitousek and Sanford, 1986; Scott et al., 1992). The rates of fine litterfall in our main secondary forest plots were very similar to those in the primary forest plots (though rates in the subsidiary secondary forests were lower); a comparable result to that found by Zou et al. (1995) for lower montane forests in Puerto Rico (Table 11). However, the litterfall rates in our study were greater than those obtained by Tanner (1980b) and Hafkenscheid (2000) from six primary/old secondary forests on ridge-tops in the Jamaican Blue Mountains (Table 11). The proportion of fine litterfall comprising the leaf fraction was comparable between our study (90%) and the other two (74–97%).

The differences in the results obtained from the Jamaican Blue Mountains could be explained by altitude; our main secondary forest plots, at 1250–1310 m, were at least 244 m lower than those of Tanner (1980b) (1554–1620 m) and Hafkenscheid (2000) (1809 m). One block of our subsidiary plots was comparable in altitude to Tanner (1980b) but the other two were 150–300 m lower. This difference in altitude/topographic position was reflected in the significant differences in soil pH and associated variables (Section 3.2.1). Eight out of our 10 plots can be categorised as ‘lower montane tropical rain forests’ whereas three out of four of Tanner’s and both of Hafkenscheid’s are classified as ‘upper montane tropical rain forests’ (Tanner, 1977a; Hafkenscheid, 2000). Such differences in altitude have a major impact on litterfall rates: mean litterfall in non-secondary upper montane forests is substantially lower than that in lower montane forests (Table 11). However, for secondary forests surprisingly little difference has been found in mean litterfall rates between mountain and lowland environments (Table 11).

In comparing the different litterfall data sets from the Jamaican Blue Mountains a second factor that must be considered is the influence of weather before and during the period of observation, in particular the impact of hurricanes that cause extensive defoliation of the forests (Bellingham et al., 1992). Tanner (1980b) reported litterfall data from two separate periods: 1974–1975 and 1977–1978. The first period had 3115 mm of rainfall (40% more than the long-term average), which he attributed to two hurricanes which passed near to the island. Daily litterfall rates were markedly higher in the hurricane period, but they were then much lower than average in the subsequent 98-day wet period. 1977–1978, however, had 1745 mm of rainfall (22% lower than the long-term average). In contrast, the 2 years of our study (1992–1994) had very similar annual rainfall that was close to the long-term average, with no exceptional seasonal events.

Our results may, nonetheless, have been influenced by the longer-term effects of the catastrophic impact of Hurricane Gilbert in 1988, which might have led to increased litterfall in 1992–1994 while the forests were still recovering from the effects of defoliation, branch damage and an overall 8% mortality (Bellingham et al., 1992, 1995; Bellingham and Tanner, 2000). The eye of Hurricane Gilbert passed within 15 km of our study sites, and many patches of the montane forest were completely defoliated (Bellingham et al., 1992). Refoliation took about 28 months (Bellingham et al., 1995) which, because it was synchronized, may have resulted in synchronized litterfall for several years. Scatena et al. (1996) found that, in the Luquillo Mountains of Puerto Rico, in the first year following the impact of Hurricane Hugo, mean total annual litterfall was 2300 kg ha^{-1}per year; then, over the following 4 years, it increased steadily to 7300 kg ha^{-1}per year (but still below the pre-hurricane level of 8700 kg ha^{-1}per year). Similarly, Walker et al. (1996) in an independent study of changes in productivity in lower montane and upper montane forest in Puerto Rico following Hurricane Hugo, found

Table 11
Comparison of rates of litter production between different categories of tropical forest (kg ha^{-1} per year)

	Secondary forests			Non-secondary mountain forests[a]		
	Lowland[b]	Mountain[c]	Combined	Unspecified/ lower montane[d]	Upper montane, Jamaica[e]	Upper montane, global[f]
Small litterfall (number of studies)	26	9 (8)[g]	35 (34)[g]	20	2	11
Range	4500–13,200	7000–27000 (12500)[g]	4500–27000 (14300)[g]	2700–11100	5500–6600	3600–11000
Mean	9100	11700 (9800)[g]	9800 (9200)[g]	7900	6140	6200
Total litterfall, 1-year-old forests (range)[h]			1000–5000			
Total litterfall, 7-year-old forests (range)[i]			7000–13000			
Total litterfall (mean)[j]		8700	8700	9100		
Fine litterfall (mean)[k]		9319				
Fine litterfall (mean)[l]		7218		9454		
Leaf litterfall (number of studies)	17		19 (18)[g]	16	2	9
Range	3700–8400		2700–15500 (8400)[g]	2500–8500	4600–5500	2300–5700
Mean	6200		6500 (6000)[g]	5500	5000	4400

[a] Forests not indicated to be secondary.

[b] Twenty studies reviewed by Proctor (1983) and those of Dantas and Philipson (1989), Hegarty (1991), Morellato (1992), Burghouts et al. (1992), Herbohn and Congdon (1993) and Sanchez and Alvarez-Sanchez (1995).

