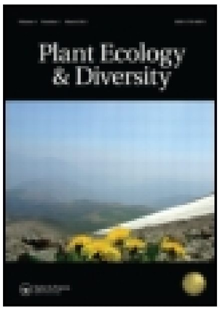

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Agnaldo Aguiar Jr. [a] , Reinaldo I. Barbosa [b] , José B.F. Barbosa [c] & Moisés Mourão Jr. [d]

[a] Roraima State Foundation for Environment and Water Resources (FEMARH-RR), Boa Vista, Brazil

[b] National Institute for Research in Amazonia (INPA), Department of Environmental Dynamics (CDAM), Boa Vista, Brazil

[c] Federal University of Roraima (UFRR), Centre for Agricultural Sciences (CCA), Boa Vista, Brazil

[d] Brazilian Enterprise for Agricultural and Ranching Research (EMBRAPA), Belém, Brazil

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Invasion of *Acacia mangium* in Amazonian savannas following planting for forestry

Agnaldo Aguiar Jr.[a], Reinaldo I. Barbosa[b]*, José B.F. Barbosa[c] and Moisés Mourão Jr.[d]

[a]*Roraima State Foundation for Environment and Water Resources (FEMARH-RR), Boa Vista, Brazil;* [b]*National Institute for Research in Amazonia (INPA), Department of Environmental Dynamics (CDAM), Boa Vista, Brazil;* [c]*Federal University of Roraima (UFRR), Centre for Agricultural Sciences (CCA), Boa Vista, Brazil;* [d]*Brazilian Enterprise for Agricultural and Ranching Research (EMBRAPA), Belém, Brazil*

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***Background*:** No studies have examined the invasion of exotic species used for forestry purposes in the savannas of the Brazilian Amazonia.
***Aims*:** We investigated the invasion process of *Acacia mangium* in savanna areas adjacent to large-scale forestry plantations in north-eastern Roraima State, Brazilian Amazonia.
***Methods*:** A tree inventory to record the presence of all *A. mangium* and native tree individuals was carried out in of 14 plots (each 50 m in width and 1500 m in length) established at five plantation sites. Biometric measurements were taken for all individuals to identify their structure and maturity. Distance categories were created for determining frequency of occurrence in 100 m sections along the plots for all individuals. Correlations and goodness-of-fit tests for discrete data ordered in categories were applied to verify the occurrence of *A. mangium* plants in relation to distance from the plantation.
***Results*:** Individuals of *A. mangium* were dispersed up to 900 m from the plantation edge 8–9 years after the plantation was established. Although most recorded individuals were in the juvenile stage, reproductive adults were found in two establishment patterns: non-nucleated and nucleated under native tree species. Crown cover of the savanna's most abundant native tree species facilitated the regeneration of *A. mangium*.
***Conclusions*:** Planting of *A. mangium* in Amazonian savannas provides a source of continuous dispersal, and invasion by the species is facilitated by environmental conditions.

Keywords: alien plant; Amazonia; biological invasion; facilitation; invasive species; tree invasions

Introduction

Large-scale forestry plantation carried out with potentially invasive species in areas of open native vegetation has produced negative environmental effects, such as reducing species richness of native plants, disturbing nutrient cycling and altering the structure of the vegetation in adjacent native areas (Richardson et al. 1989; Richardson 1998; van Wilgen and Richardson 2012). In addition to ecological damage, the introduction of exotic tree species into these natural habitats may cause losses in profits due to additional costs of monitoring programmes (Vitousek et al. 1996; Brooks et al. 2004). Plant invasions originating from commercial forestry plantations can be very effective when invasive species function as transformers of both community structure and of interactions within and among communities, leading to changes at the ecosystem level (Crooks 2002). Where impacts are manifest at the ecosystem level, delays in management can severely impair reversal of invasion or even cause secondary invasions (Yelenik et al. 2004; Wilson et al. 2011).

In general, commercial forestry plantations are established in large open areas. This model favours invasive processes because species used for forestry have rapid growth, allowing the accumulation of massive propagule banks (Pyšek et al. 2009; Richardson and Rejmánek 2011). In this process, the large introduced population can quickly become a continuous focus for new, smaller populations of propagules (Moody and Mack 1988; Lockwood et al. 2005). However, the ability to propagate new individuals does not, by itself, categorise an alien species as invasive (Simberloff 2009). By definition, a species can only be regarded invasive when it is fully naturalised and able to produce reproductive offspring in large numbers at considerable distances from the mother plants: >100 m from the source population in less than 50 years for seed-dispersing species (Richardson et al. 2000; Shine et al. 2000). Therefore, not every large-scale forestry plantation with exotic species poses a potential to become a source of invasion, but studies are necessary to adequately define the potential for both the invasion process (residency status) and the degree of naturalisation (invasion status) (Pyšek et al. 2004).

