Journal of Tropical Ecology (2000) 16:243–251. With 2 figures

Soil seed bank and growth rates of an invasive species, *Piper aduncum*, in the lowlands of Papua New Guinea

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(Accepted 1st October 1999)

ABSTRACT. Secondary fallow vegetation in parts of the Papua New Guinea lowlands is dominated by the shrub *Piper aduncum* L. that originates from South America. Here we report on its seed bank, growth rate and biomass accumulation. *P. aduncum* accounted for 69 % (408 m^{-2}) of the seed bank in the forest and 53 % (1559 m^{-2}) of the seed bank under fallow. About 90 % of the tree seed bank at the fallow site was dominated by *P. aduncum* whereas this was 78 % in the forest soil. Two-year-old *P. aduncum* had grown to 4.5 m height and had accumulated 48 Mg dry matter (DM) per ha of above ground biomass. The rate of biomass accumulation increased from 10 Mg DM ha^{-1} y^{-1} in the first year to 40 Mg DM ha^{-1} y^{-1} in the second year when 76 % of the biomass consisted of mainstems. The highest growth rate of 134 kg DM ha^{-1} d^{-1} occurred when *P. aduncum* was 17-mo-old. Aggressive invasion and monospecific stands of *P. aduncum* are explained by its dominance in the seed bank, fast growth, and high rates of biomass accumulation. *P. aduncum* is a major competitor to indigenous tree species and presents a threat to Papua New Guinea's rich biodiversity.

KEY WORDS: Introduced plant species, tropical forest, seed bank, biomass accumulation, growth rate, fallow vegetation, *Piper aduncum*

INTRODUCTION

Introducing plant species into new environments can have many unanticipated ecological effects. Whether deliberately introduced as ornamentals and economic plants or brought in accidentally, new species can have devastating effects on ecosystem quality (van Groenendael *et al.* 1998) and functioning through out-competing indigenous species and habitat modification. As a

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result, an endemic flora may become extinct (Lorence & Sussman 1986). An example which has recently gained attention in Africa and Asia is the small shrub *Chromolaena odorata* L., a native of Central and South America which was brought to Asia in the late 19th century (Slaats 1995). It then spread rapidly across Asia and arrived in Africa in the 1940s. Its spread is closely related to human activities, in particular frequent disturbances of the natural vegetation from agriculture and road maintenance (McFadyen & Skarratt 1996, Slaats 1995). An example from the Pacific is *Miconia calvescens* DC. It was introduced in Tahiti in 1936 and has become a major plant pest in the Society Islands of French Polynesia (Meyer 1996).

In the lowlands of Papua New Guinea the exotic tall shrub *Piper aduncum* L., that originates from South America now dominates much of the secondary fallow vegetation. In many parts of the lowlands *Piper aduncum* invaded similarly to *C. odorata* in Asia and Africa and *M. calvescens* in Polynesia. *P. aduncum* is indigenous to tropical America where it is found from Mexico to Bolivia. Its habitat in Central America is restricted to evergreen vegetation and near watercourses in seasonally deciduous forests, from sea level to *c.* 1500 m asl. *P. aduncum* was introduced in Indonesia in 1860, and is now commonly found in Irian Jaya and Malaysia. In the Pacific it occurs in Fiji but is not found in Hawaii or Northern Australia (Hartemink 1999).

It is unknown how and when *P. aduncum* arrived in Papua New Guinea but it was first described in the Morobe Province in 1935 (J.F. Veldkamp, Rijksherbarium Leiden, *pers. comm.* 1999). *P. aduncum* is found in many parts of the humid lowlands where 20–30 y ago it was absent (Kidd 1997, R. M. Bourke, *pers. comm.* 1998). It occurs widely in the Morobe and Madang Province at altitudes up to 600 m asl, and is found in the highland provinces up to altitudes of 1800 m asl. *P. aduncum* is frequently observed along logging tracks and on fallow sites where it often forms monospecific stands. It occurs in soil seed banks (Saulei 1989) and appears to be fast growing.

Despite the rapid invasion of *P. aduncum*, very little is known about its growth characteristics and how it can establish monospecific stands. We therefore conducted a seed bank study in fallow and forested areas in addition to measurements of its rate of height growth and biomass accumulation. These aspects are considered vital attributes (Drury & Nisbet 1973) that might explain *P. aduncum*'s spread across the humid lowlands of Papua New Guinea.