[c] Nine studies reviewed by Proctor (1983) and that of Zou et al. (1995).

[d] Eighteen studies reviewed by Proctor (1983) and those of Weaver and Murphy (1990), Morellato (1992), Zou et al. (1995), Vitousek et al. (1995), Stocker et al. (1995) and Pendry and Proctor (1996) of unspecified mountain or specifically lower-montane forest (those studies in clearly upper-montane forest were excluded from this set).

[e] Four ridge-top forests studied in 1974/1975 and 1977/1978 by Tanner (1980b) and two in 1995/1996 by Hafkenscheid (2000) — these results are included in the global upper montane range and mean values shown to the right.

[f] Nine studies reviewed by Proctor (1983) and those of Veneklaas (1991) and Hafkenscheid (2000).

[g] One study of secondary forest reviewed by Proctor (1983) had exceptionally high litterfall rates. Although there are no good a priori grounds for dismissing this study, the maximum and mean values with this study excluded are shown in brackets.

[h] Four studies reviewed by Brown and Lugo (1990).

[i] Seven studies reviewed by Brown and Lugo (1990), this wide range was maintained until at least 21 years.

[j] Zou et al. (1995) provide a direct comparison between adjacent primary (‘mature tabonuco’) and secondary ‘mid-successional’ (cleared at the beginning of this century and abandoned from agriculture in the 1920s and 1930s) forests in Puerto Rico — these results are included in the small litterfall range and mean values shown above.

[k] Our study, main secondary forest plots (from Table 7).

[l] Our study, subsidiary plots (from Table 7).

that during the first 4 years total annual litterfall increased to approach (but not reach) the pre-hurricane levels. Looking at the impact of another category of disturbance Burghouts et al. (1992) found that 10 years after heavy selective logging of lowland dipterocarp forest in Sabah, Malaysia, annual litterfall in regrowth (11,900 kg ha^{-1}per year) was slightly higher than that in unlogged primary forest (11,500 kg ha^{-1}per year).

The invasive exotic species *P. undulatum*, occupied 28% of the basal area of our main secondary forest plots (Table 1), whereas it was absent as a tree from Tanner's plots before Hurricane Gilbert. The exceptional productivity of this species (as reflected in trunk growth) is a third factor that is likely to contribute to the high rates of litterfall that we recorded. Unpublished data from Goodland and Healey (1995) plots show that, during 1991–1996, the relative basal area increment of *P. undulatum* (0.164($\pm$0.029)) was substantially greater than that of the native species (0.013($\pm$0.001)); it was also much greater than that found by Bellingham et al. (1995) for all the individual native tree species in Tanner's plots.

The final factor to be considered in comparing litterfall among the different Jamaican Blue Mountain data sets (in particular the contrast that the higher basal area of the primary forest plots was not generally matched by a higher litterfall rate) is Brown and Lugo (1990) observation that in younger secondary forests litter production is a higher fraction of the net primary productivity than stemwood biomass production. Ewel (1976) found evidence in Guatemalan lowland rain forests that during the course of succession litterfall in secondary forests might even rise to levels higher than that in adjacent primary forests. He found that litterfall in 2-year-old secondary forests was about half that in mature forests, and then increased until in a 14-year-old forest it was about 10% higher than in mature forest (though the difference was probably not significant). These observations may be explained by Swaine and Whitmore's (1988) conclusion that pioneer tree species (those that tend to dominate the early stages of secondary succession) have a higher rate of leaf turn-over than the non-pioneer 'climax' tree species that dominate later in the succession and in undisturbed primary forest.

The standing crop of leaf litter in the main secondary forest plots (mean of 4114 kg ha^{-1} (Table 9)) was very similar to that recorded in ridge-top forest by Hafkenscheid (2000) (4300 kg ha^{-1}), but lower than that recorded in five ridge-top forests by Tanner (1980b, 1981) (range 6400–11,700 kg ha^{-1}). However, they were higher than in our subsidiary primary (3456 kg ha^{-1}) and secondary (2194 kg ha^{-1}) forest plots. The annual amount of leaf litterfall in our main secondary forest plots (Table 7) was equivalent to 204% of the standing crop, a lower ratio than that in the subsidiary secondary forest plots (274%), similar to that in our subsidiary primary forest plots (215%), but much larger than the ratio found by Tanner (1980b): 62 and 83% for two ridge-top forest types. These results indicate that the forest in lower altitude, less acidic slope sites had a more rapid turnover of litter (and thus of nutrient cycling) than the higher altitude ridge-top primary forests. However, there was no evidence of systematic variation in litter turnover rates between secondary and primary slope forests.

