The adaptations of plants in fire-prone ecosystems:
savanna and dry deciduous forest of Kirindy,
Western Madagascar

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Abstract

In fire-prone ecosystems we can find particular adaptations of the plants to resist several environmental stresses and first of all the fire. In this study, we documented post-burn re-sprouting response of the woody plants in a savanna vs. a dry deciduous forest. We measured bark thickness in relation to plant size in forests and savanna trees as a key fire survival trait. We found that most of the savanna trees have relatively thick bark, especially in the juvenile stages, re-sprout vigorously and grow tall rapidly post-burn. Forest trees were thin-barked, with high mortality and slow regrowth of the few small surviving plants after a forest fire. To understand the origin of savanna we compared the proportion of endemic plants in both habitats, characterised the soils and used other additional bio-indicators. The savanna is of edaphic origin and contains both endemic and non-endemic fire-tolerant woody species.

INTRODUCTION

Each year fires blacken roughly one-half of the grasslands that cover most of the Madagascar's central highlands (Goodman & Benstead, 2003). For many researchers this ecosystem has not a primary origin, but mostly originated by the human impacts (pastoralism, "slash-and-burn" agriculture, charcoal, etc.) on the original highlands forests. There are controversial opinions about this origin, where some ecologists argue that grasslands are primary at least in some regions of the island (Bond *et al.*, 2008). This opinion is supported by the soil composition and by the presence of endemism (and micro-endemism) among plants and animals (living and extinct) of the grassy ecosystems (Dempewolf & Rieseberg, 2007).

The Kirindy forest has been exploited for several years and now is relatively protected. There have been few fires since 2008 (Raharimalala *et al.*, 2008) and no studies have been conducted on fire in the forest. In 2009, part of the forest was burnt (CFPF guide, pers. information). A nearby savanna has patches that burn almost annually. There are few studies of the evolution of fire-adaptive traits in savanna (Bond & Keeley, 2005) and, as far as we are aware, none in Madagascar, so this study therefore was conducted to compare fire response of plants in savanna and forest at Kirindy. We

identified and compared fire survival traits and fire response of the woody plants in burned and unburned forest versus a savanna.

Aims

This study focused on:

- documenting the floristic composition and diversity of savanna vs. forest shrubs and trees;
- comparing the proportion of endemic plant species in the forest and savanna;
- comparing the bark thickness of the forest and savanna trees;
- identifying the different re-sprouting modality of woody plants;
- characterising the soil of the forest and savanna;
- using additional savanna bio-indicators to develop an hypothesis of its origin.

MATERIALS AND METHODS

Study site

The data for this study were collected in a dry deciduous forest and savanna in the forestry concession of the *Centre de Formation Professionelle Forestiere* (CFPF), Western Madagascar, 60 km north of Morondava (44° 39' E; 20° 03' S), at the end of the dry season, in November 2011. The savanna is about 2 km long and 1 km wide, surrounded by deciduous dry forest. The grasses in the savanna are dominated mostly by *Heteropogon contortus* and *Hyparrhenia rufa* with patches of *Cynodon dactylon* near seasonal wetlands. The area has two distinct climate seasons, the hot and wet season of three to five months and the dry season from seven to nine months. The wet season starts at the end of November of earlier December and continues to late March or early April. The dry season is distinct from March or April to October or November. Annual rainfall averages about 780 mm and annual temperature averages about 24.8 °C (Hunziker, 1981).

Methods

We sampled trees of diverse sizes to characterised bark thickness and re-sprouting response. The sampling protocol varied in different habitats. In the unburned forest we selected common species with a range of size classes. In the burned forest we sampled all woody species along a transect (50 x 10 m) inside the most burned area. In the savanna we walked transects using a wandering quarter method to sample the few trees species in all their size classes. Any shrubs encountered along the savanna transects were also sampled for fire response.

1. Bark thickness sampling: we sampled a range of tree species but avoided shrubs as these are typically top killed by fires regardless of bark thickness. We measured the circumference at breast height of the sample of tree species in the forest and savanna. We measured bark

thickness by making an incision with a big strong knife (machete), from the bark to the cambium, of the biggest trees and a small knife for young trees or branches. Bark thickness was measured with a Vernier Calliper to the nearest 0.1 mm.

