Forest Ecology and Management 144 (2001) 19–32

Forest Ecology and Management

www.elsevier.com/locate/foreco

Biomass and nutrient accumulation of *Piper aduncum* and *Imperata cylindrica* fallows in the humid lowlands of Papua New Guinea

Alfred E. Hartemink*

International Soil Reference and Information Centre (ISRIC), PO Box 353, 6700 AJ Wageningen, The Netherlands

Received 16 May 2000; received in revised form 10 November 2000; accepted 16 November 2000

Abstract

Shifting cultivation with short fallow periods (<3 years), is an important form of land use in the humid lowlands of Papua New Guinea. The secondary forest vegetation is dominated by the shrub *Piper aduncum* which originates from South America, and *Imperata cylindrica* grasslands in areas where annual bush fires are common. No information is available on the rate of biomass and nutrient accumulation of these two fallow types. Plots with *P. aduncum* and *I. cylindrica* were planted on a Typic Eutropepts and sampled every 3 months for 23 months to assess above ground biomass and nutrient content. Total biomass of imperata was slightly higher than that of piper during the first year, but remained around 23 Mg dry matter (DM) ha^{-1} in the second year. Above ground biomass of piper increased linearly, and reached 48 Mg DM ha^{-1} at 23 months when three-quarter of the biomass consisted of wood. Growth rates of piper were on average 69 kg DM ha^{-1} per day, and increased with higher rainfall. Nutrient content of imperata was 100 kg N, 12 kg P, 62 kg K, 64 kg Ca, 40 kg Mg and 9 kg S ha^{-1} at 23 months. The concentration of K and Ca was high in piper leaves but declined over time. At 23 months, piper had accumulated 222 kg N, 50 kg P, 686 kg K, 255 kg Ca, 75 kg Mg, and 24 kg S ha^{-1}. More than half of the P, K, Ca and Mg was found in the stem (wood) which is removed from the field and used as firewood when farmers slash the fallow. piper biomass (excluding wood) returned about three times more K to the soil than imperata, but differences between total P and S contents were small. For the accumulation of biomass and nutrients, imperata fallows should not exceed 1 year. Piper accumulated large amounts of biomass and nutrients, particular K, which is an important nutrient for root crops that dominate the cropping phase in the shifting cultivation systems of the humid lowlands.

Keywords: Natural fallows; Nutrient concentration; Nutrient stocks; Nutrient cycling; Tropical secondary vegetation

1. Introduction

About three-quarter of Papua New Guinea (460 000 km^2) is under primary forest (McAlpine and Quigley, 1995). No exact figures are available on the current rate of deforestation, but estimates from the 1980s vary between 113 000 and 200 000 ha per year (FAO, 1990; Freyne and McAlpine, 1987). Deforestation takes place for logging, mining, agricultural plantations and shifting cultivation. Aerial photographs from the early 1970s compared with Land-Sat^{TM} imagery from 1996, revealed that the area under shifting cultivation has increased by only 7% (McAlpine, CSIRO, 1999, personal communication) despite the fact the human population doubled between 1966 and 1990 (Allen et al., 1995). It implies that land is cropped more often and fallow periods are shortened,

* Tel.: +31-317-471-711; fax: +31-317-471-700.
E-mail address: hartemink@isric.nl (A.E. Hartemink).

0378-1127/01/$ – see front matter
PII: S0378-1127(00)00655-1

which puts a greater demand on the soil resource (Nye and Greenland, 1960), particularly as virtually no inorganic fertilisers are being used on food crops in Papua New Guinea (Hartemink and Bourke, 2000). Forest regrowth is uncommon in the humid lowlands and the woody shrub *P. aduncum* and *I. cylindrica* grasslands dominate the fallow vegetation.

P. aduncum is a member of the family Piperaceae of which there are some economically important species in the Pacific, including *Piper nigrum* (pepper), *Piper methysticum* (kava), and *Piper bettle* of which the fruits are used with betel nut (*Areca cathecu*) in Papua New Guinea (Bornstein, 1991). *P. aduncum* is a shrub or small tree with alternate leaves and spiky flowers and fruits. It occasionally reaches an height of 7–8 m, and has very small seeds which are mostly dispersed by the wind, fruit bats and birds. *P. aduncum* is common throughout Central America where it is found between sea level and 2000 m above sea level (a.s.l.) along road sides and in forest clearance areas on well drained soils. It occurs in Mexico, Central America, Surinam, Cuba, southern Florida, Trinidad and Tobago, and Jamaica (Hartemink, 1999) and is very common in Costa Rica on open or partly shaded sites (Burger, 1971). In the Neotropics, *P. aduncum* may be locally abundant but the species rarely dominates the vegetation (Callejas, University of Antoquia, 1999, personal communication) or is found in mature vegetation. In the Amazon areas, it has been reported as an invading plant after timber exploitation (Maia et al., 1998). Extracts of *P. aduncum* are used as folk medicine in South America. The species is mentioned in several ethnopharmalogical databases, and has antifungal and antibacterial compounds (Nair and Burke, 1990).

P. aduncum was introduced in the botanical gardens of Bogor (Indonesia) in the 1860. By the 1920s it commonly occurred in a radius of 50–100 km around the botanical gardens in young secondary vegetation, close to rivers and on very steep slopes, locally in dense stands (Heyne, 1927). *P. aduncum* was noted in Jayapura in 1955 and in Biak in 1960 on Papua (Irian Jaya) (Veldkamp, Rijksherbarium Leiden, 1999, personal communication), and in Malaysia and Borneo in the 1960s (Allen, 1966; Chew, 1972). It has also been recorded in Singapore and Sumatra, and is on the list of unwanted weed species by the quarantine service of Australia (Hartemink, 1999). *P. aduncum* was introduced into Fiji in the 1920s and is now widespread in the wet and intermediate zones of Viti Levu (Smith, 1981). It is not found on Hawaii.

It is not known when and how *P. aduncum* arrived in Papua New Guinea but it is likely that the seeds came in by accidental transport from Papua or perhaps from Fiji. The botanist Mary Clements first observed *P. aduncum* in 1935 near the mission station Heldsbach in the Morobe Province. It was not very widespread in the early 1970s and *P. aduncum* is not separately listed in the standard text on New Guinea vegetation (Paijmans, 1976). However, by the late 1990s *P. aduncum* is very common in the lowlands of the Morobe and Madang Provinces, and is also observed in the Central Highlands above 2000 m a.s.l. (Rogers and Hartemink, 2000). Seeds are being spread by flying foxes (Kidd, 1997) and logging equipment. Causes for its rapid spreading remain unclear but evidence is being accumulated that areas of high native plant species richness and cover, like many areas in Papua New Guinea, and areas high in soil fertility may be highly invisible (Stohlgren et al., 1999). The invasion of *P. aduncum* in the humid lowlands of Papua New Guinea appears similar to the spreading of *Chromolaena odorata* in Asia and parts of West Africa (McFadyen and Skarratt, 1996; Slaats et al., 1996), and to the invasion of *Miconia calvescens* which was introduced as an ornamental but is now one of the major pests in the Society Islands of the Pacific (Meyer, 1996) where it is nicknamed the "green cancer" (Stone, 1999).