The concentration of N in our main secondary forest plots' fine litterfall (9.2 g kg^{-1}, Table 8) was very close to the top of the range of four values obtained by Tanner (1977b) (5.9–9.0 g kg^{-1}). However, fine litterfall P concentration in our study, 1.0 g kg^{-1}, was substantially above the range for Tanner (1977b) four forest types (0.2–0.4 g kg^{-1}). Whilst being in the upper half of the range of values obtained for tropical forests (Proctor, 1983), this value fits well within the range of litterfall P concentrations, 0.5–1.2 g kg^{-1}, obtained from a series of eight mountain secondary forests in the Philippines by Kellman (1970) (these also had high litterfall N concentrations, in the range 13–17 g kg^{-1}) and evergreen mountain forests in northern Thailand by Thaiutsa et al. (1978) (0.9–1.6 g kg^{-1}).

Litterfall mass and nutrient concentrations together determine the total recycling of nutrients in fine litterfall, which in our main secondary forest plots were 81 kg N ha^{-1}per year, and 7.7 kg P ha^{-1}per year (Table 8). These values were within the wide ranges reported in other studies in tropical forests at >1000 m altitude (28–165 kg N ha^{-1}per year and 1.1–12.0 kg P ha^{-1}per year) (Vitousek, 1984; Vitousek and Sanford, 1986; Tanner et al., 1998). However, both values were high compared to Tanner (1977b) values of 35–59 kg N ha^{-1}per year and 1.3–2.4 kg P ha^{-1}per year in primary/old-secondary ridge-top forests in the Jamaican Blue Mountains.

Healey (1989) and Tanner et al. (1990) concluded that growth in ridge-top upper montane forests in the Blue Mountains was limited by the low availability of P and N. However, the much higher litterfall P concentrations in our main secondary forest plots indicate that productivity in these forests may be much less P limited (Vitousek and Sanford, 1986). The ratio of litterfall concentrations ($g\,kg^{-1}$) to contents ($kg\,ha^{-1}$per year) of both N and P in our study lie well within the range of values of forests in the same altitudinal range reported by Tanner et al. (1998). Our results are thus compatible with recent tentative conclusions of Tanner et al. (1998) that productivity in tropical montane rain forests is, in fact, limited more by low availability of N than of P.

The rate of total N mineralisation (0.48 $\mu g\,g^{-1}$per day) in in-situ soil cores in the main secondary forest plots (Table 2) was within the wide range obtained for ex-situ incubation of cores of soil from four ridge-top forest types by Tanner (1977a) (−0.775 to +4.00), whereas the rate of nitrate-N increase, 0.52 $\mu g\,g^{-1}$per day, lay below Tanner (1977a) range of 1.3–3.4 $\mu g\,g^{-1}$per day. Tanner (1977a) found very variable rates of change in ammonium-N during incubation (for 40 days) and for three of his four soils it was negative. The amount of total N mineralised in our main secondary forest plots (Table 2) was a very high proportion, 173%, of the amount of N input over an equivalent time period and area in fine litterfall (Table 8), but within the broad range found by Tanner (1977a) (−315 to +1327% of litterfall inputs). However, it was equivalent to just 0.2% of standing stock of total N in the soil (Table 2).

As indicated in Section 3.2.1, the soils in our main secondary forest plots had values of most chemical indicators of fertility similar to those recorded in primary forests in the Blue Mountains, and, for pH, base saturation and exchangeable Ca, the values were larger. The bioassay indicated that soil fertility in the subsidiary secondary forest plots had recovered to the levels in the primary forest plots. However, Healey (1989) found a similar result of no significant difference in the above-ground growth of *Melinis minutiflora* plants grown in two very different (primary) montane forest soils from Mull Ridge and Col (Tanners 'Gap' (Tanner, 1977a)) Forest. The only significant difference between the plants was that those in the less-fertile Mull Ridge Forest soil had greater root masses. Nonetheless, the indication of equivalence in soil fertility from our bioassay has greater significance because two of the species used are trees growing in the forests concerned.

5. Conclusions

For forests in the middle of steep slopes on a tropical mountain in Jamaica, following the abandonment of agriculture, tight nutrient cycling and soil condition and fertility are effectively restored during ca. 20 years of secondary succession. In particular, the secondary forest acts as a buffer against fluctuations in runoff associated with rainfall events. The very small losses of nutrients in runoff and erosion compared with high rates of recycling through litterfall suggest that these forests are effective in restoring soil fertility. This is borne out by the similar rates of plant growth on the primary and secondary forest soils in the bioassay experiment. The secondary succession results in the re-establishment of a forest ecosystem with effective nutrient conservation that offers a high degree of protection of catchment soil and water resources and the potential to sustain another cycle of agricultural production.

Acknowledgements

This publication is an output from a research project funded by the United Kingdom Department for International Development (DFID) for the benefit of developing countries. The views expressed are not necessarily those of DFID. R4611 Forestry Research Programme. The authors are grateful to Raimond Hafkenscheid, Peter Bellingham, David Coombes, John Hall and three anonymous reviewers for reviewing the manuscript, and additionally to Peter Bellingham for data analysis. Malcolm Allison, Albert Hall, Roy Bryan and Shannon Morin provided valuable field assistance, Keith Thomas laboratory assistance and Michelle Jones prepared Fig. 1.

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