

Successful invasion of the neotropical species *Piper aduncum* in rain forests in Papua New Guinea

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Abstract. *Piper aduncum* is a neotropical invasive species which has spread throughout Papua New Guinea over the past three decades. It has become a most successful alien woody plant in New Guinea, occurring from sea level up to 2000 m a.s.l. The species prefers initial stages of forest succession and is particularly common in recently abandoned gardens representative of a system of swidden agriculture. It often attains high cover, suppresses other pioneer species and becomes the absolute dominant species in these habitats. The species is now also spreading into naturally disturbed habitats far from direct human influence, such as natural tree-fall gaps, landslides and frequently flooded stream banks. It has, however, never been found in a closed primary forest. The species germinates from faeces of mammal and bird species, and we conclude that dispersal through endozoochory contributes to this species' extraordinary success in Papua New Guinea. A similar invasion behaviour has been documented over a large geographic area, from Malaysia to Fiji. *Piper aduncum* has attributes which are common amongst successful invasive species: (1) a large native geographic range; (2) aggressively colonizing disturbed habitats in its native area; (3) relatively small seeds; (4) a short juvenile period; (5) a large seed production every year.

Keywords: Alien species; Biological invasion; Disturbance; Rain forest succession; Swidden agriculture.

Abbreviations: CCA = Canonical Correspondence Analysis; PG = Papua New Guinea; RDA = Redundancy Analysis.

Introduction

Invasions by alien species are one of the most serious threats to ecosystems around the world. Studies of invasive species do not only have important practical consequences, but are also of theoretical interest (e.g. Elton 1958; Rejmánek 2000; Sakai et al. 2001). Many studies aim to derive a set of rules predicting the ability of species to invade, and the susceptibility of a community to invasions (Rejmánek 1999). For a species, the 'taxon-specific approach' (Rejmánek 2000) often yields very successful predictions; this approach is based on the fact that a species which has been shown to be invasive in one region is also a threat to other regions with similar environmental conditions. This approach is very useful when tackling practical problems; however, it does not provide a mechanistic insight into invasion processes. From a mechanistic point of view, the approach based on an evaluation of biological characters is more interesting. Many attempts have been made to find a set of biological characters that can predict the extent to which a species will be invasive (e.g. Rejmánek & Richardson 1996). Similarly, it has been demonstrated that some community types are more, and some are less prone to invasion by alien species (Rejmánek 1989, 1996, 1999). One of the few rules that are repeatedly confirmed in various parts of the globe is the lack of invasions in undisturbed tropical forests (Rejmánek 1996). Tropical rain forests in Papua New Guinea (PG hereafter) represent one of the largest areas of this biome in the world. This area has recently been invaded by a neotropical species, *Piper aduncum*, probably the largest invasion of a woody species in this area. Are the general rules for invasibility and invadability applicable also to this species?

Piper aduncum (*Piperaceae*) is a shrub or small tree up to 8 m high. It is the most common species in its genus in the western Hemisphere. It originates from the West Indies and tropical South and Central America (from Mexico to Bolivia). In the Americas, its distribution overlaps almost exactly with the distribution of the

genus (Burger 1971). It spreads via seeds and it also has a good resprouting ability. Fruits are eaten by birds (Petir et al. 1998) and mammals, which also distribute the seeds. Fruits of all species of this genus are preferred by bats (Jarmillo & Manos 2001). *P. aduncum* is recognized as a serious weed in its native range (Vélez 1950; Lorenzi 2000) and it is also known to have spread beyond its original range within America – for example, it is reported as an alien species from three nature reserves in Florida (Gann & Bradley 1999). The species has multiple uses in its original range; e.g. it provides a traditional medicine (e.g. in Guatemala for the treatment of gonorrhoea; Caceres et al. 1995).