Another fallow type in the humid lowlands of Papua New Guinea is grasslands consisting of *I. cylindrica* (spear grass, cogon grass, alang-alang, kunai). Such grasslands occur widely in the humid tropics on various soil types (Menz et al., 1998; Santoso et al., 1996), and *I. cylindrica* is generally considered one of the world's worst weeds, especially in southeast Asia (NRI, 1996; Turvey, 1994). In Papua New Guinea, *I. cylindrica* grasslands cover millions of hectares and are found from sea level to nearly 2000 m a.s.l., with annual rainfall varying from 1250–4000 mm and on soils with a pH ranging from 5 to 9 (Holmes et al., 1980). They have been mostly formed because of annual bushfires which hinders the regrowth of woody vegetation.

Despite the widespread occurrence of *P. aduncum* and *I. cylindrica* fallows in the humid lowlands of Papua New Guinea, there is no information available on the amount of biomass and nutrients. This is no exception as there is a paucity of information on total biomass and nutrient stocks in tropical secondary vegetation (Szott and Palm, 1996). The objectives of this study were, therefore, to quantify rates of biomass and nutrient accumulation by *P. aduncum* and *I. cylindrica* (hereafter referred to as piper and imperata, respectively). Such information is important as improved or managed fallows may be required to replace existing natural fallows because they accumulate higher amounts of nutrients and biomass in shorter periods (Sanchez, 1999; Szott et al., 1999).

2. Materials and methods

2.1. Site

The study was performed between December 1996 and November 1998 near Hobu village (6°34′S, 147°02′E), which is 25 km north of the city of Lae in the Morobe Province. The site is at an altitude of 405 m a.s.l. at the footslopes of the Saruwaged mountain range. Rainfall records were only available since the start of the experiment (November 1996) and the daily rainfall pattern during the growing period is shown in Fig. 1. The end of 1997 was an exceptionally dry period and this was caused by the El Niño/southern oscillation climatic event that affected the Pacific severely in 1997/1998. Consequently, there were many bushfires in the study area and most of the fallow fields around the experimental site were burned. Total rainfall in 1997 was 1897 mm whereas in the first 6 months of 1998 the amount of rain was 2067 mm. March 1998 was a wet month with 725 mm of rain, and rainfall for 1998 was 3667 mm. Total rainfall during the experimental period (23 months) was 5323 mm. Temperatures were not available for the experimental site but average daily temperatures at the University of Technology, which is situated about 15 km south of Hobu village, are 26.3°C.

The Hobu experimental site is located on an uplifted alluvial terrace with a slope of less than 2%. Soils are derived from a mixture of alluvial and colluvial deposits dominated by sedimentary rocks and coarse to medium grained, basic, igneous rocks. The soils have water-worn gravelly and stony horizons below 0.2 m depth, effective rooting depth is over 0.7 m. Air-dried and sieved (<2 mm) soil had the following properties in the top 0.12 m: pH H_2O (1:5, w/v) = 6.2, organic C (dry combustion) = 55 g kg^{-1}, available P (Olsen) = 9 mg kg^{-1}, CEC (NH_4Oac, pH 7) = 400 $mmol_c$ kg^{-1}, exchangeable Ca = 248 $mmol_c$ kg^{-1}, exchangeable Mg = 78 $mmol_c$ kg^{-1}, exchangeable K = 16.9 $mmol_c$ kg^{-1}, clay = 480 g kg^{-1} and sand = 360 g kg^{-1}, bulk density = 0.82 Mg m^{-3}.

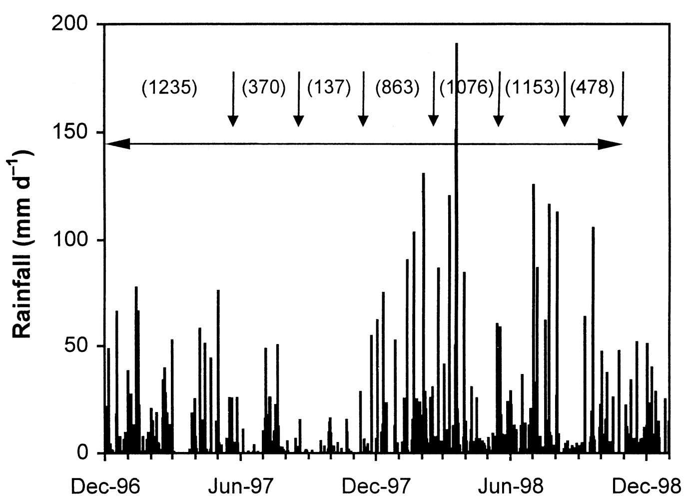

Fig. 1. Rainfall during fallow period (mm per day) at the experimental site in the Morobe Province of Papua New Guinea. Horizontal arrow indicates growing period (23 months), vertical arrows indicate sampling times for biomass and nutrients. Amount of rain between sampling times in parentheses.

The soils are classified as mixed, isohyperthermic, Typic Eutropepts (USDA Soil Taxonomy) or Eutric Cambisols (World Reference Base). Further details on soil chemical and physical properties can be found in Hartemink et al. (2000).

2.2. The shifting cultivation system

The experiment was located in an area where shifting cultivation is commonly practised and consists of a short fallow period (<3–5 years) alternated with a cropping period of about 1 year. At the end of the fallow period, piper is coppiced at 0.2–0.5 m above the ground (Fig. 2) with bushknives. The vegetation debris is left to dry for some weeks whereafter the woody parts (stems) are removed from the field, which are mostly used for firewood and sometimes for constructing hutroofs. Burning the vegetation debris is uncommon due to the prevailing wet conditions, which hampers proper drying and burning. In addition, piper stems may not sprout after burning. Taro (*Colocasia esculenta*) or maize (*Zea mays*) are commonly firstly planted after a fallow period and these are gradually interplanted with sweet potato (*Ipomoea batatas*), which is the major staple in the lowlands (Bourke, 1985), bananas (*Musa* sp.) and sugar cane (*Saccharum* sp.) (Fig. 2). After 1 year, the piper has sprouted, the bananas have grown large and the cropped site reverts back to fallow bush.

Fig. 2. Partly cleared field with *P. aduncum* as the dominant fallow species near Hobu village in the Morobe Province of Papua New Guinea. Fallow was about 4-year-old. Note dense stand of *P. aduncum* in the background and planted taro (*Colocasia esculenta*) and banana (*Musa* sp.) in cleared field.

Not much is known about the farmers' perception of piper fallows in the Morobe Province, although a number of farmers remember that it arrived in their area in the 1970s. Some farmers claim that if the piper is large, good crop yields may be expected and others say the piper makes good firewood. Most farmers know that piper consumes much soil water and quantitative differences have been observed in the volumetric soil moisture contents of soils under piper, imperata, and *Gliricidia sepium* (Hartemink and O'Sullivan, 2001). Soils after 1 year piper fallow were drier than under other fallows of the same age, which may be of an advantage since high rainfall depresses sweet potato yield (Hartemink et al., 2000).