METHOD

The Sites

The study was conducted at two sites reflecting contrasting environments where *P. aduncum* is invasive. The first site at Oomsis (6°45′S, 146°47′E), 40 km west of Lae, at *c.* 400 m asl is in a mixed species lowland rainforest (Paijmans 1976). The forest at Oomsis was selectively logged *c.* 30–35 y ago. Lowland forests in Morobe Province commonly have a basal area of 25–35 m^2

ha^{-1}, but basal areas at Oomsis are *c*. 18 m^2 ha^{-1} (H. M. Rogers, unpubl. data) suggesting the forest had not fully recovered from the logging. This was reflected by fewer large stems (> 0.5 m diameter at breast height) (H. M. Rogers unpubl. data), otherwise the forest appeared little different in structure from unlogged forest. Shifting cultivation is practised in irregular patches of less than 0.5 ha within the forest and *P. aduncum* is often abundant and sometimes dominant in abandoned fields. Within the forest, occasional stems of *P. aduncum* were present in the understorey and along hunting tracks. *P. aduncum* saplings occurred in some small gaps, often in association with saplings of *Musa* and *Macaranga* spp. Mean annual rainfall at the nearest weather station (Lae airport 20 km E, altitude 10 m asl) is *c*. 4800 mm. The mean daily temperature is *c*. 26 °C. The soils are well drained and derived from schist. They are tentatively classified as chromic luvisols (Kubo 1992).

The second site was located at Hobu (6°34′S, 147°02′E) at 405 m asl. This site was chosen as an example of a secondary vegetation fallow site where *P. aduncum* is abundant forming monospecific stands. Hobu is located *c*. 20 km northeast of Lae at the footslopes of the Saruwaged range. The mean annual rainfall of 3000 mm is fairly evenly distributed throughout the year. The mean annual temperature is *c*. 26 °C. Soils are derived from a mixture of colluvial and alluvial deposits of mostly igneous rocks. The soils have a high base status and are classified as eutric cambisols (A. E. Hartemink, unpubl. data).

Seed Bank Study

Plot locations were chosen to reflect representative sites of where *P. aduncum* had invaded closed forest (Oomsis) and fallow (Hobu) sites. For the closed forest site care was taken to ensure there were no fallow sites within *c*. 200 m. At each site 2 m^2 of soil and associated leaf litter was collected by taking eight samples measuring 0.5-m × 0.5-m to 0.05 m depth from random points within a 50-m × 50-m plot at the University of Technology, Lae. Each sample was thoroughly mixed and a subsample (3780 cm^3) of *c*. 50% of total volume (7500 cm^3) was spread to a depth of 0.03 m in plastic germination trays (0.42 m × 0.30 m), over a base of 0.02 m of autoclaved soil to provide a deeper rooting environment. Each tray (subsample) represented a germination test of 30.2% (0.0756 m^2) of the original sample. Autoclaved soils were heated to 121 °C for 90 min. For each site, a control was prepared from autoclaved soil to assess contamination from local seed rain.

Eighteen trays were placed in a germination house under coarse shade netting. Germinating seedlings were counted and removed at biweekly intervals from each tray for 16 wk from May to September 1998 during which 1788 mm of rain was recorded. Seedlings that could not initially be identified were tagged and left to grow until identification could be made.

Growth Rate Study

In October 1996, an area of *c*. 200 m^2 was cleared at Hobu. It consisted mainly of 5-y old secondary fallow vegetation dominated by *P. aduncum* and to a lesser extent by *Homalanthus* sp., *Macaranga* sp., *Trichospermum* sp. and *Trema orientalis*. All vegetation debris was removed from the plot and no burning was practised. In December 1996, a block of 90 m^2 was planted with young seedlings of *P. aduncum*, which were taken from nearby roadcuts. Spacing was 0.75-m × 0.75-m which we have frequently observed in *P. aduncum* fallows. The plots were manually weeded. After 5 mo, the heights of four plants were measured and these were cut at ground level and separated into main stems, branches, leaves and litter. Each plant part was weighed and dried at 70 °C for 72 h for dry matter determination. Every 3 mo, the biomass was assessed of four plants 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 mo old. Roots were not sampled in this study.

A few herbaceous weeds germinated in the autoclaved control trays, but no tree or shrub seedlings. The herbaceous weeds were confined to the Hobu control soil, and were mainly *Pilea microphylla* and *Cardamine hirsuta*. Because of the negligible numbers of these species, no adjustments were made to counts from the trays containing the samples.

