Distribution and population structure of *Adansonia rubrostipa* in dry deciduous forest in western Madagascar

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Abstract

We mapped and measured all of the *Adansonia rubrostipa* trees in 40 ha of dry deciduous forest in Kirindy Forest, Menabe, western Madagascar. Survey effort was split between three compartments which had been heavily logged or selectively logged for timber trees, not including *A. rubrostipa,* in the 1980s, or which remained unlogged. We recorded 304 trees ranging in stem diameter at breast height from 5 to 221 cm. Trees were most abundant and the majority of regeneration was recorded in the unlogged compartment. Regeneration was generally poor in the two logged compartments. We suggest that seed predation and poor seed dispersal contribute to a generally ageing population, and that the dense shrub cover resulting from disturbance during logging impedes seedling establishment.

Key words: Adansonia, dispersal, Madagascar, population structure, regeneration

Résumé

Nous avons localisé et mesuré tous les arbres *Adansonia rubrostipa* dans 40 ha de forêt décidue sèche, dans la forêt de Kirindy, à Menabe, dans l'ouest de Madagascar. L'effort de l'étude se partageait entre trois compartiments, un qui avait été fortement déboisé, un où certains arbres sélectionnés avaient été coupés, non compris *A. rubrostipa*, dans les années 1980, et le dernier où rien n'avait été coupé. Nous avons relevé 304 arbres allant de 5 à 221 cm de diamètre (d.b.h.). Les arbres étaient surtout abondants, et la majorité de la régénération s'observait, dans le compartiment non coupé. La régénération était généralement médiocre dans les deux compartiments exploités. Nous suggérons que la consommation des semences et leur mauvaise dispersion contribuent à une population généralement vieillissante et que le dense couvert de broussailles qui résulte de la perturbation au moment des coupes freine l'installation des semences.

Introduction

Of the eight extant species of baobabs (*Adansonia* spp.) six are endemic to Madagascar. Whilst they are iconic symbols of the unique nature of Madagascar's flora, and even held to have magical or religious significance according to some Malagasy traditions, there is concern that at least some populations of all six species are threatened with extinction caused by human activities, especially forest clearing and burning for agriculture (Baum, 2003). One of these, *Adansonia rubrostipa* Jum. & H. Perrier ('fony'), is a common baobab in the Kirindy Forest, and is widespread in the west of Madagascar from near Itampolo in the south-west to Soalala in the north-west (Baum, 1995). Due to its extensive distribution, *A. rubrostipa* is probably conservationally secure (Baum, 1995); however, concern has been raised that regeneration of *A. rubrostipa* is poor, and that seedlings are scarce in some forests, despite an absence of browsers.

Adansonia rubrostipa has the characteristic 'bottle tree' baobab form with a swollen pachycaul trunk and short

branches; this growth form is apparent from a very early stage, and together with its distinctive red and grey foliaceous bark makes the species unmistakable. The Kirindy Forest also contains *A. za* Baill. in some areas, and *A. grandidieri* Baill. occurs at the edge of the forest near Morondava in low lying, wetter areas; both of these species are readily distinguishable from *A. rubrostipa*. The timber of *A. rubrostipa* has no commercial value, and is not logged, but traditional nontimber forest products obtained from it include fruits, foliage, bark and fibre, generally harvested in a nondestructive manner (Baum, 1995, 2003).

We sought to determine the distribution and size structure of *A. rubrostipa* within the Kirindy Forest, and relate this to the known logging and regeneration history of the forest, current patterns of seed dispersal and the regeneration requirements of *A. rubrostipa*.

Materials and methods

Study area

The study was carried out near the Centre de Formation Professionnelle Forestiere de Morondava (CFPF) field station at Kirindy Forest, at approximately 44°39′E 20°03′S, 20 km east of the west coast of Madagascar and 60 km north-east of Morondava. The forest consists of 12,500 ha of dry deciduous forest mostly on sandy soils, but with a narrow band of vertisols along the seasonal Kirindy River, and some rocky outcrops to the north-east (Sorg & Rohner, 1996). The climate is hot and wet from November until March or April, cooler and drier from May to August, and increasingly hot with some rain in September and October. Mean annual rainfall is 767 mm mostly in heavy showers; mean 43 days year^{-1}. Mean annual temperature at Morondava is 24.7°C, with mean monthly maxima and minima of 30.7 and 19.0°C, respectively. Potential evapotranspiration rate is 1400–2143 mm annum^{-1} (Sorg & Rohner, 1996).