Imperata fallows are also common in the Morobe Province of Papua New Guinea particularly in areas where bushfires are common. These fires usually occur when there is a short dry spell which takes place in most years. Fires hinder the regrowth of woody vegetation and the imperata grasslands are, therefore, anthropogenous (Henty and Pritchard, 1988). Farmers slash the imperata and remove the dried grass which is often used as thatch. The land may be cropped for one or two seasons before opportunity costs for weeding become too large and the site reverts back to imperata grasslands. In Papua New Guinea, imperata is also a problem in young rubber, coconuts or timber plantations (Henty and Pritchard, 1988). However, the grasslands can support an extensive beef production system provided legumes are introduced and cattle stocking rates are low (Holmes et al., 1980).

2.3. Experimental set-up

In October 1996, an area of about 0.5 ha was cleared which mainly consisted of 5-year-old secondary fallow vegetation dominated by *P. aduncum* and to a lesser extent by *Homalanthus* sp., *Macaranga* sp., *Trichospermum* sp. and *Trema orientalis* (Rogers and Hartemink, 2000). All vegetation debris was removed from the plot and no burning was practised. In December 1996, a plot of 90 m^2 (6 m × 15 m) was planted with young piper seedlings (about 0.2 m), which were taken from nearby roadcuts. Plant spacing was 0.75 m × 0.75 m, as is frequently observed in fallows dominated by piper (Hartemink, 1999) — see also Fig. 2. During the first month, plots were manually weeded but thereafter the canopy had closed and no more weeding was necessary. At the same time a plot of 90 m^2 was left fallow. Woody regrowth was removed from this plot and within 4 weeks the vegetation was dominated by *I. cylindrica*.

2.4. Plant sampling and analysis

Five months after the piper was planted, the height of four plants was measured. A 0.75 m × 0.75 m quadrate was placed around each plant and the litter was removed and put in a paper bag. The four plants were cut at ground level and separated into main stems, (side) branches, and leaves. Each plant part was weighed and subsamples were taken to the laboratory. Every 3 months, the above ground biomass (i.e. stem, branches, leaves, litter) of four plants was assessed in a stratified sampling scheme leaving a border row between the sampled plants. In total seven samplings were made and the last sampling was done when the plants were 23-month-old (see Fig. 1). Flowers and fruits, which appeared after about 18 months, were included in the leaf biomass. Piper fruits were sampled at 23 months for nutrient analysis. Roots were not sampled in this study.

Above ground biomass of the imperata was sampled at the same dates as the piper and four quadrates of 0.75 m × 0.75 m were randomly placed in the imperata plot. The imperata was clipped at ground level and litter could not be separated from the above ground biomass. Total biomass was weighed in the field and subsamples were taken to the laboratory. The imperata data for 14 months after planting were lost.

In the laboratory, all plant samples were rinsed with distilled water and oven dried at 70°C for 72 h. Samples were ground (mesh 0.2 mm) and sent for nutrient analysis to the laboratories of the School of Land and Food of the University of Queensland. One subsample was digested in 5:1 (nitric:perchloric acids) and analysed for P, K, Ca, Mg and micronutrients (B, Cu, Mn, Zn) using ICP AES (spectro model P). A second subsample was digested according to the Kjeldahl procedure and analysed for C, N and S on an Alpkem rapid flow analyser series 300.

2.5. Data analysis

Dry matter contents were calculated based on ovendried data of the subsamples. Biomass data of piper and imperata were averaged and subjected to analysis of variance. Standard error (S.E.) of the difference in means (S.E.D.) was calculated for total biomass of piper and imperata and the individual plant parts of piper. Total nutrient uptake was calculated by multiplying dry matter with nutrient concentration and S.E.D. were calculated for both the piper and imperata data. Since the data for the 14-month-old imperata were lost, the degrees of freedom (d.f.) were 15 for imperata and 18 for piper. All statistical analysis was conducted using Statistix 2.0 for Windows.

3. Results

3.1. Accumulation of above ground biomass

During the first year, above ground biomass of imperata was larger than that of piper, and the biomass of both fallows was on average below 20 Mg dry matter (DM) ha^{-1} (Fig. 3). Total above ground biomass of *P. aduncum* increased with time, but variation in piper biomass was considerable and data from the first four sampling were not statistically significant ($P > 0.05$). After 14 months, piper above ground biomass increased significantly and reached 48 Mg DM ha^{-1} at 23 months. Imperata biomass increased significantly ($P < 0.05$) between 5 and 8 months. No significant difference was found in the biomass between 8 and 11 months but imperata biomass had significantly increased again at 17 months and remained around 23 Mg DM ha^{-1} between 17 and 23 months (Fig. 3). DM content of the imperata biomass was 35% at 5 months, 45% at 8 months and around 55% between 11 and 23 months, when

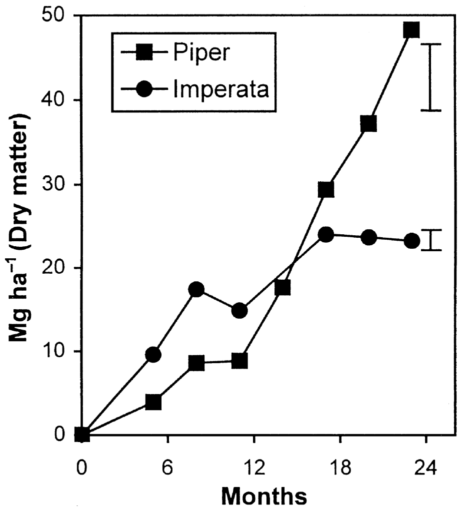

Fig. 3. Total biomass accumulation of *P. aduncum* and *I. cylindrica* during a 23 months period in the humid lowlands of Papua New Guinea. Bars indicate standard error of the difference in means (18 d.f. for piper data, 15 d.f. for imperata data).

a considerable portion of the above ground biomass was dead.

The large increase in above ground biomass of piper was mainly due to the growth of the main stems (Fig. 4) and the piper formed on average three stems per plant (Fig. 5). In the first 14 months, piper stems formed less than 50% of the total above ground biomass but at 23 months more than three-quarter of the total biomass consisted of woody stems (Table 1). Leaves formed half of the piper biomass at 5 months, but were less than 16% of the total biomass at 23 months despite the

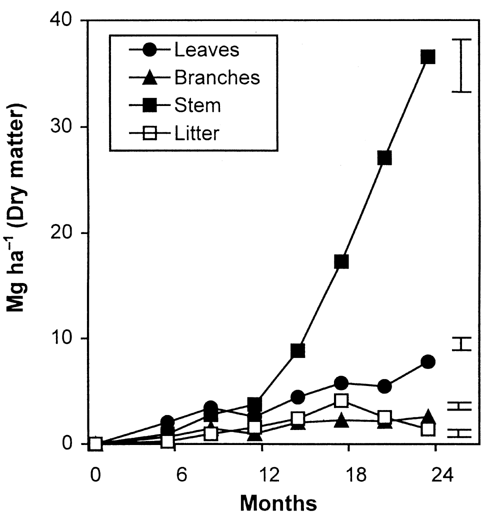

Fig. 4. Biomass accumulation in leaves, stem, branches, and litter of *P. aduncum* during a 23 months period in the humid lowlands of Papua New Guinea. Bars indicate standard error of the difference in means (18 d.f.).