P. aduncum was introduced to Indonesia in the 1860s, and is now commonly found throughout New Guinea, Indonesia, Malaysia, Solomon Islands, and Christmas Island (Backer et al. 1963; Du Puy 1993; Hashimoto et al. 2000; Rogers & Hartemink 2000). The species is also an invader and a serious weed in Fiji where it was introduced in the 1920s (Parham 1958). It is called 'yaqona ni onolulu' [Honolulu] in Fiji but it has never been reported from Hawaii. It was introduced to New Guinea probably during World War II. The oldest vouchers in the National Herbarium in Lae are from Lae in 1952 and from West Papua in 1955. There is also a voucher from Vanuatu (coll. Pat Curry) with a comment "informant said that Americans introduced the plant in 1941, not known why". The massive spread of the species started in the study area in the 1970s. This is reflected in the vernacular name of the plant in Salemben village (Petir et al. 1998), ca. 50 km NW of our study area (see below), which is Na Independens, or Independence Tree (PG attained independence in 1975). Although there are only 14 collections of *P. aduncum* in the Lae herbarium (half of them from the Morobe province, i.e. within easy reach from the Lae herbarium), the plant occurs in many other parts of the country. In addition to the northern lowlands, where it is very common, it is also found along the roads in the Highlands up to 2000 m a.s.l. In the Highlands, local people sometimes actively plant *P. aduncum*; from there it can easily spread further. The plant is also common in relatively remote places with little human migration and trade, for example, in the upper Yuat River (Elem village) along the margins of the Sepik basin. It has been speculated that it could have been introduced to New Guinea to control soil erosion.

P. aduncum is probably the most invasive species in this large genus with > 1000 species. It belongs to the section *Radula*, together with another somewhat invasive species – *P. hispidum* Sw. Another two invasive species are in the section *Lepianthes* (*P. peltatum* L. and *P. umbellatum* L.). These two sections belong to the neotropical clade (ca. 700 species) of the genus (Tebbs 1993; Jarmillo &

Manos 2001). Recently, *P. auritum* has been introduced to some Pacific Islands (Fiji, Tonga, Pohnpei).

Swidden (shifting, slash and burn) agriculture is a prevailing practice in many parts of the world, including all non-swamp lowlands of Papua New Guinea. In a typical swidden cycle in northern lowlands in PG, 0.5–1 ha of forest, preferably secondary regrowth, is cleared for a new garden. Part of the wood is used and part is burned *in situ*. The garden is planted with a mixture of crops, which are harvested for about a year, and then the garden is abandoned. Succession starts immediately after the forest has been cleared, and is characterized by the emergence of woody pioneer species, including several species of *Macaranga* (Lepš et al. 2001), and many other species. Woody species are present as weeds in the cultivated garden, either as seedlings or resprouters, and soon develop into a relatively species-rich community: 38 woody species were found in a 20 m × 20 m quadrat in an abandoned garden (Lepš et al. 2001). Until recently, this succession was dominated by local species. In recent decades, however, the course of the early succession has been altered by the invasion of *Piper aduncum* L. (Kidd 1997; Rogers & Hartemink 2000). In the succession, *P. aduncum* sometimes attains a canopy cover of 75% (visual estimate), and suppresses the native species. This is considered disadvantageous by local people, because *P. aduncum* has fewer uses in house construction, medicine etc. than have the native pioneer species. However, the sticks from *P. aduncum* are used as firewood, for fencing and for terracing in some parts of New Guinea (Bourke 1997), including our study area. Local farmers also believe that gardens which have been cleared from locally dominating *P. aduncum* are less fertile than those in areas where the secondary succession was not dominated by *P. aduncum*.

P. aduncum also enters early in the succession in other disturbed habitats, such as river banks swept by floods, natural forest gaps and landslides (which are probably good natural analogues for a garden succession; Johns 1986). In our experience, it is by far the most successful terrestrial invading plant species in PG, and is also successful in other countries in the region. The aim of this paper is to examine the ecology, particularly the habitat preferences (which include both the abiotic conditions and biotic interactions) of this species in northern PG, and compare the species with native species of similar habitat preferences. We aim to use this information to explain the invasion success of *P. aduncum*.