2. Fire response: we observed re-sprouting response of woody plants in the savanna following a fire within the last year; we also observed the re-sprouting response of trees in a forest burned two years ago. Re-sprouting was characterised as basal, ground (clonal) and epicormic. Plant height (shrubs) or stem diameter of each sample plant was noted.

3. General features in the savanna: we collected observations on termites and birds as bio-indicators. For the termites, we quantified their density in savanna and forest on similar soils in a 50 x 50 m quadrat in each habitat. For birds we noted the presence of typical grassland birds in the savanna. Soil was sampled by auger at selected points along savanna transects.

RESULTS

Bark thickness

We compared the bark thickness and stem circumference of all the tree species surveyed in the forest and savanna. Figure 1 shows there are two main patterns, with thick bark in the savanna species and much thinner bark in the forest species.
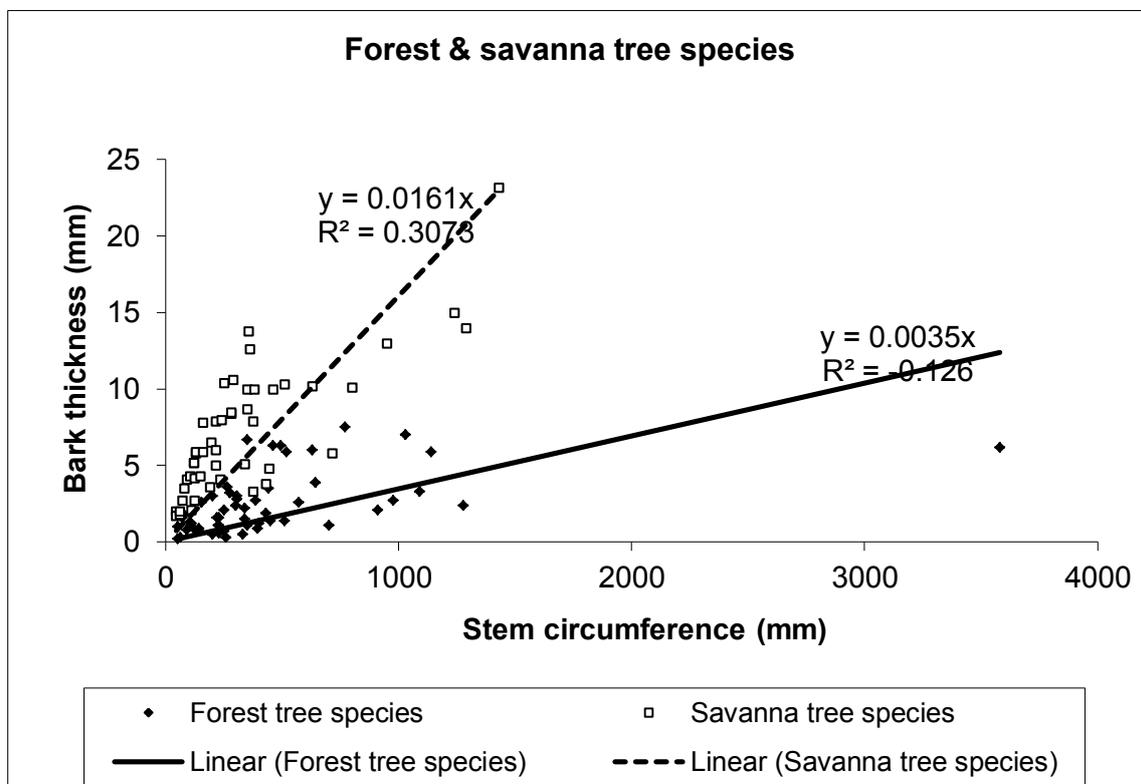
Figure 1. Relationship between bark thickness and stem circumference in the savanna (n = 48; *P* < 0.01) and forest trees (n = 36; *P* < 0.05).

On the next graph (Figure 2) we plotted the same variables but we have chosen only individuals with stem circumferences below 400 mm (<12 cm diameter). This represents the threshold below which the plants are typically killed in savanna fires. The two patterns are clearer and become more evident with young trees of savanna having thicker bark than forest trees. Savanna bark thickness increased at a four times faster rate with increasing circumferences than forest trees.