For the naturalisation process to be persistent, both the environmental conditions and the characteristics of the introduced species must facilitate the invasion (Kolar and Lodge 2001). Although it is difficult to define the characteristics that make an invasive species, it is necessary to develop effective management strategies (Magee et al. 2010). In open vegetation ecosystems, exotic species that produce large quantities of bird-dispersed seeds have a high

*Corresponding author. Email: reinaldo@inpa.gov.br

probability of propagating under native trees and shrubs (Milton et al. 2007). In general, native plants in open areas are distributed sparsely and can become focal points for birds (Dean et al. 1999). These native tree individuals not only serve as perches for seed-dispersing birds but also provide critical shade for seedlings (Vieira et al. 1994; Verdú and Garcia-Fayos 1996). The shade provided by the crowns of native individuals can produce a positive effect on seedlings of the weed species because of lower soil temperature and reduced evapotranspiration (Belsky et al. 1993; Holl 2002). These factors lead to gradually dispersing to greater distances from the initial population, and to the seedlings of the invasive species having greater chances of survival when they are under these trees (Debussche and Isenmann 1994). Therefore, certain features of some vegetation types, such as open landscapes, are more conducive to invasion by alien trees (Richardson et al. 1994).

The invasive potential of exotic species in open areas has been relatively well studied in different parts of the world such as Europe, Africa and the Pacific Islands (Henderson 2007, Richardson and Rejmánek 2011), while in Latin America research on plant invasions has made little progress (Gardener et al. 2012). In Brazil this subject received little attention until the late 1990s, with studies restricted primarily to the conifers in the southern and south-eastern regions of the country (Simberloff et al. 2010). Various introductions of exotic species in Brazil for ornamental (e.g. Mengardo et al. 2012) or forestry purposes have caused ecological and economic problems due to different stages of biological invasion in the vicinity of the plantations (Zenni and Ziller 2011). Examples include *Pinus elliottii* in the subtropical grasslands of São Paulo (Abreu and Durigan 2011) and Paraná (Ziller and Galvão 2004), and *Acacia mearnsii* in Rio Grande do Sul (Mochiutti et al. 2007). In all cases, environmental conditions, where the natural vegetation was grassland or shrub land, or where forest vegetation has been cleared, favoured the biological invasion and increased the cost of management to prevent the loss of native plant diversity in areas adjacent to these plantations in Brazil.

In the Brazilian Amazon, commercial plantations of exotic species are rarely associated with biological invasions, given that these plantations occupy a relatively small area and are relatively recent. The Brazilian government initiated a commercial forestry programme in 1995 termed the ‘Edaphoclimatic zoning for planting fast-growing tree species in the Amazon’ (Lima et al. 1999). This programme was established under the ‘Pilot Programme to Conserve the Brazilian Rain Forest’ (PPG7) and sought to reduce deforestation rates in the region by supplying the market with wood from areas with fewer legal restrictions (abandoned deforested areas and savannas) instead of primary forests. *Eucalyptus* spp. and *Acacia mangium* Willd. (Fabaceae) have been the most commonly planted exotic species in this programme, which is managed by Embrapa (Brazilian Enterprise for Agricultural and Ranching Research) (Souza et al. 2004). Of these species, *A. mangium* merits special attention. It was introduced in large-scale commercial plantations in Amazonian savannas without any prior verification of its biological invasion risks, despite evidence demonstrating that it had a high invasive potential (Djègo and Sinsin 2006; Kull et al. 2007; Richardson and Rejmánek 2011).

The largest example in the region is the commercial forestry of *A. mangium* occupying 30,000 ha of savanna in the state of Roraima, northern Brazilian Amazon. This savanna area is a Neotropical ecosystem with tropical environmental characteristics, including soil, light and climatic factors (rainfall and temperature) conducive to dispersal and naturalisation of *A. mangium* (see Species description). In addition, native tree species located in the vicinity of commercial plantations can act as focal points of dispersal agents, facilitating the establishment of *A. mangium*. Therefore, the environmental characteristics of the native savanna in conjunction with the life-history traits of *A. mangium* can provide favourable conditions for a biological invasion of this species.

The objective of this research was to determine the invasion process of *A. mangium* in the Roraima savanna based on observations in areas adjacent to the five commercial plantations. In these sites we quantified the residency status of this exotic species, namely the dispersal and establishment patterns, and assessed the naturalisation status, or individuals producing new seedlings beyond 100 m from the plantation areas. Our specific questions were: (1) Can *A. mangium* disperse over long distances (>100 m from commercial plantations)?; (2) Is the occurrence of dispersed individuals uniformly distributed over long distances?; (3) Of the total dispersed individuals, what is the proportion of plants in the reproductive stage after 8–9 years?; (4) Do the native trees in the savanna function as nurse trees for the invasive species (establishment pattern)?; and (5) Is the invasion process facilitated by the presence and/or attributes (e.g. canopy cover) of the native tree species that promote nucleation?

Results from this study are intended to encourage discussion of land-management policies and conservation strategies in the region to prevent future introduction of invasive species in Amazonian savanna and other open vegetation ecosystems in Brazilian Amazonia.