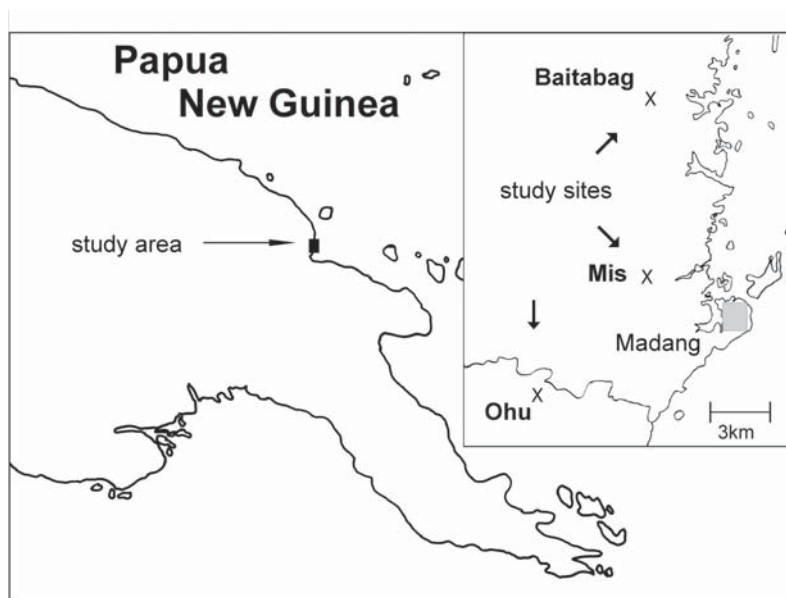


Fig. 1. The study area and its location within Papua New Guinea.

Study area

The study area was situated in the lowlands of the Madang Province, extending from the coast to the slopes of the Adelbert Mountains and bounded by the Gogol and Sempri Rivers. Fieldwork was concentrated in primary and secondary lowland forests near the Baitabag, Pau, Ohu and Mis Villages (145°41-8' E; 5°08-14' S; ca. 0-200 m, Fig. 1). General descriptions of a similar, nearby forest site can be found in Bowman et al. (1990). The average annual rainfall in the Madang area is 3558 mm, with a moderately dry season from July to September; mean air temperature is 26.5 °C and varies little throughout the year (McAlpine et al. 1983).

Methods

We monitored the distribution of 60 locally common species of woody plants, representing 19 families and 40 genera, including *P. aduncum* (listed in Table 1, below). These species were selected for the study of insect herbivores along forest successional gradient (Lepš et al. 2001; Novotný et al. 2002). Their distribution was recorded in a total of 116 quadrats, 400 m² each, distributed among seven habitats: recently abandoned gardens (24 quadrats), young secondary forests (20), old secondary forests (23), primary forests (22), riverine habitats (12), gaps after tree falls (12), and landslides (3). The first four vegetation types form a successional series, the latter three are habitats with natural disturbances. The gardens included in the study represented areas from 500 m² to 1 ha, cleared, most often within an area

of secondary forest, as a part of the swidden agricultural cycle. Young secondary forest usually did not contain trees over 20 cm DBH (diameter at breast height), whilst old secondary forest had such trees. Primary forest always contained numerous large trees (often DBH > 100 cm), lianas, and epiphytes. The riverine habitat was a rocky bed with a stream large enough to prevent the forest canopy from closing. The gaps were caused by a treefall in the primary forest and usually > 400 m² in size. The landslides were always on the steep slopes, usually ca. 1000 m². In the landscape mosaic, we attempted to place the quadrats into homogeneous habitat patches.

Plots of 5 m × 80 m were used in riverine habitat, while 20 m × 20 m quadrats were used in other habitats. Presence of all individuals in quadrats was recorded and for individuals taller than 1.5 m, the DBH was measured. For smaller individuals, a DBH of 1 mm was adopted for the calculation of basal area. The representation of each species in a plot was characterized by its number of individuals and its basal area (i.e. sum of cross-sectional areas of all the trees at breast height). The quadrats were censused in 2000 and early 2001.

For the data analysis, classical methods of univariate statistics and constrained ordinations CCA (Canonical Correspondence Analysis and Redundancy Analysis) were applied, using the CANOCO for Windows package (ter Braak & Šmilauer 1998).

Results

Piper aduncum was found in all vegetation types except primary forests and showed a clear preference for abandoned gardens (Fig. 2). It was present in all the garden plots, 92% of riverine plots, 80% of young secondary and 65% of old secondary forest plots, 75% of the gaps, and in two landslides out of the three. The highest density values were found in the gardens, followed by riverine habitats; the abundance in gaps was comparable to that in secondary forest. In terms of basal area, the optimal site conditions are found in garden and young secondary forest. This difference reflects the fact that in riverine habitats there are many seedlings and small saplings of this species, but they seldom reach a larger size. In old gardens, *P. aduncum* attained a density of up to 300 individuals and a basal area of up to 0.5 m² per 400-m² plot. The three landslides were highly variable: in one of them, *P. aduncum* was the dominant, whereas it was absent from another one.