Forest & savanna tree species <400 mm SC

The graph shows bark thickness (mm) on the y-axis (0 to 16) versus stem circumference (mm) on the x-axis (0 to 400).

$y = 0.0282x$
$R^2 = 0.5071$

$y = 0.0068x$
$R^2 = 0.0858$

Legend:
◆ Forest tree species   □ Savanna tree species
—— Linear (Forest tree species)   - - - - Linear (Savanna tree species)
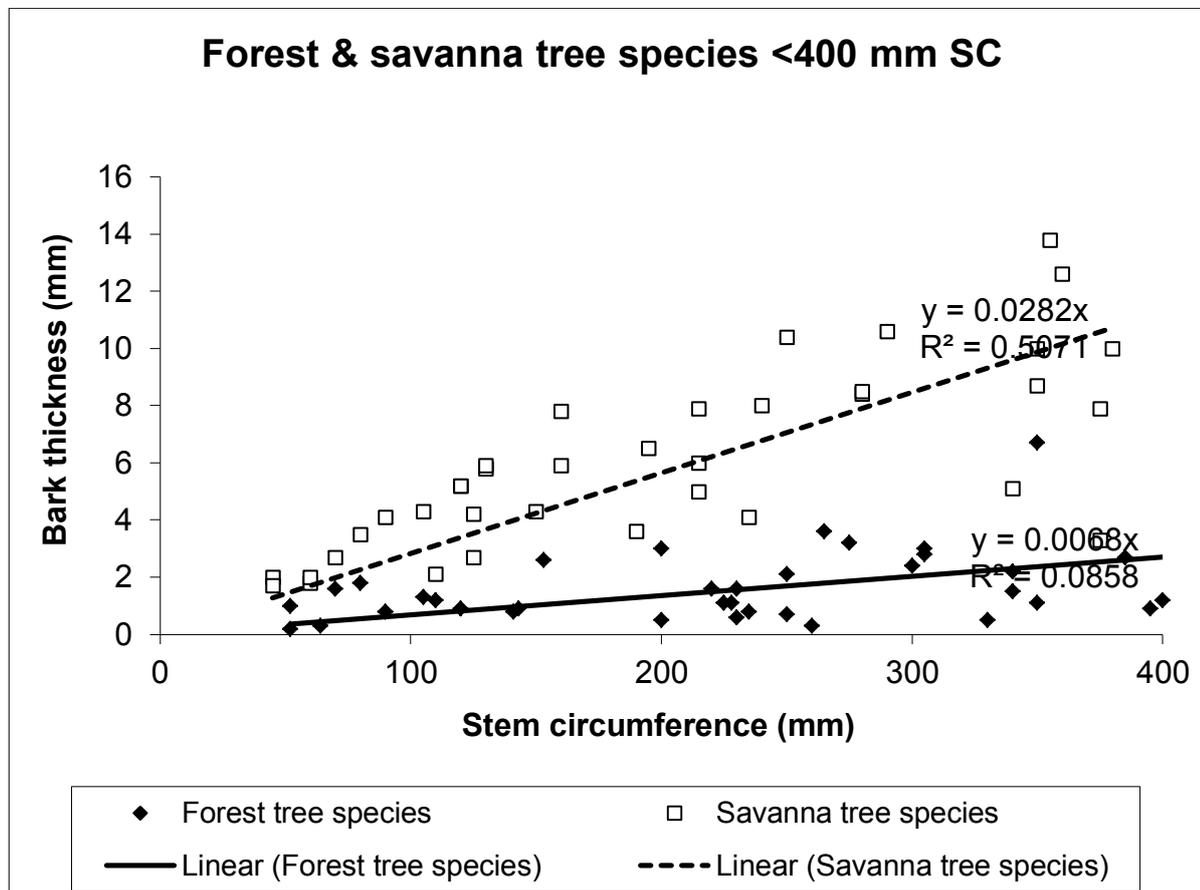
Figure 2. Relationship between bark thickness and stem circumference <400 mm in the savanna (n = 36; *P* < 0.01) and forest (n = 36; *P* < 0.05) trees.