Data collection

Three grids were mapped for all *A. rubrostipa* trees in early November 2005, after two rainfall events in October which had initiated leaf production but before the wet season proper (52 mm 21 October, 55 mm 25 October). Visibility in the understorey was 15–20 m. Existing grids established in the forest by the Deutsches Primatenzentrum (DPZ) were utilized, which consisted of narrow (*c.* 1 m)

paths approximately 25 m apart, above which the forest canopy typically was closed. One grid (CS4 *sensu* Sorg & Rohner, 1996) was in forest that had been heavily logged in the 1980s; the second one (CN5) in forest had been selectively logged, and the third one (CS7) was unlogged. The heavily logged forest was approximately 1.5 km south of the selectively logged forest, and approximately 2 km west of the unlogged forest. At least 34.5 km of trails were surveyed, totalling 10 ha of unlogged forest and 15 ha of each of the two logged forests. Individual trees were mapped to within a 25 × 25 m grid square, and diameter at breast height (d.b.h.; 1.3 m above ground level) measurements were recorded. Standing dead and fallen trees were not recorded.

An index of dispersion (as variance/mean) was calculated for all trees on each grid; for some analyses 25 × 25 m grid cells were grouped into 50 × 50 m cells in order to populate sufficient cells to calculate reliable indices. The survey was carried out as a class exercise on a Tropical Biology Association course; supplementary surveys and verification of all trees were carried out by D.J.M.

Results

In total, 304 individual trees of *A. rubrostipa* were recorded; densities varied between the three grids, with the greatest number of individuals in the unlogged forest and the least number in the selectively logged forest (Table 1). Densities were locally much higher than indicated for the whole grids, with up to four trees in a 50 × 50 m grid block in logged forest types and seventeen trees in a 50 × 50 m block in unlogged forest. The population structure of all three grids was dominated by large trees –

Table 1 Tree size, density and dispersion (calculated for 50 × 50 m cells) in three deciduous dry forest blocks at Kirindy

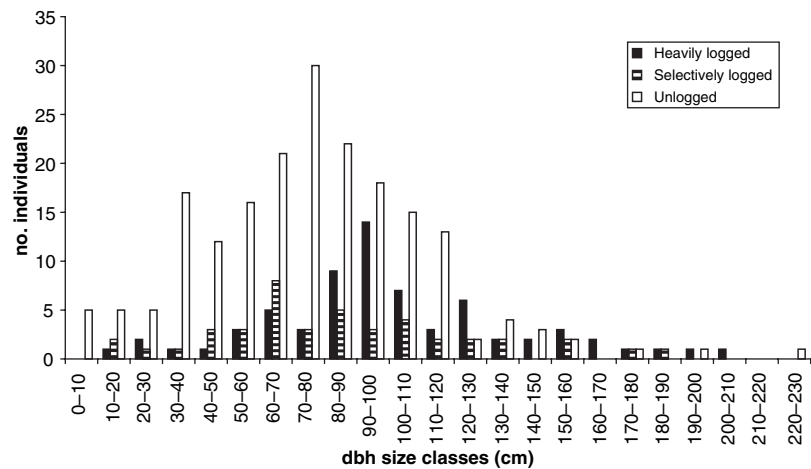|	Heavily logged	Selectively logged	Unlogged
Mean stem d.b.h. ± SD	100.6 ± 39.53	85.4 ± 39.96	76.7 ± 34.35
No. stems	68	43	193
Mean stems ha^{-1}	4.5	2.9	19.3
Index of dispersion	0.88	1.75	3.79
Number of stems <50 cm d.b.h.	5	7	44
Number of stems >110 cm d.b.h.	22	10	27

Fig 1 Distribution of diameter at breast height size classes of *Adansonia rubrostipa* in three deciduous dry forest blocks with different logging histories at Kirindy

the modal d.b.h. class was 90–100, 60–70 and 70–80 cm in grids heavily logged, selectively logged and unlogged forest, respectively (Fig. 1). Few small trees were found on either of the logged grids; however, nearly 25% of the stems in the unlogged forest were <50 cm d.b.h., and the mean stem diameter was also smaller than in the logged forest grids (Table 1).