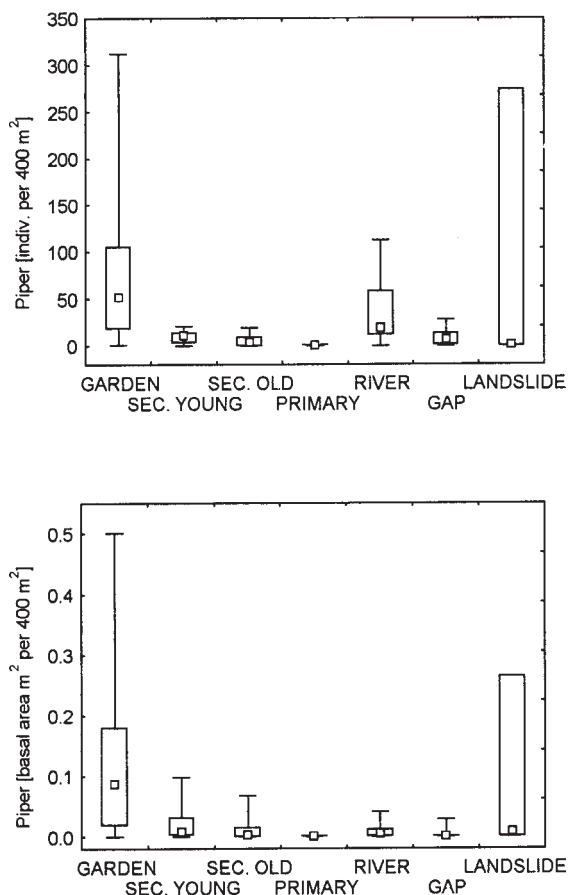


Fig. 2. Density (above) and basal area (below) of *Piper aduncum* in the studied habitats. Whiskers denote ranges, boxes correspond to the interquartile range and the square represents the median. To keep the original variability, the numbers are presented per quadrat (i.e. per 400 m²).

According to a species correlation analysis based both on the number of individuals and basal area in the 116 quadrats, the species most similar to *P. aduncum* is *Leucosyke capitellata*, a native early successional small tree. Both species are of similar growth form, and also of similar height. Also, the pattern of habitat preferences is very similar between the two species (Fig. 3), but *Leucosyke* is less frequent, and never reached abundance as high as *P. aduncum*. Three common native pioneer species, *Melanolepis multiglandulosa*, *Macaranga aleuritoides* and *M. brachytricha*, are shown for comparison in Fig. 3. Although they are common, they seldom attain such a high basal area as *P. aduncum* in gardens. The three species, however, are trees and persist in the forests longer in the succession, because they grow taller and thicker than *P. aduncum*.

The habitat preferences of all studied species and habitat similarities based on these preferences are presented in the CCA ordination diagram (Fig. 4), with species composition (Table 1) as the dependent vari-