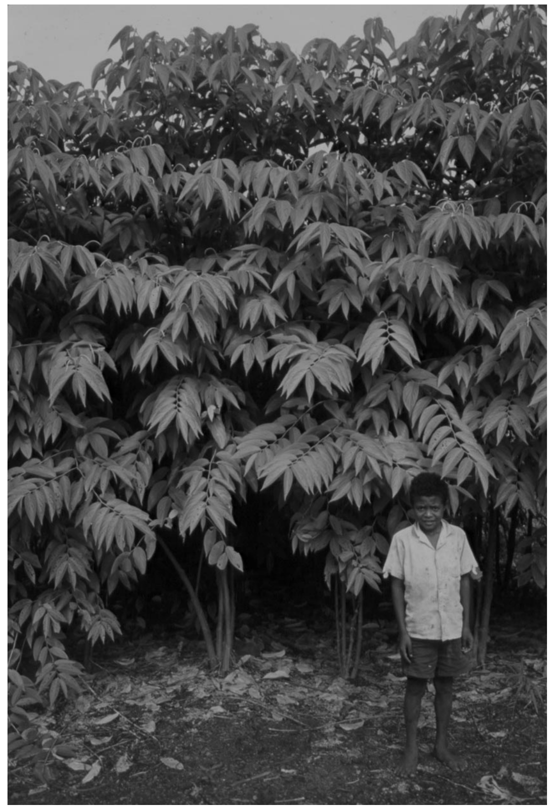

Fig. 5. Eighteen-month-old *P. aduncum* at the experimental site near Hobu village. Total aboveground biomass was about 30 Mg ha^{-1} and the trees were about 3.5 m. Trees had formed first flowers and fruits. Note absence of undergrowth.

Table 1
Biomass in leaves, stem, branches and litter of *P. aduncum* as percentage of the total above ground biomass, over a 23 months period in the humid lowlands of Papua New Guinea

Plant part	Months after planting						
	5	8	11	14	17	20	23
Leaves	52	40	29	25	20	15	16
Stem	24	32	42	50	59	73	76
Branches	17	17	11	11	8	6	5
Litter	6	11	18	14	14	7	3

significant increase from 2.0 to 7.8 Mg DM ha^{-1}. Overall a widening wood–leaf ratio was observed with increasing age of the piper. Litter biomass differed significantly between the various sampling times and ranged from 0.3 to 4.1 Mg DM ha^{-1} (Fig. 4). The growth of the piper will eventually level off and in the Morobe Province of Papua New Guinea it was observed that other secondary species slowly invade monospecific piper stands after about 5 years.

Growth rates of piper varied considerably, and ranged from 3.0 to 133.5 kg DM ha^{-1} per day during the 23 months of observation. Rates of biomass accumulation of imperata were highest between 5 and 8 months when it reached 82.1 kg DM ha^{-1} per day. Average growth rates over the whole period were 69.1 kg DM ha^{-1} per day for piper and 31.5 kg DM ha^{-1} per day for imperata. Piper shrubs were on average about 0.9 m ($\pm$0.06 m) at 5 months after planting but the average height increased to 2.5 m ($\pm$0.19 m) at 14 months, and to 4.5 m ($\pm$0.17 m) at 23 months. During the time of the experiment, it was observed that the height and biomass gain of the piper was affected by the amount of rain between the sampling times which varied considerably (Fig. 1). Between 8 and 11 months after planting, only 137 mm of rain fell and there was no increase in above ground biomass (Fig. 3), although there was a significant increase in the litter biomass during this period (Fig. 4). The amount of rain between a sampling time (in mm per day) was plotted versus the growth rate (kg DM ha^{-1} per day), and the relation was as follows:

$$\text{growth rate (kg ha}^{-1}\text{ per day)} = 8.1 \times \text{rainfall (mm per day)} + 13.6 \quad (r^2 = 0.413,\ P < 0.05).$$

Although, the data are few and do no take into account age effects on the growth rates of piper, a clear increasing trend was found in growth rate with increasing rainfall. On average, piper growth rates increased with about 81 kg DM ha^{-1} per day for each 10 mm of rain per day. No relation could be established between the growth rates of imperata and rainfall.

3.2. Nutrient concentration and accumulation

Nutrient concentration was measured in leaves, stems, branches, and litter of piper and the whole above ground biomass of imperata (Table 2). Piper leaves contained on average 22.7 mg N kg^{-1} at 5 months but levels significantly decreased thereafter and were almost halved at 23 months. N concentrations in piper stem, branches and litter also significantly decreased over time. Imperata contained less than 6.5 mg N kg^{-1} and N concentrations declined significantly between 5 and 8 months, but did not change between 8 and 23 months. The P concentration of piper leaves and stem was similar and declined significantly over time. Piper branches contained relatively high P concentration whereas imperata leaves contained low P levels. Piper leaves and branches contained high concentrations of K, which decreased during the 23 months growing period. Piper litter contained more K than imperata leaves, which had very low concentration of K. Variation in Ca concentration of piper leaves was considerable and concentrations were mostly below those of the piper litter. Concentration of Ca in imperata was low but remained constant over the 23 months period. Piper litter contained the highest Mg concentrations and mostly exceeded those in the piper leaves. S concentrations were highest in the piper branches.

Piper leaves contained relative high concentrations of B particularly when compared to imperata (Table 3). Mn concentrations decreased over time in the piper leaves but increased significantly in the above ground biomass of imperata. Piper branches contained relatively high concentrations of Cu and levels decreased with time. Zinc concentrations were highest in piper leaves, although branches contained relative high concentrations of Zn.

At 23 months after planting fruits of the piper were analysed for their nutrient concentration and the data were compared to the nutrients in the leaves (Table 4). Piper fruits contained on average slightly higher nutrient concentrations than the leaves at 23 months, particularly N, P, S and Cu. However, compared to leaf analytical results of the first 11 months (Table 2), piper fruits were poorer in nutrients except for P which levels are relatively high.