Materials and methods

Species description

Acacia mangium occurs naturally from eastern Indonesia and Papua New Guinea to north-eastern Australia (Pedley 1964; Moran et al. 1989). It is considered an invasive tree species in many regions of the world, such as Asia, Indonesia, Pacific Islands, Indian Ocean Islands, Africa (southern) and South America (Richardson and Rejmánek 2011). The species has a rapid growth rate and tolerates relatively acidic soils (pH 4.5–6.5), grows in areas with an annual precipitation ranging from 1000–4500 mm, and annual mean (min–max) temperatures between 12–34 °C. It does not tolerate frost and excessive shading (Atipanumpai 1989; Jøker 2000; CABI 2003). Given its robustness and adaptability, it has been widely planted in commercial plantations for products such as pulp, firewood, charcoal, construction material, veneer and furniture, for soil protection, and as a food-source for bees (Doran and Turnbull 1997; Lim et al. 2003; Midgley and Turnbull 2003; Silva 2010). *A. mangium* has life-history characteristics that favour wide dispersal, including flowering for up to 8 months of the year (Wang et al. 2005), high seed production (Saharjoa and Watanabe 2000), and bird-dispersed seeds (Gibson et al. 2011).

Acacia mangium *in the Roraima savanna*

Acacia mangium was experimentally introduced into Roraima in 1995 by Embrapa and first used by only one private entity in 1997. First seeds were brought from south-eastern Brazil. The species was used for business purposes by *Ouro Verde Agrosilvopastoril Ltda*. (now known as *F.I.T. Manejo Florestal Ltda*.) in 1999 (Arcoverde 2002; Meier-Doernberg and Glauner 2003). The original plan was to supply raw materials for production and export of cellulose pulp by the company *Brancocel Indústria e Comércio de Celulose Ltda*. Brancocel ceased its activity in Roraima in 2006, but Ouro Verde carried on the project and its activities and concluded the planting of 30,000 ha of *A. mangium* in 2008. Regional studies have shown that this species has a large seed production (66,800–115,000 seeds per kg seed) and low germination rate (ca. 3%) under natural conditions (Smiderle et al. 2005; 2009). The physical dormancy of the seeds due to their impermeability to water contributes to the threat of invasion over long periods of time until favourable germination conditions occur. This is a true orthodox species with seeds that have high longevity and low loss of viability, even when stored for long periods (Yap and Wong 1983). In high-density homogeneous stands in Roraima *A. mangium* is prone to pathogen problems that can affect its growth (Halfeld-Vieira et al. 2006). Rhizobia (root-nodulating bacteria) were not introduced from Australia (or other places) to facilitate its establishment in Roraima plantations, but *A. mangium* is often nodulated by *Bradyrhizobium* spp. in soils where it has been introduced (Galiana et al. 2002).

Study area

Fieldwork was carried out from October 2007 to February 2008 in the vicinity of five *A. mangium* plantations established by Ouro Verde in 1999 and 2000 in the savanna of the State of Roraima, in northern Brazil (Figure 1). Savannas and grasslands occupy ca. 5% (200,000 km^2) of Brazilian Amazonia (Santos et al. 2007). The Roraima savanna (locally known as lavrado) is the largest continuous non-forest ecosystem in the Amazon (ca. 43,000 km^2) in the area near Brazil's border with Venezuela and Guyana (Barbosa and Campos 2011). At the time of fieldwork the plantations were 8–9 years old.

The dominant natural vegetation in all of the sampled areas is a lowland (79–114 m a.s.l.) open savanna dominated by three tree species: *Curatella americana* L. f. (Dilleniaceae), *Byrsonima crassifolia* (L.) H.B.K. (Malpighiaceae) and *B. coccolobifolia* Kunth (Miranda et al. 2002; Barbosa et al. 2005). The level of disturbance around plantations is low because Brazilian environmental laws currently require that natural areas be maintained around development projects. The soil in this region is classified as sandy-clay from the Boa Vista Geomorphological Formation (Brazil-MME 1975; Schaefer and Dalrymple 1995). According to the Köppen classification, the climate is Awi, or sub-humid tropical with a defined dry season. Rainfall is seasonal with two climatic periods: dry (December to March) and wet (April to August). This region is characterised by the following annual averages: 1600–1700 mm rainfall, 27–28 °C temperature, and 70–75% relative humidity, based on data from the National Institute of Meteorology of Brazil (INMET) available for the city of Boa Vista, capital of Roraima (Barbosa 1997).

Experimental design

A tree inventory to record the presence of all *A. mangium* and native tree individuals was made in 14 plots (each 50 m in width by 1500 m in length) covering a total sampling area of 105 ha, established at the five plantation sites (Figure 1). Given that all of the plantation sites had unequal areas and irregular perimeters, plots were established at the four cardinal points (north, south, east, and west) of each plantation. From 20 possible plots, three were redirected to other cardinal directions due to physical restrictions such as roads, agricultural crops and rural constructions while six plots were excluded from the sampling (Appendix 1 available via online Supplementary Material). Only savanna ecosystems around plantations were considered (non-flooded and non-disturbed).