RESULTS

Seed Banks

In total 41 species were recorded of which 15 species were common to both sites (Table 1). Twenty species were identified to genus or family level and 21 to species level. In total 981 seedlings m^{-2} germinated from Oomsis (forest) and 4826 m^{-2} from Hobu (fallow). At both sites, the shrub *P. aduncum* was the dominant seed bank species, accounting for 69% of the seed stocks at Oomsis and 53% of the seed stocks at Hobu. About 90% of the woody species seed bank at Hobu was dominated by *P. aduncum* whereas this was 78% at Oomsis. Other secondary tree species were the second most common seed stock life form at Oomsis (18%) followed by herbs (12%). In contrast, at Hobu herbs were the second most common seed stock (40%), followed by secondary tree species (6%). For both sites, vines and grasses made up less than 1% of the seed stocks.

The progress of germination at each site for the different life forms and *P. aduncum* is shown in Figure 1. The first seedlings were observed after 5 d. In the Oomsis soil only a few secondary trees, herbs and *P. aduncum* had germinated during the first 4 wk, but thereafter the rate of *P. aduncum* germination increased. In the Hobu soil, the rate of germination for *P. aduncum* increased dramatically from 4 wk onwards. For both sites, the rate of *P. aduncum* germination had reached its peak before 8 wk.

The number of seedlings emerging per tray was variable. For the Oomsis samples, seedlings of *P. aduncum* ranged from 10 to 95 per tray (mean 52 ± 31), and secondary tree seedlings ranged from 4 to 24 (mean 13 ± 8). For the Hobu soil, *P. aduncum* seedlings ranged from 121 to 479 per tray (mean 211 ± 126), and herbs ranged from 21 to 278 (mean 154 ± 93).

Table 1. Species and number of seedlings germinated (per m^2) from soil samples of Oomsis (forest site) and Hobu (fallow site), Papua New Guinea. Germination period was 16 wk.

		Site	
	Species	Oomsis	Hobu
Vines	*Cissus* sp.	—	2
	Mikania micrantha Kunth	—	2
	Wedelia biflora (L.) DC	—	3
	Total	0	7
Grasses	*Echinochloa colonum* Beauv.	—	2
	Imperata cylindrica (L.) P. Beauv.	—	5
	Paspalum cartilagineum L.	3	28
	Rottboellia exaltata L.f.	—	2
	Total	3	37
Herbs	*Alocasia* sp. (Schott) G. Don. F.	3	5
	Amaranthus sp.	—	2
	Cardamine hirsuta L.	—	104
	Compositae	—	5
	Dichrocephala bicolor (Roth) Schltdl.	2	38
	Eupatorium odoratum L.	36	686
	Zingiberaceae	—	20
	Hedyotis corymbosa (L.) Lamk	—	2
	Musa sp.	66	25
	Oxalis sp.	2	38
	Peperomia pellucida (L.) Kunth	—	2
	Physalis angulata L.	—	12
	Pilea microphylla (L.) Liebm.	13	845
	Solanum sp.	—	15
	Sonchus oleraceus L.	—	38
	Urticaceae	—	81
	Total	122	1918
Primary trees	*Alstonia spectabilis* Monach.	2	2
	Neonauclea sp.	—	2
	Total	2	4
Secondary trees	*Anthocephaluschinenesis* (Lamk) Rich	33	—
	Cordia dichotoma Forst.	—	10
	Elaeocarpus sp.	2	—
	Ficus sp.	—	17
	Gardenia sp.	15	2
	Glochidion sp.	35	—
	Homalanthus sp.	7	3
	Macaranga sp.	43	40
	Muntingia calabura L.	3	—
	Octomeles sumatrana Miq.	3	20
	Phyllanthus sp.	—	2
	Pipturus sp.	18	170
	Trema orientalis (L.) Bl.	—	7
	Trichospermum sp.	20	8
	Total	179	279
Shrubs	*Piper aduncum* L.	675	2578
	Mussaenda sp.	—	3
	Total	675	2581
	Grand Total	981	4826

—, not present.