Although, imperata accumulated more biomass during the first 12 months (Fig. 3), nutrient

Table 2
Major nutrient concentration (g kg^{-1}) of *P. aduncum* leaves, stem, branches and litter and *I. cylindrica*, over a 23 months period in the humid lowlands of Papua New Guinea

	Fallow species	Plant part	Months after planting							
			5	8	11	14	17	20	23	S.E.D.[a]
N	Piper	Leaves	22.7	16.2	16.3	15.9	16.5	15.1	13.9	0.56
		Stem	8.1	5.4	3.6	6.1	3.3	2.7	2.6	0.21
		Branches	8.0	5.7	7.4	7.2	5.4	5.8	5.1	0.22
		Litter	9.6	8.5	9.0	8.7	7.1	5.7	5.1	0.52
	Imperata[b]	Whole plant	6.3	5.1	4.0	nd[c]	4.2	4.9	4.3	0.57
P	Piper	Leaves	2.6	1.8	1.9	1.7	1.7	1.7	1.1	0.30
		Stem	2.2	1.2	1.0	1.6	1.4	0.7	0.9	0.15
		Branches	2.7	1.6	3.2	2.7	3.1	2.4	2.2	0.25
		Litter	0.8	0.9	0.8	0.9	0.8	0.5	0.5	0.04
	Imperata[b]	Whole plant	0.9	0.9	0.8	nd[c]	0.6	0.8	0.5	0.07
K	Piper	Leaves	34.0	29.4	25.2	20.3	20.9	25.4	16.2	4.09
		Stem	31.2	17.8	11.0	15.9	16.2	14.1	13.4	1.50
		Branches	44.2	33.6	28.6	25.0	29.1	25.3	22.2	2.40
		Litter	15.2	14.6	10.0	2.3	5.4	3.5	3.3	1.42
	Imperata[b]	Whole plant	12.6	7.7	6.6	nd[c]	4.5	4.3	2.6	0.65
Ca	Piper	Leaves	17.3	18.1	19.3	20.9	14.4	15.5	8.8	2.64
		Stem	6.1	3.0	2.2	3.3	2.0	1.6	4.3	1.68
		Branches	12.9	9.6	7.9	8.6	11.4	9.8	7.2	0.64
		Litter	34.9	30.8	31.7	33.1	24.1	8.8	9.7	2.48
	Imperata[b]	Whole plant	2.9	2.6	2.6	nd[c]	2.5	2.6	2.8	0.29
Mg	Piper	Leaves	3.6	4.5	7.1	6.7	3.1	3.6	2.3	0.79
		Stem	2.6	1.5	1.2	1.6	1.0	0.8	1.2	0.35
		Branches	5.2	6.0	8.2	8.1	4.8	3.5	4.0	0.76
		Litter	5.3	7.8	8.4	6.7	5.4	2.3	2.0	0.51
	Imperata[b]	Whole plant	1.7	1.7	1.7	nd[c]	2.2	2.3	1.7	0.11
S	Piper	Leaves	1.3	1.2	1.0	1.0	0.9	1.0	0.5	0.16
		Stem	0.8	0.4	0.2	0.3	0.2	0.2	0.3	0.10
		Branches	2.1	2.9	2.9	2.7	3.2	3.3	2.9	0.40
		Litter	0.7	0.8	0.7	0.8	0.8	0.4	0.5	0.06
	Imperata[b]	Whole plant	0.4	0.4	0.3	nd[c]	0.4	0.4	0.4	0.06

[a] Standard error of the difference in means (18 d.f. for piper, 15 d.f. for imperata).
[b] For imperata whole plants (excluding roots) were sampled.
[c] Not determined.

accumulation of piper was much higher (Fig. 6). N uptake by piper was almost linear and equalled 222 kg ha^{-1} at 23 months. Total N accumulation of piper was more than double the N accumulation by imperata. Accumulation of P was 50 kg ha^{-1} in the above ground biomass of the piper fallows, but varied greatly for imperata. K accumulation in piper was linear and reached 686 kg ha^{-1} compared to 62 kg K ha^{-1} under imperata fallows at 23 months. Piper also accumulated considerable amounts of Ca and two times more Mg than imperata, although there was some variation in the data. S accumulation by piper reached 24 kg ha^{-1} at 23 months, which was about three times higher than in imperata.

Variation in the nutrient uptake data was considerable which resulted from variation in both dry matter production and nutrient analysis. Despite this variation it was found that the order of nutrient accumulation for piper followed: $K \gg Ca > N > Mg > P > S$ whereas the order for imperata was found to be $N > K = Ca > Mg > P > S$. Total C accumulation by 23 months for piper was 19.6 Mg ha^{-1} (±5.1)

Table 3
Minor nutrient concentration (mg kg^{-1}) of *P. aduncum* leaves, stem and branches and *I. cylindrica*, over a 23 months period in the humid lowlands of Papua New Guinea

	Fallow species	Plant part	Months after planting							
			5	8	11	14	17	20	23	S.E.D.[a]
B	Piper	Leaves	34.5	42.8	19.7	22.7	33.0	26.2	14.1	3.93
		Stem	14.7	21.1	7.5	14.1	14.6	2.6	8.3	5.25
		Branches	18.0	34.0	11.5	16.4	20.2	13.1	10.0	5.04
	Imperata[b]	Whole plant	2.9	9.8	10.7	nd[c]	8.4	5.9	3.1	2.24
Cu	Piper	Leaves	6.8	11.0	4.1	0.2	2.0	3.1	0.8	1.06
		Stem	18.5	13.5	10.9	5.4	4.5	3.9	0.5	2.26
		Branches	29.2	16.3	8.5	3.5	5.4	6.8	4.8	4.47
	Imperata[b]	Whole plant	12.0	7.5	3.7	nd[c]	2.8	4.2	0.1	1.79
Mn	Piper	Leaves	28.0	28.3	29.9	23.2	11.9	18.6	10.8	3.57
		Stem	8.7	4.5	3.7	6.3	2.5	2.0	4.5	1.51
		Branches	13.6	10.6	9.3	9.6	6.2	7.6	6.3	0.87
	Imperata[b]	Whole plant	22.6	27.8	24.9	nd[c]	28.7	32.6	35.6	3.25
Zn	Piper	Leaves	40.7	44.7	37.9	37.0	29.9	23.2	15.0	5.21
		Stem	31.2	15.7	20.1	15.7	7.6	4.8	9.5	2.87
		Branches	40.6	37.4	31.2	29.3	29.6	18.4	15.4	2.88
	Imperata[b]	Whole plant	18.3	10.6	13.0	nd[c]	11.8	13.2	7.7	2.47

[a] Standard error of the difference in means (18 d.f. for piper, 15 d.f. for imperata).
[b] For imperata whole plants (excluding roots) were sampled.
[c] Not determined.

whereas 9.5 Mg C ha^{-1} ($\pm$1.3) was accumulated in the above ground biomass of the imperata.

3.3. Nutrient cycling

Accumulation of some major nutrient was more or less linear whereas the contents of other nutrient levelled off or decreased with time (Fig. 6). As the fallows will eventually be slashed and the nutrients will be returned to the soil when the biomass is decomposed, the pattern of nutrient accumulation has implications for the optimum time for slashing the fallows. The data suggest that there is no obvious advantage of having imperata fallows for longer than 1 year because no extra biomass or nutrients will be accumulated. However, for piper it was found that accumulation of biomass and N, P, K and S was found to be almost linear which implies that longer fallow periods means more biomass and nutrients. Accumulation of Ca and Mg showed, however, a plateau after 18 months.