Total height (Ht) – the distance between the base of the stem and the top of the canopy – and diameter of the base (Db) of each plant measured in cm at 2 cm above the ground were measured for all *A. mangium* plants. Seedlings and small saplings were measured with a 1 mm precision calliper, and larger saplings and adult plants were measured with a measuring tape. Height and diameter were used for classifying the *A. mangium* specimens into four life stages based on previous field observations: (1) seedlings (young plants in the initial vegetative phase; $Ht < 0.3$ m and/or $Db < 2$ cm), (2) saplings (young plants in the intermediate vegetative phase; $0.3 \text{ m} = Ht < 1.0$ m), (3) juveniles (larger saplings in the advanced stage of vegetative development; $1.0 \text{ m} = Ht < 2.5$ m), and (4) adults (individuals approaching or at the reproductive stage; $Ht = 2.5$ m). *A. mangium* individuals were also classified into establishment patterns: nucleated (one or more *A. mangium* plants under the canopy projection of a native tree) and non-nucleated (plants located beyond the canopy projection of native trees).

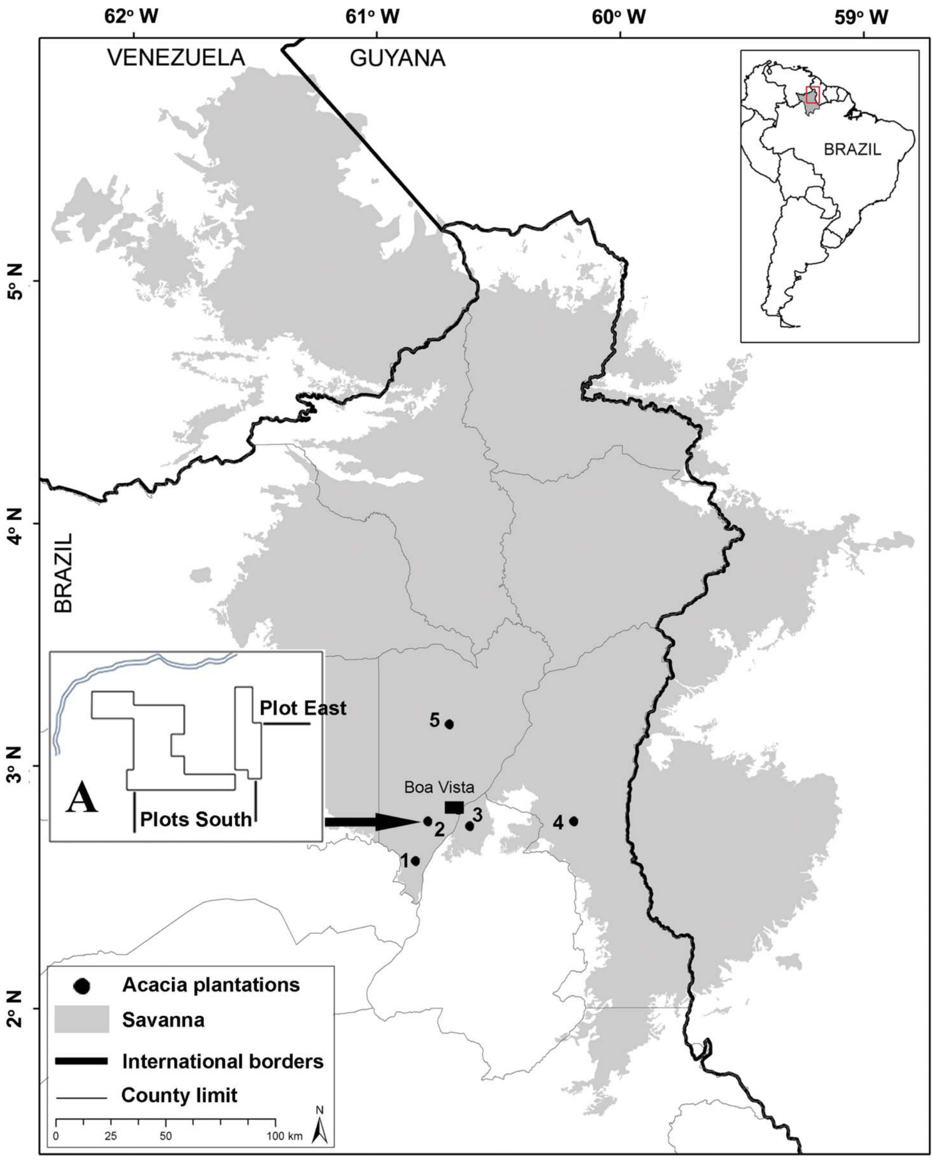

Figure 1. Geographical location of *Acacia mangium* plantation sites in the savanna region of the Brazilian State of Roraima. 1, Mucajaí (02° 40′ 58″ N / 60° 57′ 10″ W); 2, Alvorada (02° 43′ 47″ N / 60° 45′ 27″ W); 3, Santa Cecília (02° 44′ 52″ N / 60° 38′ 30″ W); 4, Serra da Lua (02° 43′ 25″ N / 60° 21′ 59″ W); and 5, Jacitara (03° 12′ 41″ N / 60° 48′ 58″ W). A. Plot distribution on the Alvorada site: physical restrictions excluded the plot North and redirected the plot West to South direction (see Appendix 1, supplementary material).