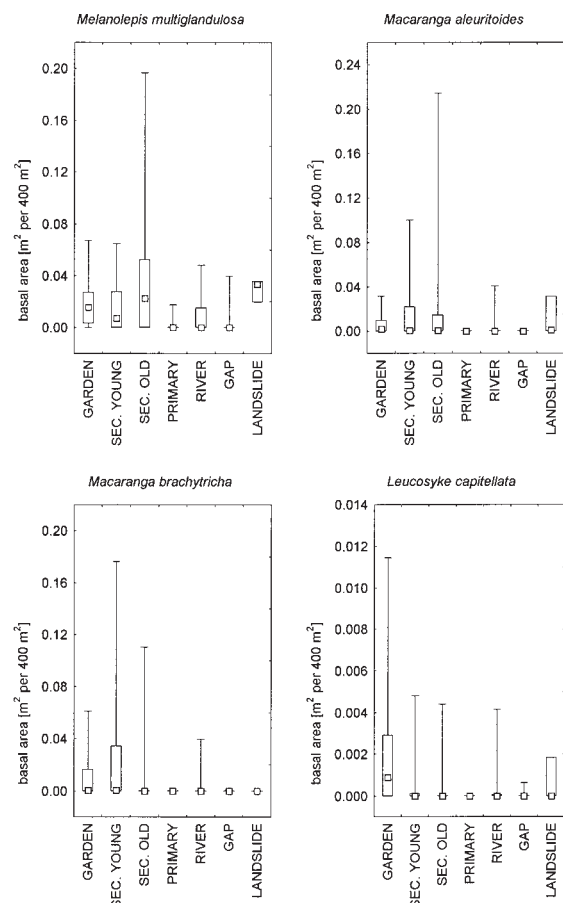


Fig. 3. Basal area of four common pioneer species in the studied habitats: *Melanolepis multiglandulosa*, *Macaranga aleuritoides*, *M. brachytricha* and *Leucosyke capitellata*. Symbols as in Fig. 2.

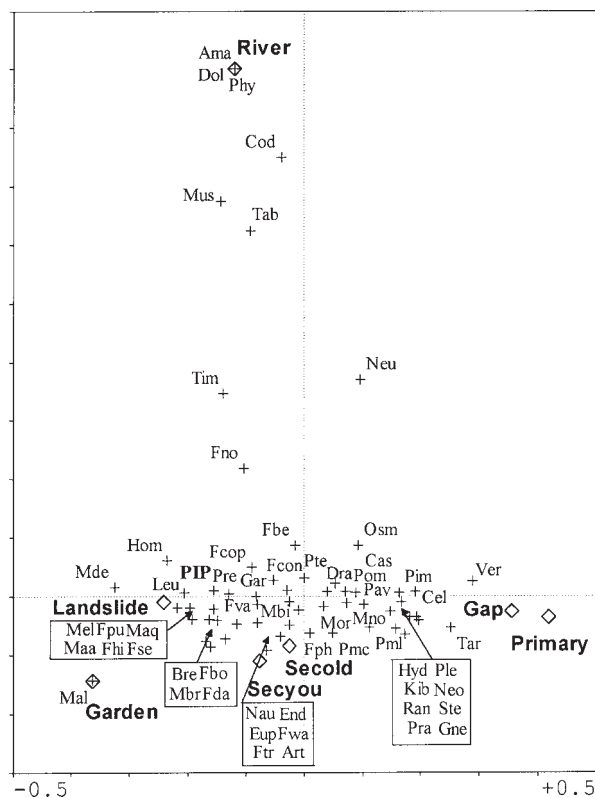


Fig. 4. Ordination diagram of CCA, with species composition (log transformed basal area) explained by the habitat type (categorical variable). The species names and their abbreviations are listed in Table 1. Habitats are shown by their centroids (Secyou = Secondary young forest, Secold = Secondary old forest). The relationship was highly significant ($P = 0.001$, Monte Carlo permutation test, 999 permutations).

able and habitat type (categorized as a set of dummy variables; see ter Braak & Šmilauer 1998) the sole explanatory factor. The ordination diagram shows that the envisaged successional trend is well reflected by the gradual change in species composition, and that the riverine habitat is an outlier. The species composition of the landslides is similar to that of the early successional communities on abandoned gardens. The gaps are very similar to the primary forest. Interestingly, *P. aduncum* is more common in gaps than most of the indigenous pioneer species. *P. aduncum* is most similar in distribution to typical pioneer species, such as *Leucosyke capitellata*, *Macaranga densiflora*, *M. quadriglandulosa*, *M. aleuritoides*, *M. brachytricha*, *Premna obtusifolia*, *Homalanthus novoguineensis* and *Melanolepis multiglandulosa* (see also Lepš et al. 2001).

Within plots from old gardens, there was no significant correlation between *P. aduncum* density or basal area and number of studied plant species present. Similarly, redundancy analysis of gardens, taking the basal

Table 1. Plant species studied; and their abbreviations in the ordination diagram (Fig. 4).