The distribution of trees was close to random in the heavily logged and clumped in the other two forest types when calculated for 50 × 50 m cells (Table 1); using 25 × 25 m cells for the unlogged forest also indicated a clumped distribution (index of dispersion 2.13). There were sufficient small trees (<50 cm d.b.h.) in the unlogged forest to also calculate their dispersion index – using 50 × 50 m cells the index was 4.84 suggesting strong clumping; up to thirteen stems <50 cm d.b.h. were recorded in a single 50 × 50 m cell. Dispersion of large trees (>110 cm d.b.h.) could be assessed using 50 × 50 m cells in both the heavily logged and unlogged forests; the resulting indices were 1.30 and 1.32, respectively, suggesting close to random distributions.

Discussion

The primary limitations of our data set are uncertainty about the rate of growth of *A. rubrostipa*, and our inference that stem diameter correlates with age. We infer relatively fast stem diameter increments in juveniles from observations of saplings, mainly off our grids, where rapid stem thickening of relatively young saplings was apparent; Guy (1970, cited in Guy, 1982) also noted faster growth rates in younger than in older *A. digitata* L. trees in Africa. No

growth rate data could be located for Madagascar, but mean annual diameter increments for *A. digitata* range from 0.15 cm in Zambia (Swart, 1963, cited in Barnes, 1980) to 8.6 cm in Kenya in an area with two wet seasons; we recorded an annual growth rate of 0.4 cm for a single, 7-year-old sapling cut down during path maintenance, assuming that one growth ring equates to 1-year growth, as observed for *A. digitata* by Swart (1963, cited in Caughley, 1976). Both Bowman (1997) and Guy (1982) point out that due to the large number of conflicting studies, it is unsafe to assume a simple relationship between age and size in *Adansonia* spp. Nevertheless, given the enormous range in stem diameters recorded on the grids (5–221 cm) we feel confident that there is no or minimal overlap between the 'younger' size class trees <50 cm d.b.h. and the 'older' size class trees >110 cm d.b.h., when they occur in close proximity to each other.

Adansonia rubrostipa is an abundant tree in Kirindy Forest, indeed, it occurs at much higher densities than have been recorded for *A. digitata* in Africa (Barnes, 1980; Wilson, 1988) or *A. gibbosa* (A.Cunn.) Guymer ex D.Baum in Australia (Bowman, 1997), and it is clearly regenerating albeit at a low level, but the data suggest a senescing population. Its size distribution, with greatest abundance of mid-sized trees (Fig. 1), contrasts strongly with those of other trees in the same forest, which show the more usual 'reverse-J' distribution, with very large numbers of small trees and progressively fewer larger stems. For example, 158 of 368 stems of *Commiphora guillaumini* Perr. in the unlogged forest were <10 cm d.b.h. (M.P. Curran and E.Nti Acheampong, unpublished data), and 64 of 93 stems of *Colvillea racemosa* Bojer were <20 cm d.b.h. in the

logged forest (S.U. Korogone, A. Minlend and H.J. Razafi-manahaka, unpublished data). Studies on other *Adansonia* species have also shown reverse-J distributions [Weyer-haeuser, 1985; Wilson, 1988 (in Tanzania); Bowman, 1997; Dhillion & Gustad, 2004], although poor recruitment and low seedling numbers have also been recorded (Caughley, 1976; Barnes, 1980). For *A. digitata*, Barnes (1985) and Wilson (1988) (in Kenya, Mali, Sudan and Zambia) found monomodal peaks in size class distributions, with few large or small individuals, and attributed this distribution to elephant damage, which show a preference for small trees. Bowman (1997) found poor recruitment by *A. gibbosa* in Australia, and suggested changed fire regimes since European displacement of Aboriginal peoples as the cause. Neither of these theories seems likely to explain our observations in the context of Madagascar.