The inventory of native tree species involved adults only, i.e. those with sufficient structure and maturity to act as nurse trees. We considered as nurse trees all native plants with Ht = 1.5 m and Db = 5 cm (Mourão et al. 2010). In these cases, we also measured the crown diameter (Dm – the mean of the minimum and maximum canopy diameters) to use as the basis for limiting the maximum canopy projection area for the measurement regenerating *A. mangium* (nucleated plants). The taxonomic identification of the native plants was carried out in the field as these plants are common and are easily identified in the region. The perpendicular distance of all plants (*A. mangium* and native trees) in relation to the edge of each plot was measured to establish their position.

Data analysis

Dispersal distance. To investigate the relationship between frequency/abundance of *A. mangium* and distance from plantation edge, the 1500 m-long plots were divided into 100 m-long sections and frequency vs. distance were correlated by using Spearman's correlation (r_s). The categories for determining frequency were obtained on the basis of the sum of occurrences observed in the 14 sampled plots, independent of location. This particular protocol was adopted based on the assumption that *A. mangium* dispersal probability would be equal in all of the plantation sites given similar environmental conditions. The Kolmogorov–Smirnov goodness-of-fit test ($d_{0.05}$) for discrete data ordered in categories (Zar 1999) was used for testing the null hypothesis that the occurrence of *A. mangium* plants was distributed uniformly in relation to distances from the plantation. The same test was applied to determine if life stages and establishment patterns are also distributed uniformly. Finally, a two-dimensional contingency table (4 stages × 2 patterns) was constructed to determine if the dispersed *A. mangium* individuals could reach the reproductive life stage independent of the establishment pattern ($\chi^2_{0.05}$).

Native plants. The total number of individuals of native species with nurse-tree characteristics was calculated and the individuals were ordered into 100 m groups. Four classes of native tree species were created: three of these individually representing each of the species with greatest abundance (*Curatella americana*, *Byrsonima crassifolia* and *B. coccolobifolia*) and one class containing all of the other species (Others). All of the individual native plants were categorised into three canopy-diameter classes (<1 m, 1–3 m and >3 m), representing the most important feature for establishment of the *A. mangium* individuals under their canopies. Finally, two nucleation categories were also created: native individuals with and without *A. mangium* plants under their canopies. The data were organised into a three-dimensional contingency table (4 species × 3 canopy classes × 2 nucleation categories), with a chi-square test ($\chi^2_{0.05}$) then being applied in order to test if the establishment process was facilitated by presence/absence and canopy diameter of the native tree species. Partial dependence tests ($\chi^2_{0.05}$) were also carried out by using two-dimensional contingency tables between the nominal variables, presence/absence and canopy cover.

Results

Dispersal distance

A total of 625 *A. mangium* individuals were counted in the 14 sampled plots; 85.1% of these represented seedlings and saplings (Table 1). They occurred up to a distance of 900 m from the plantations (0.84–872.45 m). *A. mangium* dispersal was not uniformly distributed throughout the whole sampling distance; the highest frequency of occurrence (363 individuals; 58.1%) was observed up to 100 m from the plantations ($d_{0.05}$; $P < 0.001$). The correlation coefficient between total number of recorded *A. mangium* plants and distance from the source plantation was negative ($r_s = -0.617$), but non-significant ($P = 0.08$).

An individual analysis of each life stage indicated that the occurrence of adult plants (9) was low and significantly independent of distance ($d_{0.05}$; $P < 0.01$). Five dispersed plants reached the reproductive phase close the plantations (<200 m), and other ones were not uniformly distributed throughout the remaining sampling distances. The frequencies of occurrence of the other life stages were not distributed uniformly either ($d_{0.05}$; $P < 0.001$) because the majority of seedlings (63.5%), saplings (51.7%) and juveniles (59.5%) were found within the first 100 m from the source plantation.

Frequencies of occurrence of the non-nucleated (88.5%) and nucleated (38.6%) *A. mangium* plants under native trees were also higher within the first 100 m ($d_{0.05}$; $P < 0.05$) from the source plantation. Occurrence of life stages was significantly dependent of establishment patterns ($\chi^2_{0.05,3} = 11.291$; $P < 0.01$). Saplings and juveniles were more frequent under nurse trees, while adults and seedlings occurred in the same proportion between nucleated and non-nucleated establishment patterns (Figure 2).

Table 1. Total number of *A. mangium* individuals, distributed by life stage, establishment pattern and distance class around five plantation sites, Roraima, Brazil.