After the piper fallows are slashed, farmers in the area remove the woody biomass (stems) from the fallow fields. Therefore, the amount of nutrients returned to the soil is the total amount of nutrients in the above ground biomass minus nutrients removed

Table 4
Major and minor nutrient concentration of *P. aduncum* fruits and leaves at 23 months after planting in the humid lowlands of Papua New Guinea

Plant part	Major nutrient (g kg^{-1})						Minor nutrient (mg kg^{-1})			
	N	P	K	Ca	Mg	S	B	Cu	Mn	Zn
Fruits	17.0	3.7	17.1	9.9	2.3	1.5	11.6	3.7	10.2	16.7
Leaves	13.9	1.1	16.2	8.8	2.3	0.5	14.1	0.8	10.8	15.0

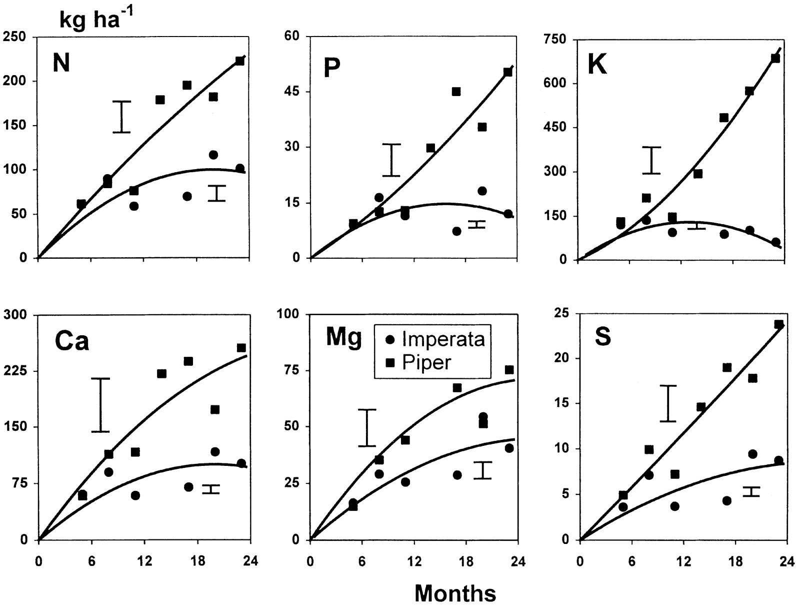

Fig. 6. Total nutrient uptake in the above ground biomass of *P. aduncum* and *I. cylindrica* during a 23 months period. Bars indicate standard error of the difference in means (18 d.f. for piper data, 15 d.f. for imperata data).

with the wood (Table 5). This makes the difference with the imperata smaller (Fig. 6) as considerable amounts of nutrients, particularly K and Ca, are removed with the wood. Piper returned about three times more K to the soil than imperata but differences between total P and S contents were small.

4. Discussion

4.1. Biomass accumulation

Variation in the rate of biomass accumulation by *P. aduncum* was considerable and caused by the irregular amount of rain between the sampling times. Growth rates were increased with higher rainfall, and after 23 months large amounts of above ground biomass had accumulated. Total biomass of piper is even higher but no measurements were made on below ground biomass. Various root–shoot ratios have been reported in the literature. In the humid lowlands of Venezuela, pioneer trees allocated high amounts of energy to root production and root–shoot ratios varied between 0.14 and 0.41 (Uhl, 1987). Below/above ground ratio for the fast growing *Inga edulis* in the humid lowlands of Peru were between 0.12 and 0.15 at 17–29 months after planting (Szott et al., 1994). Observations on the roots of *P. aduncum* were made

Table 5
Major nutrient content of *P. aduncum* stem and total above ground biomass at 23 months after planting in the humid lowlands of Papua New Guinea

	Content in kg ha^{-1} ± 1 S.D.					
	N	P	K	Ca	Mg	S
Total biomass[a]	222 ± 58	50 ± 17	686 ± 289	255 ± 259	75 ± 44	24 ± 12
Stems (wood)	93 ± 23	35 ± 12	495 ± 220	155 ± 226	44 ± 38	11 ± 11
Difference	129 ± 36	15 ± 5	191 ± 76	100 ± 52	31 ± 13	13 ± 4

[a] Nutrients in leaves, stem, branches, and litter (see Fig. 6).

Fig. 7. Rooting of 7-month-old *P. aduncum* at the experimental site near Hobu village. Note relatively shallow rooting pattern.

7 months after planting by digging 0.5 m deep trenches around piper plants. Piper had not an excessive root mat and the majority of the roots were concentrated in the top 0.18 cm (Fig. 7). If a root–shoot ratio of 0.15 is assumed, the total above and below ground biomass of the *P. aduncum* is 56 Mg ha^{-1} at 23 months. This is exceptionally high and caused by the piper's genetic potential, the dense spacing, and the fertile soils as the site had been fallow for about 5 years prior to the planting of piper. The large biomass accumulation may explain why *P. aduncum* is such an invasive species because it shades out native species. In addition, it produces large amounts of seeds which are easily dispersed.

There is only one other study which has reported above ground biomass of *P. aduncum*. Hashimotio et al. (2000) measured the biomass of a forest fallow dominated by *P. aduncum* in the humid lowlands of East Kalimantan (Indonesia) and found an above ground biomass of about 12 Mg ha^{-1} after 2 years, and 45–56 Mg ha^{-1} in 10–12-year-old forests fallow dominated by *P. aduncum*. The soils at the site were very acid and of low fertility (Ultisols), which may explain the lower biomass.

On poor fertility Ultisols in the humid lowlands of Peru, Szott et al. (1994) measured above and below ground biomass accumulation and found 19 Mg DM ha^{-1} for the fast growing tree *Inga edulis* per year. In the humid lowlands of Venezuela above ground biomass accumulation rates of natural regrowth varied from 5 to 9 Mg DM ha^{-1} per year (Uhl, 1987). In a recent overview of fallows in the humid and subhumid tropics, the highest biomass was about 30 Mg DM ha^{-1} after 2 years (Szott et al., 1999). Two-year-old *Chromolaena odorata* on Ultisols in the humid lowlands of Ivory Coast had accumulated about 16 Mg DM ha^{-1} (Slaats et al., 1996). *Gmelina arborea*, a widely used tree on forest plantations, produced between 56 and 137 Mg ha^{-1} in 5–7 years (Halenda, 1993). Above ground biomass of 2-year-old *Acacia mangium* in Cameroon was 44 Mg ha^{-1} (Duguma et al., 1994) whereas the biomass in 6-year-old bamboo in Bandung (Indonesia) was 76.7 Mg ha^{-1} (Christanty et al., 1996).

None of the studies on secondary fallow in the humid tropics reported such high rates of biomass accumulation as in this study with *P. aduncum*. Although, some studies were conducted on high base status soils (Szott et al., 1999), growth of secondary vegetation in humid lowlands is mostly nutrient limited (Gehring et al., 1999).

Biomass accumulation of *I. cylindrica* (maximum 24 Mg DM ha^{-1}) was much lower than of *P. aduncum* and rates decreased with time, which is common in non-woody fallows (Szott et al., 1994). Above ground biomass of imperata in southeast Asia can reach

18 Mg DM ha^{-1} (NRI, 1996). The above ground biomass of 1-year-old imperata in East Kalimantan was ranging from 5.5 to 10.7 Mg ha^{-1} (Hashimotio et al., 2000), and in the drier parts of Papua New Guinea biomass of imperata ranged from 7.9 to 16.6 Mg ha^{-1} (Holmes et al., 1980). Again, the large biomass accumulation of the imperata in this study, reflects the high soil fertility and favourable rainfall.