To compare phylogenetically related species we have chosen two species of *Poupartia*: *P. sylvatica* from the forest and *P. birrea* (= *Sclerocarya caffra*) from the savanna. The species show a clear difference: *P. birrea* had much thicker bark both in the young and adult plants than *P. sylvatica*. The relationship is clearly not linear with larger savanna trees having relatively thin bark for their size. In Figure 4, we have selected only juvenile plants with a stem circumference less than 400 mm. The bark thickness of the savanna species increased at three times the rate of the forest species with increasing stem size.
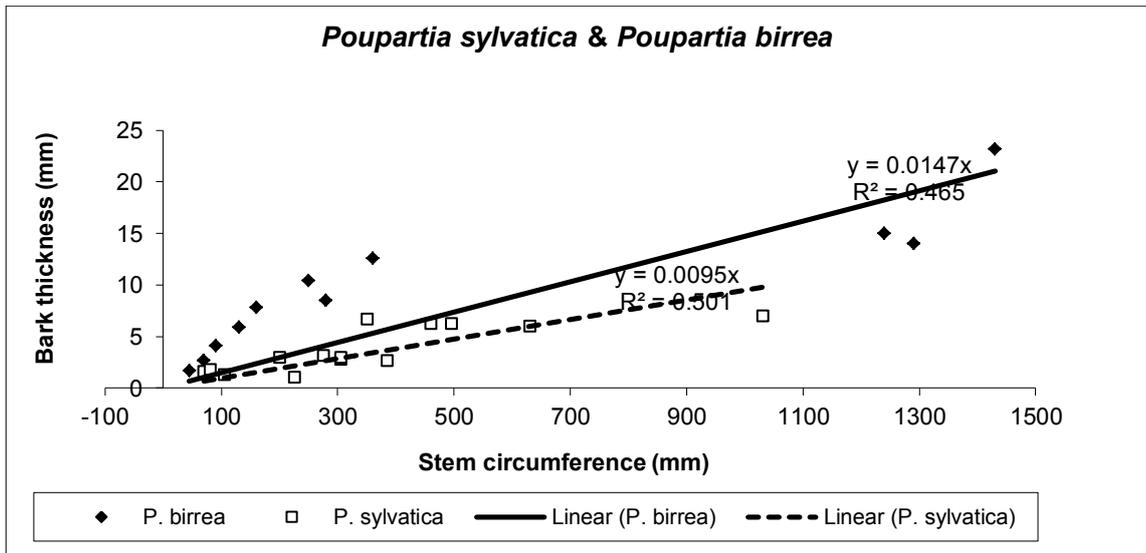
Figure 3. Relationship between bark thickness and stem circumference among *Poupartia sylvatica* (*n* = 16; *P* < 0.01) and *Poupartia birrea* (*n* = 36; *P* < 0.01).
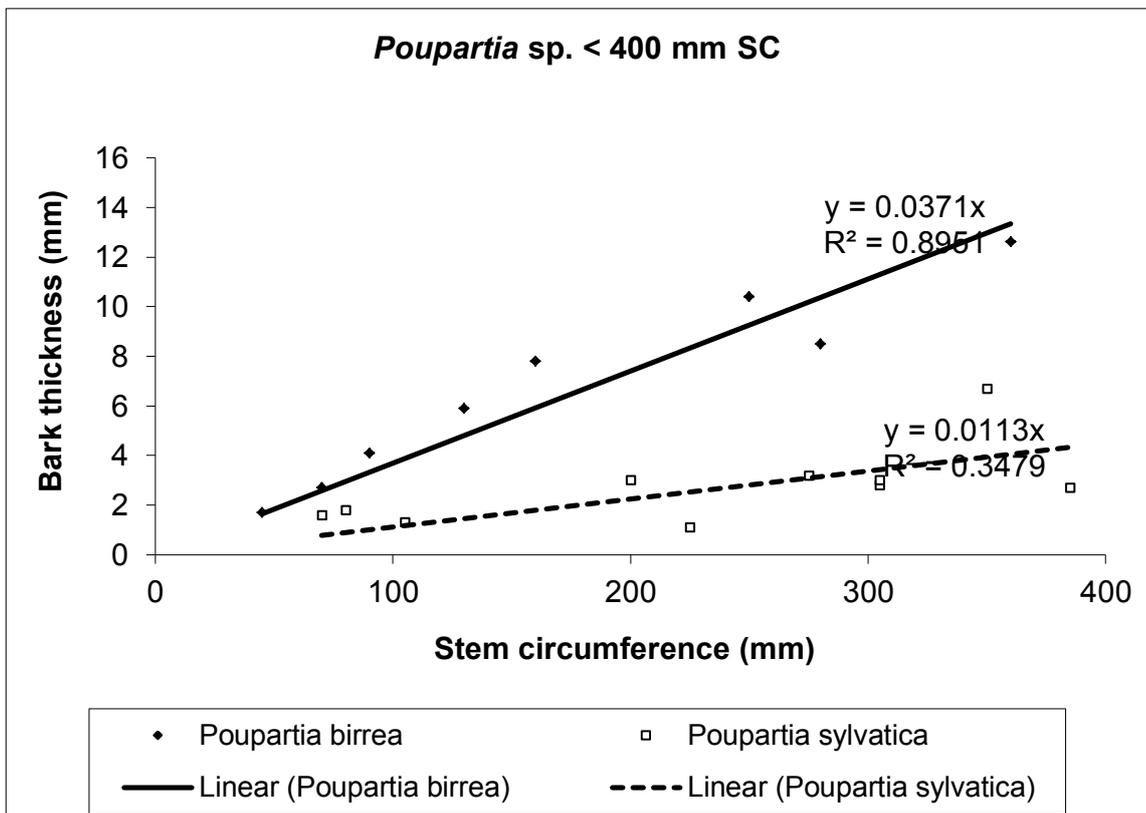
Figure 4. Relationship between bark thickness and stem circumference <400 mm among *Poupartia sylvatica* (*n* = 9; *P* < 0.05) and *Poupartia birrea* (*n* = 8; *P* < 0.01).