Distance class (m)	Life stage: Seedling	Sapling	Juvenile	Adult	Total: *n*	%
000–100	188	122	50	3	363	58.1
100–200	34	16	9	2	61	9.8
200–300	12	9	7	0	28	4.5
300–400	19	20	1	0	40	6.4
400–500	7	16	2	1	26	4.2
500–600	1	2	2	0	5	0.8
600–700	12	5	5	0	22	3.5
700–800	23	44	6	3	76	12.2
800–900	0	2	2	0	4	0.6
900–1500	0	0	0	0	0	0.0
n	296	236	84	9	625	–
%	47.36	37.76	13.44	1.44	–	100

Native plants

We recorded 968 native plant individuals representing a total of 18 native tree species up to 900 m from the plantation edge (Table 2). Of this total, 6.1% (59) of the trees were classified as being a nucleation point for *A. mangium*. Seven species appeared to act as 'nurse trees' in that they were able to support *A. mangium* recruitment. The most abundant of these nurse-tree species were *Byrsonima crassifolia* (40.7%), *B. coccolobifolia* (28.3%) and *Curatella*

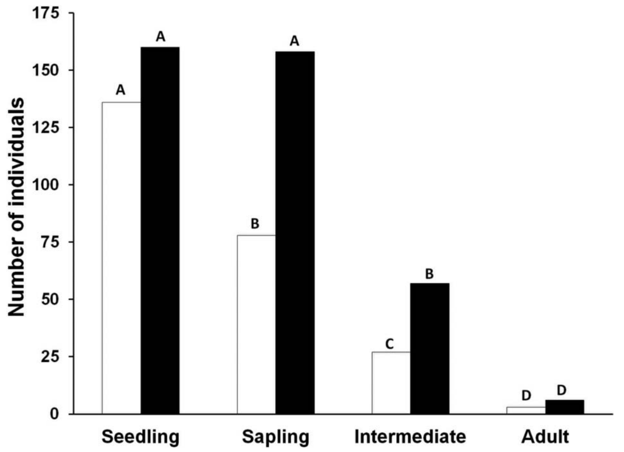

Figure 2. Numbers of *Acacia mangium* individuals, distributed by life stage and establishment pattern (non-nucleated, open bar; nucleated, filled bar) observed in the vicinity of the five plantation sites, Roraima, Brazil. Different letters indicate significance at $\alpha = 0.05$ between life stages and establishment patterns.

Table 2. Native species and numbers of individuals, with and without nucleation by *A. mangium*, around five plantation sites, Roraima, Brazil.

	Without nucleation			With nucleation			
Species	<1 m	1–3 m	>3 m	<1 m	1–3 m	>3 m	Total
Byrsonima crassifolia (L.) Kunth[a]	14	330	33		12	5	394
Byrsonima coccolobifolia Kunth	27	223	21		1	2	274
Curatella americana L.f.	6	85	65		12	17	185
Bowdichia virgilioides Kunth	3	28	10		2	3	46
Himatanthus articulatus (Vahl) Woodson	9	14	2			1	26
Casearia sylvestris Sw.	3	6	2		1	1	13
Psidium guineense Sw.		2			1	1	4
Connarus favosus Planch.	2	2					4
Roupala montana Aubl.		4					4
Erythroxylum suberosum A.St.-Hil.	1	2					3
Vitex schomburgkiana Schauer		2	1				3
Xylopia aromatica (Lam.) Mart.		2	1				3
Aegiphila integrifolia (Jacq.) B.D.Jacks.		2					2
Byrsonima cf. *intermedia* A. Juss.		2					2
Eugenia punicifolia (Kunth) DC.		2					2
Anadenanthera peregrina (L.) Speg.	1						1
Genipa americana L.		1					1
Cecropia sp.			1				1
N	66	707	136	0	29	30	968
%		93.9			6.1		100

[a]Two nucleated individuals were dead.

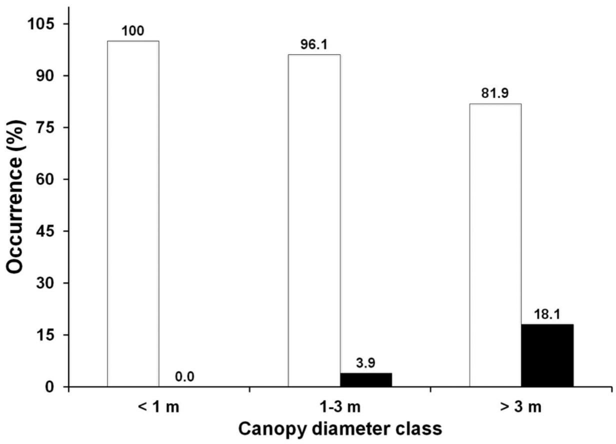

Figure 3. Occurrence (%) of native plants, with and without nucleation by *Acacia mangium*, around five plantation sites, Roraima, Brazil. Open bar, non-nucleated; filled bar, nucleated.

americana (19.1%). Of these species, the highest number of nucleation occurrences was for the *C. americana*, with 29 individuals (49.1% of the total).