Agavaceae: *Dracaena angustifolia* Roxb. = Dra; **Apocynaceae:** *Tabernaemontana aurantica* Gaud. = Tab; **Araliaceae:** *Osmyxylon sessiliflorum* (Lauterb.) W.R. Philipson = Osm; **Areaceae:** *Hydriastele microspadix* (Becc.) Burret = Hyd; **Euphorbiaceae:** *Breynia cernua* (Poir.) Muell. Arg. = Bre; *Codiaeum ludovicianum* Airy Shaw = Cod; *Endospermum labios* Schodde = End; *Homalanthus novoguineensis* (Warb.) K. Schum. = Hom; *Macaranga aleuritoides* F. Muell. = Maa; *M. brachytricha* A. Shaw = Mbr; *M. bifoveata* J.J. Smith = Mbi; *M. densiflora* Warb. = Mde; *M. novoguineensis* J.J. Smith = Mno; *M. quadriglandulosa* Warb. = Mqu; *Mallotus mollissimus* (Geisel.) Airy Shaw = Mall; *Melanolepis multiglandulosa* (Reinw. ex Bl.) Reichb.f. & Zoll. = Mel; *Phyllanthus lamprophyllus* Muell. Arg. = Phy; *Pimelodendron amboinicum* Hassk. = Pim; **Eupomatiaceae:** *Eupomatia laurina* R. Br. = Eup; **Fabaceae:** *Pterocarpus indicus* Willd. = Pte; **Flacourtiaceae:** *Casearia erythrocarpa* Sleum. = Cas; **Gnetaceae:** *Gnetum gnemon* L. = Gne; **Loganiaceae:** *Neuburgia corynocarpa* (A. Gray) Leenh. = Neu; **Malvaceae:** *Sterculia schumanniana* (Lauterb.) Mildbr. = Ste; **Monimiaceae:** *Kibara cf. coriacea* (Bl.) Tul. = Kib; **Moraceae:** *Artocarpus communis* J.R. et G. Forst. = Art; *Ficus bernaysii* King = Fbe; *F. botryocarpa* Miq. = Fbo; *F. conocephalifolia* Ridley = Fcon; *F. copiosa* Steud. = Fcop; *F. dammaropsis* Diels = Fda; *F. hispidoidea* S. Moore = Fhi; *F. nodosa* Teysm. & Binn. = Fno; *F. phaeosyce* Laut. & K. Schum. = Fph; *F. pungens* Reinw. ex Bl. = Fpu; *F. septica* Burm. = Fse; *F. trachypison* K. Schum. = Ftr; *F. variegata* Bl. = Fva; *F. wassa* Roxb. = Fwa; **Piperaceae:** *Piper aduncum* L. = PIP; **Rubiaceae:** *Amaracarpus nymantii* Valeton = Ama; *Dolicholobium oxylobum* K. Schum. = Dol; *Gardenia hansemannii* K. Schum. = Gar; *Morinda bracteata* Roxb. = Mor; *Mussaenda scratchleyi* Wernh. = Mus; *Nauclea orientalis* (L.) L. = Nau; *Neonaclea clemensii* Merrill & Perry = Neo; *Pavetta platyclada* Lauterb. & K. Schum. = Pav; *Psychotria leptothyrsa* Miquel = Ple; *P. ramuensis* Sohmer = Pra; *P. micralabastra* (Laut. & Schum.) Val. = Pml; *P. micrococca* (Laut. & Schum.) Val. = Pmc; *Randia schumanniana* Merrill & Perry = Ran; *Timonius timon* (Spreng.) Merr. = Tim; *Versteegia cauliflora* (K. Schum. & Laut.) Val. = Ver; *Tarena buruensis* (Miq.) Val. = Tar; **Sapindaceae:** *Pometia pinnata* Forster = Pom; **Ulmaceae:** *Celtis philippensis* Blanco = Cel; **Urticaceae:** *Leucosyke capitellata* (Poir.) Wedd. = Leu; **Verbenaceae:** *Premna obtusifolia* R.Br. = Pre. Vouchers deposited in the National Herbarium at Lae, PNG, Bishop Museum (Honolulu) and Smithsonian Institution (Washington).

area of *P. aduncum* as the explanatory variable for remaining species representation does not provide significant results (RDA was used instead of CCA because the variability within the set of garden samples was much lower than in the complete data set; see ter Braak & Šmilauer (1998) for technical explanation). However, the basal area of *P. aduncum* is negatively correlated with the sum of basal areas of the remaining species studied ($r = -0.21$), and also with basal areas of the other dominant pioneer species (*Melanolepis multiglandulosa*: $r = -0.23$, *Macaranga brachytricha*: $r = -0.21$). However, none of the correlations is significant.