As regards size class distribution of trees in the savanna, we noted three main height-classes. Most of the plants that we surveyed were small and clustered in a height class less than 2 m. These plants are likely to be top killed by fire because of thin bark and low stature. The second class shows the intermediate height, where the plants have reached a size with a higher probability of escaping

damage from low severity fires. The third class shows the scattered adults, which have reached enough height to escape being top killed from the fire.
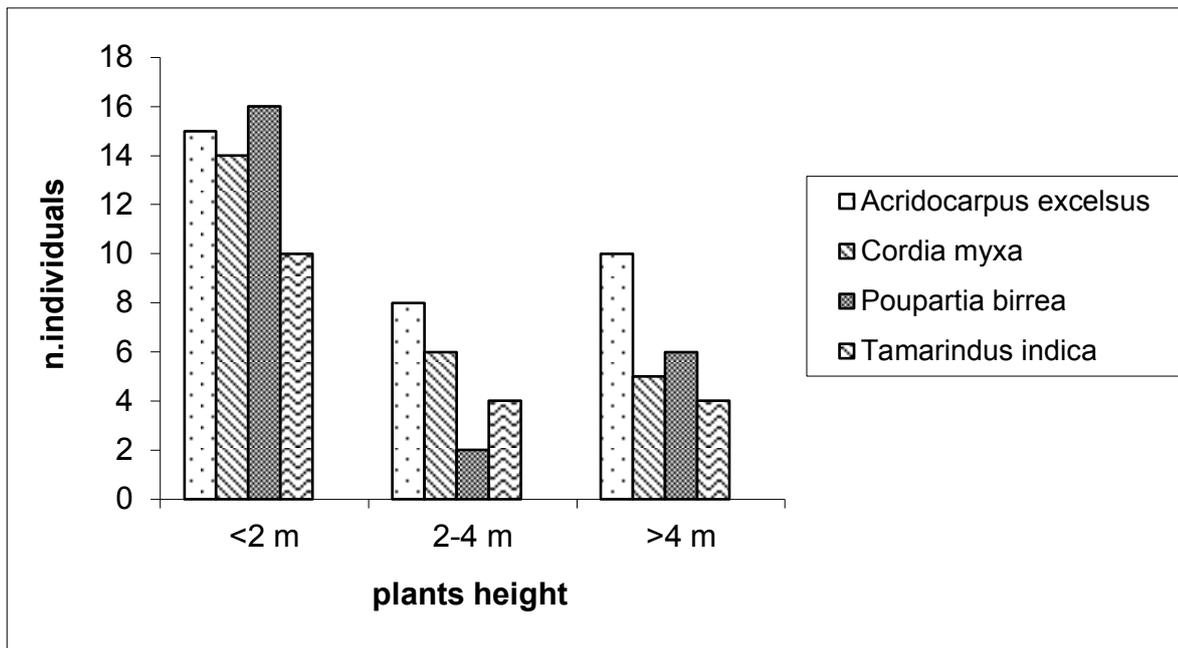
Figure 5. Relationship between plant height and number of the individuals of four savanna tree species. Plants <2 m height are vulnerable to top kill in savanna fires. Plants at 2-4 m height are large enough to escape top-kill in less intense fires. Plants >4 m height are usually not top killed by fire