The occurrence of nucleated native plants increased with the diameter of their canopy (Dm; $\chi^2_{0.05,17} = 27.587$; $P < 0.001$); the largest proportion was observed in individuals with Dm >3 m (18.1%) (Figure 3). Partial tests ($P < 0.001$) indicated that nucleation by *A. mangium* tended to occur under the three most abundant native trees species around plantations and under individuals with a canopy diameter >1 m. The greater the Dm class of the native plants was, the greater the probability of *A. mangium* occurring under this canopy-diameter class was.

Discussion

The presence of *Acacia mangium* individuals up to 900 m from the plantation edge 8–9 years after its introduction, independent of life stage or establishment pattern, indicates that this species can naturally disperse over long distances in natural Amazonian savanna regions. These findings are the same as those recorded for the natural dispersal of *A. auriculiformis* around commercial plantations on Unguja Island, Tanzania, with the number of *A. mangium* decreasing with increasing distance from plantations (Kotiluoto et al. 2008). The fact that the highest frequency of occurrence of *A. mangium* at short distances from the plantations (<100 m) is not related to diameter of canopy cover indicates that natural fruit dehiscence and hydrocory (seed dispersal by rain water) may play an important role in seed dispersal close to source plantations. Large numbers of propagules naturally being dispersed over short distances from the mother tree is a common characteristic of the genus *Acacia* (Zengjuan et al. 2006; Marchante et al. 2010). It is not possible to state whether *A. mangium* is dispersed at long distances by invertebrates, or whether their seeds are displaced by rodents as has been found in other species of the genus *Acacia* (Holmes 1990; Whitney 2002). However, we can suggest that ornithochory may be the strongest primary mechanism by which *A. mangium* is dispersed over long distances in the savanna of Roraima.

The largest number of specimens observed in the seedling and sapling life stages in the vicinity of the *A. mangium* plantations is directly related to the age of the plantations (8–9 years) at the time of the fieldwork. The youngest generation of plants most likely corresponds to the propagules that arrived during the preceding 1 or

2 years, whereas the individuals classified as juveniles or adults most likely represent the earlier generations from which the source stands reached their first reproductive phase (4–5 years of age). This establishment pattern is similar to that observed in *A. mearnsii* in the state of Rio Grande do Sul, Brazil, with the majority of individuals representing young age classes (Mochiutti et al. 2007). On the other hand, the youngest *A. mangium* individuals from the first generations in our study must have had high mortality rates due to frequent outbreaks of fire in the vicinity of the plantations. Fire is very common in Amazonian savannas and contributes significantly to high mortality of young individuals of all species present (Barbosa and Fearnside 2005). However, surviving plants of *A. mangium* have a very good chance of reaching the reproductive and seed dispersal phases beyond the plantation edges. Results from our study corroborate this scenario because nine dispersed individuals had reached their reproductive adult stage within 4–5 years over a sampled area of 105 ha around plantations. Considering that early maturity and high production of low-mass seeds are essential characteristics for a plant to acquire invasive status (Rejmánek and Richardson 1996), the dispersed *A. mangium* in Amazonian savannas have a good chance of establishing satellite populations owing to their dispersal capabilities. Early maturity and high production of low-mass seeds increase the likelihood of seeds being dispersed over long distances and reaching reproductive maturity (Richardson et al. 2004).

Our results indicate that *A. mangium* individuals growing under the canopy cover of native tree species can have a greater chance of reaching the adult phase as compared with individuals growing outside of the canopy cover. Several studies indicated that seedling or sapling nucleation under nurse trees could reduce invasion by *A. mangium* due to competition for light (Osunkoya et al. 2005). However, seedlings and saplings growing under native trees in open savannas do not seem to be negatively affected by low levels of light. In addition, native trees in open areas are able to create a favourable micro-environment including high concentrations of organic material, increased water-storage capacities in the soil, and high root penetration that facilitate establishment of seedlings and saplings (Vetaas 1992). In a study on native seedlings and saplings in the savanna (Cerrado) of the Central Brazilian Plateau, the mortality rate of individuals under the canopy of nurse trees due to recurring fire was lower than that of individuals that established themselves away from the canopy (Hoffmann 1996). Given that we observed the majority of *A. mangium* to be under or around native trees, we expect that the probability of reaching reproductive maturity will be highest for these individuals.