Baobabs produce abundant fruit on a yearly basis (up to 104 fruits recorded on a single *A. rubrostipa* each containing hundreds of seeds; Du Puy, 1996), but both fruits and seeds may be destroyed prior to dispersal. With an absence of large terrestrial herbivores in Madagascar, fruit and seed predation is limited to lemurs and birds. Unripe fruit are eaten during the dry season by red-fronted brown lemurs [*Eulemur fulvus rufus* (Audebert, 1799)], red-tailed sportive lemurs [*Lepilemur ruficaudatus* (A. Grandidier, 1867)] and Verreaux's sifaka [*Propithecus verreauxi verreauxi* (A. Grandidier, 1867)], and both *P. v. verreauxi* and the vasa parrots *Coracopsis nigra* (Linnaeus, 1758) and *C.vasa* (Shaw, 1811) eat the pedicel or receptacle, sometimes leading to 100% of fruit on a tree being removed whilst immature (Du Puy, 1996; Ganzhorn & Kappeler, 1996). Fruits have a thick (*c.* 6 mm) pericarp which rarely cracks or breaks when hitting the ground, and fallen fruits are often destroyed by weevils (Curculonidae) and, after some time, by termites. The locally endemic giant jumping rat *Hypogeomus antimena* (A. Grandidier, 1869) is implicated in the removal of the pulp and seeds of up to 92% of fallen fruit below some trees in Kirindy (Du Puy, 1996), and presumably predates the seeds. Records of actual seed dispersal rather than predation are rare, although Perrier de la Bâthie (1955; cited by Baum, 1996) makes note of lemurs feeding on fruit, and one of us (C.N.) has seen giant couas [*Coua gigas* (Boddaert, 1783)] swallowing whole seeds from opened fruits. Baum (1995, 1996, 2003) suggests that the legitimate dispersers of baobab seeds may have included the extinct sub-fossil lemurs (especially *Archaeolumur*) and the elephant bird (*Aepyornis*).

Accepting high predation rates and limited dispersal, there still appears to be very poor recruitment of small trees within the forest blocks we surveyed, especially in the two logged sites. It is possible but unlikely that we missed seedlings in our surveying; we did record trees as small as 5 cm d.b.h. on the grids, and in a smaller survey to the east of the unlogged forest located seedlings of <2 m in height and stems <1 cm d.b.h. *Adansonia rubrostipa* is characteristic of dry and intermediate soils (Rakotonirina, 1996), so we avoided surveying on the deeper vertisols along the Kirindy River, and all three grids surveyed were underlain by sandy soils. The most distinctive difference between the environment of the three forest types surveyed and of the rocky area to the east of the survey area was the light environment. The two logged grids had dense understorey vegetation and limited light penetration to ground level [2–13% diffuse site factor (dsf) *sensu* Anderson, 1964], particularly the selectively logged forest which suffered many tree falls as a result of cyclonic winds in February 2004 – these opened the canopy but have led to extensive thickening of the understorey vegetation. The unlogged forest had a more complete canopy but permitted more light to reach the forest floor (8–15% dsf) by suppressing the shrub layer; most regeneration was occurring at the eastern edge of the grid where an uneven and shorter stature gave rise to more variable light climate (7–28%). The rocky area to the east of the unlogged forest, where regeneration was most abundant, had a more open canopy, and higher and more variable light levels (13–39% dsf; M. Curran and E. Nti Acheampong, unpublished data). A similar association between seedlings and open habitat has been shown for *A. digitata* (Dhillion & Gustad, 2004). Previous studies at Kirindy (J. Helps and L. Kernegger, unpublished data) showed *A. rubrostipa* seeds to show low germination rates and be strongly dependent on full sunlight for germination (25% of 300 seeds germinated in full sunlight, <10% germinated in shaded conditions; cf. Esenowo, 1991; Danthu *et al.*, 1995). It is possible that regeneration from seed is infrequent, possibly dependent on wind removal of the foliage, and that our data illustrate a cohort of densely established seedlings passing through in time, but we feel this is unlikely given the huge range of stem diameters recorded, often in extreme proximity. Consequently, we suggest that regeneration of *A. rubrostipa* is dependent on large (multiple tree-fall) canopy gaps that coincide with gaps in the understorey too – these may be relatively rare phenomena,

although cyclonic disturbance of tall forest would generate such habitat.

In summary, our data suggest that seed predation and poor dispersal may limit recruitment of *A. rubrostipa* away from parent plants, but that this is confounded by requirements for high light levels at initial establishment. Thick shrub layers associated with responses to disturbances, both natural and artificial, may cause temporary cessation of the sort of understorey conditions conducive to regeneration after natural disturbance events. However, viable seed clearly are being produced and dispersed some distance from the parent trees, and regeneration, albeit at a low level, is occurring.

Acknowledgements

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