Discussion

Invasions by woody species are relatively rare in the moist tropics and successful invaders seldom enter the primary forest habitats (Rejmánek 1996). The preference of *P. aduncum* for the early successional stages is in agreement with this general trend. From a general perspective, this trend confirms the importance of resource fluctuation for invasion (Davis et al. 2000). Undisturbed tropical moist forest does not experience pronounced fluctuations, as other vegetation types do, neither in their composition, nor in their environment, and we may expect that resource levels (nutrients or water) are rather constant. The importance of disturbances for successful invasion has been stressed before (e.g. Hobbs 1989; Rejmánek 1989), especially disturbances associated with human settlements (Noble 1989). Although *P. aduncum* invasion confirms this pattern – it is most common in abandoned swidden agriculture fields – the species is now frequently found in naturally disturbed habitats and its survival is completely independent of any human activities.

In its new habitat, *P. aduncum* behaves as a typical pioneer species. This corresponds to its ecology in its native region, South America (García et al. 2000). Similarly, it is the most abundant species in fallow forests in the tropical lowlands of Borneo (Hashimoto et al. 2000), and it is also found in similar habitats in Viti Levu (Fiji, M. Rejmánek pers. com.). Based on its behaviour in Fiji (where it is found up to 1000 m a.s.l.), Meyer (2000) considers it one of seven very aggressive invasive plant species still apparently confined to one or a few Pacific Islands. All this shows that the taxon-specific approach (i.e. prediction of species invasiveness in one area from its known invasions), although not intellectually exciting, is a powerful tool for practical protection. The introductions into various islands were probably independent, but the invasive behaviour of the species is similar in geographically distant areas.

Recently, we have studied secondary regrowth in abandoned gardens in the area (Novotný et al. in prep.). The study comprised later stages of our recent category ‘garden’ and the ‘secondary young forests’. In 25 quadrats, 20 m × 20 m each, we have measured and identified all the individuals reaching breast height. Native species formed the vast majority of the total of 171 species found. However, *P. aduncum*, and another alien species, *Spathodea campanulata* P. Beauv. (*Bignoniaceae*), were the two most common species, comprising 21% and 14% of the total basal area in all the plots, respectively. At most, *P. aduncum* formed 62% of the basal area in a quadrat. As *P. aduncum* seldom reaches DBH > 10 cm, its high basal area is achieved by large numbers of individuals. The community is formed by two very

abundant alien species, and many native species, most of them very scarce. Both alien species, however, are absent from undisturbed primary forest.

Interestingly, another species included in our study, *Timonius timon*, is a highly successful invader in Palau (Micronesia). Among the 15 species of *Rubiaceae* studied, this is the most ruderal one; it prefers the early successional stages (Fig. 4); similar to *P. aduncum*, it also appears in riverbed habitats.

Although there seem to be very few invasive species in the genus *Piper*, it is not surprising that this particular species is highly invasive, because: (1) it quickly colonizes many types of disturbed habitats in its native range; and (2) it has a large geographic distribution, being found over the entire range of the genus in the American tropics. These two attributes are reliable predictors of species invasiveness (Richardson & Bond 1991; Rejmánek 1999). The species fulfils the condition for invasiveness for woody species in disturbed landscapes (Rejmánek & Richardson 1996; Rejmánek 2000): the juvenile period is much shorter than 10 yr (as was suggested earlier), and the species produces a large seed crop every year. The seeds are very small (0.17 mg; $n = 300$). This is well below the upper limit for invasiveness (50 mg) as suggested by Rejmánek (2000). According to him, however, the species with seed weight below 3 mg should be limited to wet and preferably mineral substrates. Although the abandoned gardens would not be considered wet habitats within New Guinea, the whole area is part of the wet tropics – with precipitation over 3500 mm.yr⁻¹; water availability is probably similarly high as in ‘real’ wet habitats in drier areas.