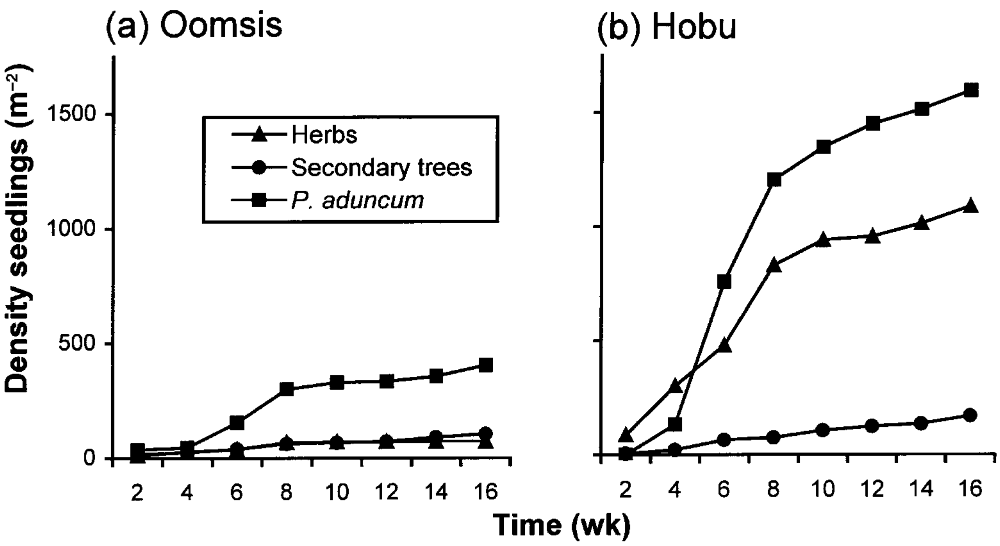

Figure 1. Cumulative germination of herbs, secondary trees and *Piper aduncum* from soil samples of (a) Oomsis and (b) Hobu, Papua New Guinea.

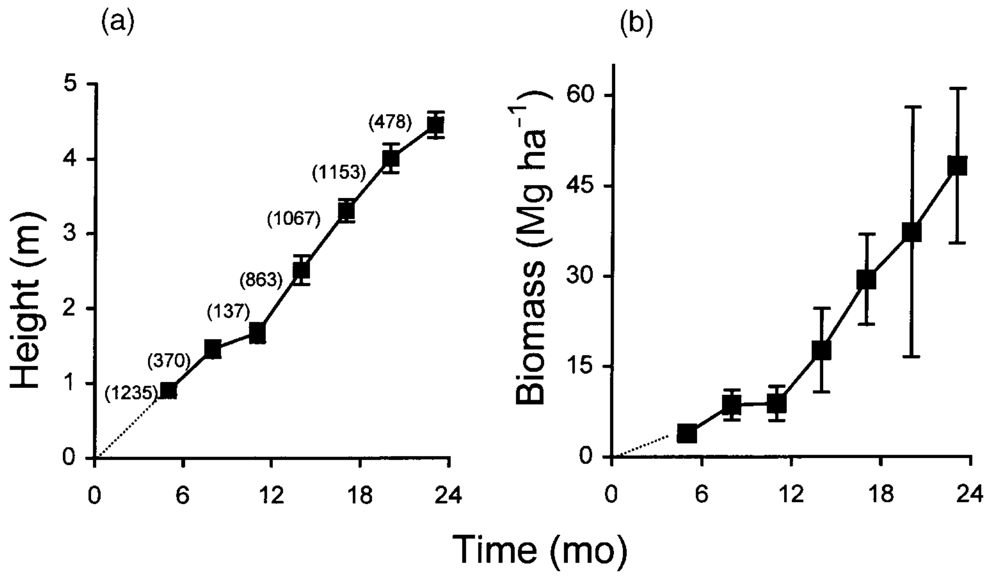

Figure 2. Mean (± SD) (a) growth (m), and (b) biomass accumulation (Mg ha^{-1}) of *Piper aduncum* at Hobu, Papua New Guinea. Amount of rain (mm) between sampling times in parenthesis in (a).

Growth Rates

After 5 mo, *P. aduncum* at Hobu had grown to about 0.9 m height (Figure 2a) and total above ground biomass was 3.9 Mg dry matter (DM) ha^{-1} (Figure 2b). This corresponds to a growth rate of 23 kg DM ha^{-1} d^{-1}. At one year, the average height of the *P. aduncum* plants was 1.7 m and dry biomass had increased to 8.8 Mg ha^{-1}. In the second year the *P. aduncum* height increased from 3.3 m at 17 mo to 4.5 m at 23 mo. Biomass accumulation was 29.4 Mg ha^{-1} at 17 mo and 48.3 Mg ha^{-1} at 23 mo.

More than 50% of the above ground biomass consisted of leaves and less than 25% was found in the main stem after 5 mo of growth. We observed a gradual change in the biomass distribution with time. The percentage in leaves and small branches both decreased whereas around 75% of the above ground biomass was found in the main stems after 23 mo of growth. Branches and litter accounted for less than 10% of the total dry biomass after 23 mo.

The average rate of aboveground biomass accumulation over the 2-y period was 85 kg DM ha^{-1} d^{-1} but rates were variable. The highest rate occurred between 14 and 17 mo and was 134 kg DM ha^{-1} d^{-1}. Between 8 and 11 mo, a period with little rain, aboveground biomass gain was only 3 kg DM ha^{-1} d^{-1}. It appeared that the growth rate of *P. aduncum* both in biomass and height is favoured by high rainfall (Figure 2b). Although rainfall at the site is fairly well distributed throughout most years, 1997 was an exceptionally dry year due to El Niño, which affected most of Papua New Guinea. Only 1897 mm of rain fell in 1997 compared to 2067 mm in the first 6 mo of 1998. During the first 11 mo of our study, 1742 mm of rain fell whereas in the second year of growth 3590 mm fell.