4.2. Nutrient accumulation

Nutrient concentration of piper leaves were higher than those of imperata which contained low levels of all major and minor nutrients. In both fallow types, nutrient concentrations decreased with time which is usually found. There was little difference in the nutrient concentration of piper leaves and fruits at 23 months, except for P which was high in piper fruits. It appears that nutrient concentrations cannot fully explain why the fruits are favoured by Neotropical bats, which are held responsible for the rapid spread of *P. aduncum* (Kidd, 1997; Thies et al., 1998).

Except for N, nutrient content in the above ground biomass of piper exceeds those published in the literature for 2-year-old natural and managed fallows. Nutrients in the imperata biomass were low and K contents declined with time possibly due to leaching of K from the biomass because a portion of the above ground biomass was dead after 1 year. Piper returns large amounts of K to the soil, which is the main nutrient for the root crop dominated farming systems in Papua New Guinea. Piper also contains considerable amounts of S which is often deficient in agricultural crops in the humid lowlands (Hartemink and Bourke, 2000). In the study area, piper is not burned after it is slashed, so most of the nutrients could potentially become available when the vegetation debris decomposes. Burning would accelerate nutrient availability but may also cause considerable losses (Mackensen et al., 1996; Nye and Greenland, 1964). Overall, the piper fallow accumulated more nutrients than the grass fallow with imperata, which is commonly found (Jaiyebo and Moore, 1964; Nye and Greenland, 1960). No estimate could be made of total nutrient stocks and decaying roots provide another important source of nutrients when the fallows are slashed (Greenland and Kowal, 1960).

At 23 months, piper fallows had fixed 19.6 Mg C ha^{-1} which is twice the amount of C fixed by imperata. The sequestration of C by tropical secondary forests is an important sink, which helps to offset the negative effects of anthropogenic CO_2 emission (Lal et al., 1998). Relatively, little has been published about C sequestration by fallow vegetation in the humid tropics. On poor fertility soils in Cameroon 10–20 Mg C ha^{-1} was found in bush fallow vegetation (Kotto-Same et al., 1997), whereas up to 35 Mg C ha^{-1} has been reported in mature tropical fallows (Houghton, 1995; Lal et al., 1997). The data from this experiment show that *P. aduncum* can fix large amount of C in a relative short period (23 months) and that it is a better C sink than imperata grassland, which was also concluded for the humid lowlands of East Kalimantan (Hashimotio et al., 2000).

5. Conclusions

The trend to shorter fallow periods in the shifting agriculture systems of the Papua New Guinea lowlands calls for management alternatives that accelerate nutrient accumulation like the use of improved fallows (Sanchez, 1999). This study has, however, shown that *P. aduncum* is an effective nutrient and biomass accumulator out yielding published data on natural and improved fallows (Szott et al., 1999; Szott et al., 1994). Biomass and nutrient accumulation of piper is faster than that of natural regrowth in Papua New Guinea, thus providing a quicker soil cover and capturing nutrients which otherwise may have been leached. An advantage of *P. aduncum* fallows is that it continues to fix C whereas C fixation stagnates in imperata fallows at about 15 months. In the absence of bush fires, piper may also smother imperata grasslands, which are usually difficult to reclaim (Nye and Greenland, 1960; Santoso et al., 1996). Piper fallows may, however, also have negative effects including a loss of biodiversity (Rogers and Hartemink, 2000) and costly programs to eradicate it as was experienced with other bioinvaders in the Pacific (Stone, 1999). Piper has no N fixing capacity which is a disadvantage compared to managed fallow species on high base status soils in the humid tropics (Buresh and Cooper, 1999). Additional research is required to evaluate the effects of piper on long-term crop yields in the shifting agricultural systems of Papua New Guinea.

Acknowledgements

This study was undertaken as part of a research programme on integrated nutrient management for sustainable sweet potato cultivation in the humid lowlands of Papua New Guinea. The programme was funded by the Papua New Guinea University of Technology and the Australian Centre for International Agricultural Research. I am greatly indebted to Mr. Spencer Poloma, Mr. Gelang Gwaidong and Mr. Philip Vovola of the Papua New Guinea University of Technology for technical assistance during fieldwork, and to Dr. Jane O'Sullivan and Ms. J. Mercer of the University of Queensland for chemical analysis of the plant samples. Mr. Niels Batjes of ISRIC is thanked for his comments on the draft of this paper.

References

Allen, B.J., Bourke, R.M., Hide, R.L., 1995. The sustainability of Papua New Guinea agricultural systems: the conceptual background. Global Environ. Change 5, 297–312.

Allen, B.M., 1966. *P. aduncum* L. in Malaya. Malayan Nature J. 19, 307.

Bornstein, A.J., 1991. The Piperaceae in the southeastern United States. J. Arnold Arboretum 1 (Suppl.), 349–366.

Bourke, R.M., 1985. Sweet potato (*Ipomoea batatas*) production and research in Papua New Guinea. Papua New Guinea J. Agric. Forestry Fisheries 33, 89–108.

Buresh, R.J., Cooper, P.J.M., 1999. The science and practice of short-term improved fallows: symposium synthesis and recommendations. Agroforestry Syst. 47, 345–356.

Burger, W.C., 1971. Piperaceae. Fieldiana: Botany 35, 79–96.

Chew, W.L., 1972. The genus piper (Piperaceae) in New Guinea, Solomon Islands, and Australia. J. Arnold Arboretum 53, 1–25.

Christanty, L., Mailly, D., Kimmins, J.P., 1996. Without bamboo, the land dies: biomass, litterfall, and soil organic matter dynamics of a Javanese bamboo talun-kebun system. Forest Ecol. Manage. 87, 75–88.

Duguma, B., Tonye, J., Kanmegne, J., Manga, T., Enoch, T., 1994. Growth of ten multipurpose tree species on acid soils in Sangmelima, Cameroon. Agroforestry Syst. 27, 107–119.

FAO, 1990. Forest resource assessment 1990. Global Synthesis. FAO, Rome.

Freyne, D.F., McAlpine, J.R., 1987. Land clearing and development in Papua New Guinea. In: Lal, R., Nelson, M., Scharpenseel, H.W., Sudjadi, M. (Eds.), Tropical Land Clearing for Sustainable Agriculture. Proceedings of an IBSRAM Inaugural Workshop. IBSRAM, Bangkok, pp. 153–163.

Gehring, C., Denich, M., Kanashiro, M., Vlek, P.L.G., 1999. Response of secondary vegetation in eastern Amazonia to relaxed nutrient availability constraints. Biogeochemistry 45, 223–241.

Greenland, D.J., Kowal, J.M.L., 1960. Nutrient content of the moist tropical forest of Ghana. Plant and Soil 12, 154–174.

Halenda, C.J., 1993. Aboveground biomass production and nutrient accumulation of *Gmelina arborea* plantation in Sarawak, Malaysia. J. Tropical Forest Sci. 5, 429–439.

Hartemink, A., Bourke, R.M., 2000. Nutrient deficiencies of agricultural crops in Papua New Guinea. Outlook Agric. 29, 97–108.