Fire response

The re-sprouting modality of the woody plants shows a very different trend in the savanna *versus* the burned forest. In the savanna we found three main re-sprouting responses: basal, ground (clonal) and epicormic. After a fire event, all smaller plants re-sprout from the base, but many of the taller trees do not. Epicormic re-sprouting was also very common on the lower branches of the adult trees. Palms seem to show clonal re-sprouting. In the burned forest, we have found only the basal re-sprouting modality and only among very few young plants. The absence of epicormic re-sprouting was striking. Forest trees that were tall enough to escape leaf scorch sometimes survived undamaged.
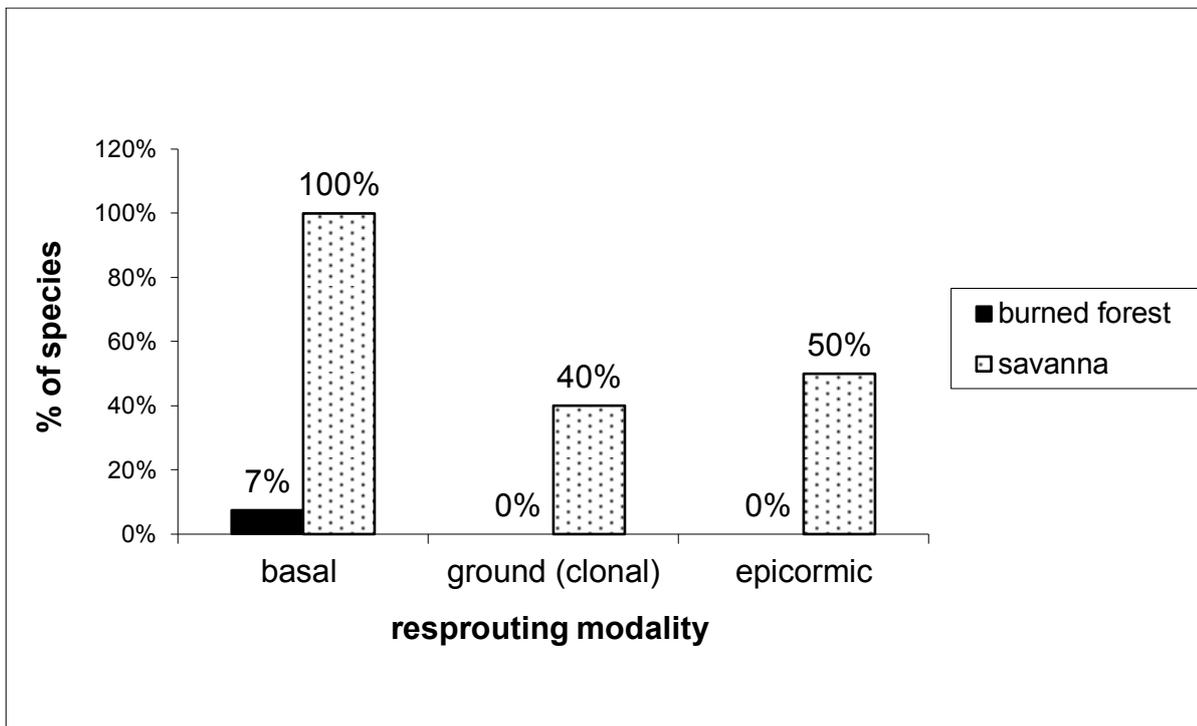
Figure 6. Re-sprouting response among woody plants in savanna and burned forest.