DISCUSSION

Large numbers of viable *P. aduncum* seeds occurred in forest and fallow soils. The size of the seed banks were comparable to those of lowland tropical forests and regrowth sites in other parts of the world (Garwood 1989), with the forest soil seed bank being typically smaller than that of fallow soils (Thompson 1992). However, the P. aduncum seed bank occurred in numbers greater than other species conferring a competitive advantage during regeneration. There was considerable variation in number of seedlings per tray. The large variations may be attributed to non-uniform dispersal of seeds in the soil, non-uniform incorporation of seed into the top 0.05 m of soil, or the influence on germination of spatial variation of the soils at each site (Thompson 1992).

The difference in size of the *P. aduncum* seed bank between Oomsis and Hobu may simply reflect differences in seed rain because of high parent tree density at Hobu. However, frequency and scale of disturbance, and litter layer can also influence seed bank size. The soils at Hobu are frequently disturbed by clearance for cultivation, which favours establishment of species that are fast growing and can reach reproductive maturity at a young age (< 5 y). Repeated occupancy of pioneers at a site maintains a high density of their seed in the soil (Saulei & Swaine 1988). By contrast, within closed forest at Oomsis disturbances by smaller scale single treefalls appear to be more common, where opportunities for massive establishment by *P. aduncum* and replenishment of the soil seed bank are less common. Another explanation for seed bank differences is the difference in the depth of the litter layer at Hobu and Oomsis. Oomsis soils had a litter layer of up to 0.05 m depth compared to a thin or non-existent litter layer at Hobu. Accumulated litter might delay or prevent seeds reaching the soil giving more chance for predation (Cintra 1997).

P. aduncum height growth of 1.7 m y^{-1} is rapid in comparison with pioneers from other tropical forests. For example in lowland Caribbean forests, common pioneer trees have a mean height growth of only 0.4 m y^{-1} to 1.3 m y^{-1} (Vandermeer *et al.* 1998). *P. aduncum*'s fast height growth enabled it to quickly outgrow associated pioneer tree species like *Macaranga* and *Pipturus* sp. Maximum growth rates of *P. aduncum* were 134 kg DM ha^{-1} d^{-1}, which is high. Slaats (1995) found rates up to 24 kg ha^{-1} d^{-1} for the pioneer shrub species *Chromolaena odorata* in lowlands of the Ivory Coast. Apparently, the humid conditions in combination with the relatively fertile soils in the Papua New Guinea lowlands favour rapid growth.

Although fast growth rate and abundant seed bank are characteristic of tropical pioneer species (Swaine & Whitmore 1988), in this study *P. aduncum* had a mega seedbank in relation to associated pioneers (e.g. *Macaranga*), and had a particularly high growth rate. We consider these two factors vital attributes (Drury & Nisbet 1973), partly explaining its persistence. However, *P. aduncum* also has the ability to resprout once damaged, which is a trait that would favour persistence in disturbance-prone environments where the vegetation is not completely removed.

P. aduncum's presence in small gaps in closed forest, and its proliferation on frequently disturbed fallow sites suggest it has a catastrophic and gap-phase regeneration pattern (Veblen 1992). Therefore, in Papua New Guinea's lowland forests, which are subjected to catastrophic natural disturbances, such as landslides or stand-devastating windthrow (Johns 1986), *P. aduncum* may pose a serious threat to the indigenous flora by out-competing other pioneer species. Moreover, anthropogenic factors contribute to the spreading of *P. aduncum* through logging and shifting cultivation. Forest fires, which were particularly severe in the 1997/98 El Niño southern oscillation, may present new frontiers for *P. aduncum* invasion. A possible advantage of the *P. aduncum* invasion is, however, that man-made grasslands (mainly *Imperata cylindrica*) may revert to bushfallow vegetation.

ACKNOWLEDGEMENTS

The research was funded through grants of the Research Committee of the Papua New Guinea University of Technology. Mr John Simaga and Mr Armstrong Bellamy identified the seedlings, and technical assistance from Mr Spencer Poloma, Mr Gelang Gwaidong and Mr Luke Kawe is gratefully acknowledged. Mr Hans van Baren and Mr Niels Batjes of ISRIC are thanked for their comments on the draft of this paper.

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