Hartemink, A.E., 1999. *P. aduncum* fallows in the lowlands of Papua New Guinea. In: Cairns, M. (Ed.), Indigenous Strategies for Intensification of Shifting Cultivation in Southeast Asia. ICRAF, Bogor, pp. 193–196.

Hartemink, A.E., O'Sullivan, J.N., 2001. Leaf litter decomposition of *P. aduncum*, *Gliricidia sepium* and *I. cylindrica* in the humid lowlands of Papua New Guinea, Plant and Soil, in press.

Hartemink, A.E., Poloma, S., Maino, M., Powell, K.S., Egenae, J., O'Sullivan, J.N., 2000. Yield decline of sweet potato in the humid lowlands of Papua New Guinea. Agric. Ecosyst. Environ. 79, 259–269.

Hashimotio, T., Kojima, K., Tange, T., Sasaki, S., 2000. Changes in carbon storage in fallow forests in the tropical lowlands of Borneo. Forest Ecol. Manage. 126, 331–337.

Henty, E.E., Pritchard, G.H., 1988. Weeds of New Guinea and their Control. Department of Forests, Lae.

Heyne, K., 1927. De nuttige planten van Nederlandsch Indië. I, 2e druk. Departement van Landbouw, Nijverheid en Handel, Buitenzorg.

Holmes, J.H.G., Lemerle, C., Schottler, J.H., 1980. *I. cylindrica* for cattle production in Papua New Guinea. Papua New Guinea Agric. J. 31, 51–62.

Houghton, R.A., 1995. Changes in the storage of terrestrial carbon since 1850. In: Lal, R., Kimble, J.M., Levine, E., Stewart, B.A. (Eds.), Soils and Global Change. CRC Press, Boca Raton, FL, pp. 46–65.

Jaiyebo, E.O., Moore, A.W., 1964. Soil fertility and nutrient storage in different soil-vegetation systems in a tropical rainforest environment. Tropical Agric. 41, 129–139.

Kidd, S.B., 1997. A note on *P. aduncum* in Morobe Province, Papua New Guinea. Sci. New Guinea 22, 121–123.

Kotto-Same, J., Woomer, P.L., Appolinaire, M., Louis, Z., 1997. Carbon dynamics in slash-and-burn agriculture and land use alternatives of the humid forest zone in Cameroon. Agric. Ecosyst. Environ. 65, 245–256.

Lal, R., Kimble, J.M., Follett, R.F., 1997. Land use and soil C pools in terrestrial ecosystems. In: Lal, R., Kimble, J.M., Follett, R.F., Stewart, B.A. (Eds.), Management of Carbon Sequestration in Soil. CRC Press, Boca Raton, FL, pp. 1–10.

Lal, R., Kimble, J.M., Follett, R.F., Stewart, B.A. (Eds.), 1998. Soil Processes and the Carbon Cycle. CRC Press, Boca Raton, FL.

Mackensen, J., Holscher, D., Klinge, R., Folster, H., 1996. Nutrient transfer to the atmosphere by burning of debris in eastern Amazonia. Forest Ecol. Manage. 86, 121–128.

Maia, J.G.S., Zohhbi, M.G.B., Andrade, E.H.A., Santos, A.S., da Silva, M.H., Luz, A.I.R., Bastos, C.N., 1998. Constituents of the essential oil of *P. aduncum* L. growing wild in the Amazon region. Flavour Fragrance J. 13, 259–272.

McAlpine, J., Quigley, J., 1995. Papua New Guinea Natural Resources, Land Use and Population. CSIRO, Brisbane.

McFadyen, R.C., Skarratt, B., 1996. Potential distribution of *Chromolaena odorata* (siam weed) in Australia, Africa and Oceania. Agric. Ecosyst. Environ. 59, 89–96.

Menz, K., Magcale-Macandog, D., Wayan Rusastra, I. (Eds.), 1998. Improving Smallholder Farming Systems in imperata Areas of Southeast Asia: Alternatives to Shifting Cultivation. ACIAR Monograph No. 52, Canberra, p. 280.

Meyer, J.Y., 1996. Status of *Miconia calvescens* (Melastomataceae), a dominant invasive tree in the Society Islands (French Polynesia). Pacific Sci. 50, 66–76.

Nair, M.G., Burke, B.A., 1990. Antimicrobial piper metabolite and related compounds. J. Agric. Food Chem. 38, 1093–1096.

NRI, 1996. Imperata Management for Smallholders. Natural Resources Institute, UK, p. 53.

Nye, P.H., Greenland, D.J., 1960. The Soil Under Shifting Cultivation. Technical Communication No. 51, Commonwealth Bureau of Soils, Harpenden.

Nye, P.H., Greenland, D.J., 1964. Changes in the soil after clearing tropical forest. Plant and Soil 21, 101–112.

Paijmans, K., 1976. New Guinea Vegetation. Australian National University Press, Canberra.

Rogers, H.R., Hartemink, A.E., 2000. Soil seed bank and growth rates of an invasive species, *P. aduncum*, in the lowlands of Papua New Guinea. J. Tropical Ecol. 16, 243–251.

Sanchez, P.A., 1999. Improved fallows come of age in the tropics. Agroforestry Syst. 47, 3–12.

Santoso, D., Adiningsih, S., Mutert, E., Fairhurst, T., van Noordwijk, M., 1996. Soil fertility management for reclamation of imperata grasslands by smallholder agroforestry. Agroforestry Syst. 36, 181–202.

Slaats, J.J.P., van der Heiden, W.M., Stockmann, C.M., Wessel, M., Janssen, B.H., 1996. Growth of the *Chromolaena odorata* fallow vegetation in semi-permanent food crop production systems in southwest Côte d'Ivoire. Netherlands J. Agric. Sci. 44, 179–192.

Smith, A.C., 1981. Piperaceae. Flora Vitiensis Nova 2, 57–65.

Stohlgren, T.J., et al., 1999. Exotic plant species invade hot spots of native plant diversity, Ecol. Monogr. 69, 25–46.

Stone, R., 1999. Keeping paradise safe for the natives. Science 285 (5435), 1837.

Szott, L.T., Palm, C.A., 1996. Nutrient stocks in managed and natural humid tropical fallows. Plant and Soil 186, 293–309.

Szott, L.T., Palm, C.A., Buresh, R.J., 1999. Ecosystem fertility and fallow function in the humid and subhumid tropics. Agroforestry Syst. 47, 163–196.

Szott, L.T., Palm, C.A., Davey, C.B., 1994. Biomass and litter accumulation under managed and natural tropical fallows. Forest Ecol. Manage. 67, 177–190.

Thies, W., Kalko, E.K.V., Schnitzler, H.U., 1998. The roles of echolocation and olfaction in two Neotropical fruit-eating bats, *Carollia perspicillata* and *C. castanea* feeding on piper. Behav. Ecol. Sociobiol. 42, 397–409.

Turvey, N.D., 1994. Afforestation and Rehabilitation of imperata Grassland in Southeast Asia: Identification of Priorities for Research, Education, Training and Extension, Technical Report No. 28, ACIAR, Canberra, p. 52.

Uhl, C., 1987. Factors controlling succession following slash-and-burn agriculture in Amazonia. J. Ecol. 75, 377–407.