During our surveys, we have identified 12 woody plant species in the savanna and 32 woody plant species in the forest. If we look at endemic composition, there are about 1/3 of endemic species in savanna and about ¾ of endemic species in the forest. The most common woody plants in the savanna were non-natives (*Poupartia birrea*, *Cordia myxa*, *Ziziphus mauritiana*). Most of the savanna Madagascar endemics were shrubs but one, *Acridocarpus excelsus*, is a fire-tolerant tree in the savanna. The Madagascan savanna shrubs were not observed in the forest and may be open habitat specialists (e.g. *Acacia (Mimosa) delicatula*).
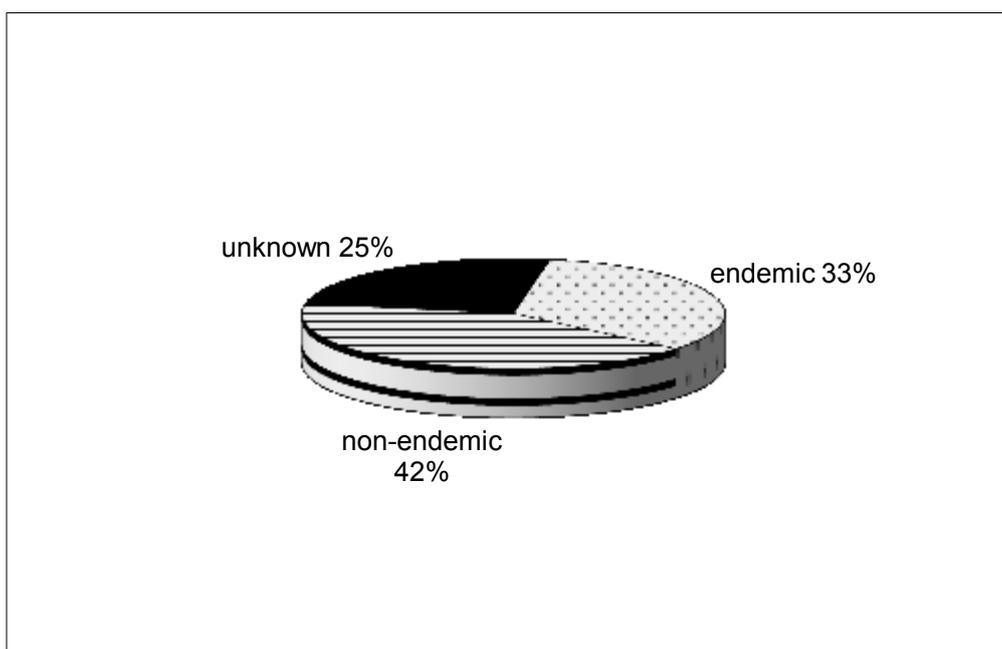
Figure 7. Percentage of endemism among savanna woody plants.
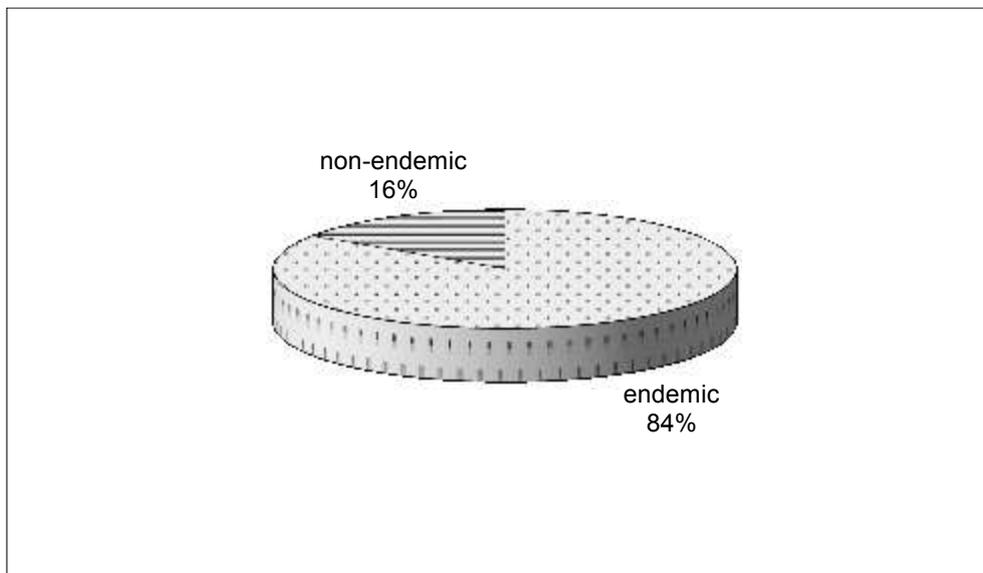
Figure 8. Percentage of endemism among forest woody plants.