The native plant species investigated in this study play a key role in maintaining the biological diversity of the Roraima savanna region, functioning as nurse trees that facilitate the growth and long-term establishment of other native species (Mourão Jr. et al. 2010). Thus, *A. mangium* seems to be adapting to this dynamic that is already present in the native ecosystems. This invasive establishment pattern is common in other species of the genus *Acacia*, such as *A. cyclops* in South Africa, which has a high frequency of propagules under native trees/shrubs in relation to the surrounding vegetation (Glyphis et al. 1981). However, it is not yet possible to state whether *A. mangium* individuals will significantly compete with native plants and consequently alter the plant community structure of the Roraima savanna. Nevertheless, it is reasonable to expect a certain level of disturbance to native plant communities as a result of changes in composition and abundance (Holmes and Cowling 1997; Andersen et al. 2004). When *A. mangium* reaches adulthood, it can form thickets and cause excessive amounts of shading for the native species that initially provided the environment for its establishment (Flores-Flores and Yeaton 2000). This feature is the factor that maximises the plant's ability to utilise environmental advantages; this is a very common attribute in the genus *Acacia*, and is similar to that observed for *A. dealbata* in Europe (Lorenzo et al. 2010). *A. mangium* is a good nurse tree for plants that can tolerate heavy shade (Norisada et al. 2005; Yang et al. 2009); however, this can become a problem for heliophilic savanna species. For example, in our study, two native tree individuals were found dead under nucleation by *A. mangium*. Although mortality of native trees in the Roraima savannas can have other causes beyond proximity of *A. mangium* plants, this observation indicates a possible interference of *A. mangium* individuals in the establishment patterns and growth of the native species.

A. mangium growing under native plants showed an association with the native species and their canopy cover. Trees with Ht = 1.5 m, Db = 5 cm and Dm = 1 m were conducive to supporting *A. mangium* in its different life stages. Debussche and Isenmann (1994) and Verdú and Garcia-Fayos (1996) demonstrated that trees with large canopies are focal points that serve as perches for birds as seed dispersers in environments with open vegetation. Similarly, trees with extensive crowns in the Roraima savannas attract more birds that can deposit seeds through faeces, with subsequent establishment of seedlings. Therefore, seedling establishment under canopy trees is favoured in relation to locations outside of canopy cover because of the perch effect (Pausas et al. 2006; Milton et al. 2007).

We observed that the frequency of *A. mangium* establishment under the canopies of native species with low height, small stem base diameter, and canopy diameter was very low. Thus, we expect *Curatella americana*, *Byrsonima crassifolia* and *B. coccolobifolia* to serve as the most commonly nucleated species because they are the most abundant and largest trees in the Roraima savanna and have the largest biometric attributes (Barbosa and Fearnside 2004). Furthermore, their fleshy fruits (*Byrsonima* spp.) and sweet arils (*C. americana*) attract frugivorous birds (Monasterio and Sarmiento 1976; Sanaiotti and Magnusson 1995) that also transit in *A. mangium* plantations. Thus, as was also observed by Cowling et al. (1997) and Gosper et al. (2005), the characteristics of landscape structure and native species are factors that affect both frugivory and the dispersal of invasive plants. We therefore conclude that the community structure of the savanna and complex plant–animal interactions involving both native species and *A. mangium* should have been assessed before the commercial plantations were established.

Our results strongly indicate that Amazonian savannas provide favourable environmental conditions for all establishment phases (introduction, dispersal, and naturalisation) of *A. mangium*. This study also shows the possibility of *A. mangium* effectively becoming an invasive species and affecting the native plant community structure of Amazonian savanna ecosystems. Evidence indicates that terrestrial ecosystems invaded by *Acacia* spp. are not easily restored to their natural state, resulting in high maintenance costs (Macdonald and Wissel 1992; Le Maitre et al. 2011; Marchante et al. 2011). The highly invasive characteristics of *A. mangium* in coastal savannas and forest boundary regions in French Guiana have resulted in recommendations that this species be restricted, or even phased out, throughout the country (Delnatte and Meyer 2012).

Conclusions

Based on our own results, we conclude that *A. mangium* could rapidly become a serious threat to the biodiversity of Amazonian savannas in the vicinity of large-scale plantations, especially in the states of Roraima and Amapá. Incorporating conservation strategies, based on empirical studies, into public policy is crucial to preventing a biological invasion by *A. mangium* of Amazonian savannas. We also suggest that the current process of International Forestry Certification take into account the invasive potential of *A. mangium,* forming an important part of risk assessment for such forestry projects. Although it is necessary that companies operating in Amazonia continue to prosper, it is also necessary that they be prepared to contribute to controlling biological invasions. Failing to do so, they should lose their environmental certification. Our findings concerning the invasion process by *A. mangium* used for forestry in Amazonian savannas can be useful for preventing the recurrence of the same problems in other areas (see Richardson et al. 2008).

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Notes on contributors

Agnaldo Aguiar Jr. is an agronomist and has completed his Master’s degree on the biological invasions by *Acacia mangium* in the savanna of Roraima.

Reinaldo Imbrozio Barbosa leads a research group established in Roraima. He is a senior researcher in ecology, with special interests in ecology of savannas, forest fires, and environmental services in Amazonian ecosystems.

José Beethoven Figueirêdo Barbosa is an associate professor and teaches graduate courses in Agronomy and Natural Resources. His main interest is on biological invasion and management of natural resources.

Moisés Mourão Jr. is a biologist/statistician specialising in the analysis of data collections related to Amazonian agroecosystems.

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