In the study area, *P. aduncum* is able to achieve very high cover values and it might suppress other pioneer species. However, we were not able to demonstrate significant negative correlations between its basal area or abundance and basal area or abundance of other species. It seems that due to the extreme variability in the basal area values (Figs. 2 and 3) the test was very weak. Prevailing negative correlations suggest that there is indeed some suppression of other pioneer species. However, most of the pioneer species are able to grow, albeit with suppressed dominance, even in the stands with dense *P. aduncum*. The representation of *P. aduncum* decreases with successional age and the species is probably outcompeted in later successional stages.

The rapid spread of this species is undoubtedly facilitated by its endozoochorous dispersal. In a study from Brasil, seeds of the species were among the most often found in bat faeces. The seeds were found in faeces of several species, and their germinability was not affected by their transition through the gut (García et al. 2000). This corresponds to the behaviour of *P. aduncum* in PG where we found that the seeds germinate from faeces of

flying foxes, cuscuses, birds, and dogs. Similarly, Petir et al. (1998) noted that the seeds are eaten by birds. Further, Rogers & Hartemink (2000) found *P. aduncum* to be the most abundant species in the seed bank, both in the fallow and in the secondary forest. Several authors (e.g. Binggeli 1996; Rejmánek & Richardson 1996, Rejmánek 2000) consider vertebrate dispersal to be responsible for the success of many woody invaders in both disturbed and also undisturbed habitats. In our view, the vertebrate dispersers were particularly important in the spread of the species to naturally disturbed plots, like landslides or gaps in otherwise pristine forest.

In closed forests, including secondary forests, *P. aduncum* seedlings were virtually absent. This corresponds to the finding of Garcia et al. (2000) that its germination is greatly suppressed by dark conditions. The very small seeds do not provide sufficient energy for seedlings to survive in the shade of rain forest ground floor. However, we noted that the species sometimes penetrated the forest along footpaths, even into the primary forest in our study area. Our experience suggests that, at least in our study area, the representation of *P. aduncum* in gaps and landslides decreases with the distance from the source population near villages, in abandoned gardens or on river banks. It seems that *P. aduncum* is more abundant in larger gaps.

An important trait facilitating the spread of *P. aduncum* within the system of swidden agriculture is its ability to resprout. In some cases, young stems of *P. aduncum* are not completely removed when the secondary forest is being cleared for a new garden, but are only cut off at ca 1.5 m above the ground and used as a support for crops (e.g. yams). However, in a short survey in one such newly abandoned field we found that the resprouting of *P. aduncum* was comparable or lower than that of other species (in our rapid survey of four species in a 1-yr old garden, based on 25 trees each, the resprouting rates were *P. aduncum* 56%, *Melanolepis multiglandulosa* 88%, *Premna obtusifolia* 96%, and *Pterocarpus indicus* 100%).

According to our experience, the species attains maximum cover after 6-8 yr of secondary succession, when its canopy is 5 to 7 m tall. Later on, the species is overgrown by other, taller pioneer trees: for example, fast growing *Melanolepis multiglandulosa* or some of the *Macaranga* species are able to reach heights well over 15 m. The growth rate of *P. aduncum*, albeit very high (Rogers & Hartemink 2000), is not superior to that of other, native pioneer species. Also, our unpublished data suggest that the abundance of leaf chewing insects is within the range of other species in the area (Novotný et al. in prep.); consequently, the species success is not due to low leaf chewing herbivore load.

The success of the species is probably affected by

the turnaround time in the swidden agriculture. Recently, the turnaround time in the investigated area has been about 10 yr. The plots that are cleared contain large numbers of seeds of *P. aduncum*. Probably, *P. aduncum* would benefit from shortening of this time, because after the tenth year, its abundance decreases. We were not able to demonstrate the supposed decrease in soil fertility in the gardens heavily infested by *P. aduncum*. However, it might well be another consequence of the shorter turnaround time, because the younger plots are also more infested by *P. aduncum*. Our unpublished data show that the decomposition rate of *P. aduncum* leaves does not differ from the native species, and the C/N ratio is relatively low (14), but still within the range of native species.

On the basis of the above comparisons it seems that the greatest advantage of *P. aduncum* in comparison with indigenous pioneer species is its ability to disperse with seeds. The seeds are germinable after their passage through the gut of herbivores. Consequently, the seeds are present in the seed bank in places that are distant from maternal plants, where they can germinate after a disturbance event, e.g. in natural gaps. This makes the species a very efficient invader.

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