DISCUSSION

The first results of this study indicate that the savanna tree species have relatively thicker bark than forest species. We showed that especially among juveniles, savanna trees present thicker bark for a given stem diameter than forest tree species. This strategy allows the insulation of the xylem from fire heat (Balfour & Midgley, 2006). At the same time, the savanna plants show a relatively quick grow comparing with the forest plants, to allow them to escape from the "fire-trap", as in the forest the young plants grow fast to reach the light. It is clear that a first requirement for trees to resist fire in a surface fire regime such as savanna is to develop a thick bark especially during the juvenile stages (Midgley *et al.,* 2011). This mechanism is not present among the woody plants of the dry deciduous forest. Our analysis revealed also that the savanna woody plants respond to burning with diverse modes of re-sprouting such as basal, clonal and epicormic; these traits were not shown in the forest except in a few cases of basal re-sprouting from shrubs and smaller trees while they lose the ability to sprout as adults (Bond & Midgley, 2001) The "savanna-strategy", together with a thick bark, ensures a great probability of survival after fire.

Our observations suggest that the savannah patch is of edaphic origin. The soils for much of the patch are heavy clays. Small bare areas of similar clay soils occur near the Kirindy camp and seem to exclude the Kirindy forest species which prefer sandier soils. The abundant grasses are tolerant of the clay soil as are many of the shrubs which only occurred in the savanna and often on a totally clay soil where other trees are not able to grow. The presence of 1/3 of endemic savanna plants also suggests that this ecosystem is not of an anthropogenic origin but has long been a component of this region (for further explanation see the appendix).

Looking forward in a management and conservation prospective of the fire-prone ecosystems of the study area, we can say that the forest is not threatened by fire. The forest-savanna boundary is composed by different shrubs and, possibly, fire-resistant tree species, with different architecture and spatial distribution. In other tropical regions, forest tree species adjoining savannas are more fire tolerant than forest interior species. This is an efficient barrier to prevent the incoming of fire into the forest (Hoffmann *et al.*, 2009). At Kirindy, the most vulnerable forest types to get fire from the savanna into the forest are probably the bamboos patches which border the savanna in a few spots.

For ecosystems with a long history of fire, the anthropogenic suppression of fire has led to the loss of as many as 50% of the plants species. Changes in faunal composition have also been reported, for example, loss of termites and even greater species loss especially when fire suppression leads to complete biomes switches, such as from savanna to forest (Bond & Keeley, 2005). Although anthropogenic fires have extended areas of flammable vegetation, there is now evidence that natural fires occurred long before humans and that flammable ecosystems pre-date anthropogenic burning by millions of years (Bond & Keeley, 2005).

ACKNOWLEDGEMENTS

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APPENDIX

Soils

For a better understanding of the edaphic conditions of the forest, forest edge and savanna, we sampled soils using an auger. The soil profile (about 40 cm depth) in the forest (see Figure 9) show a strong composition in sand (80%) and less in clay (20%), where the first layers are more sandy, dry and grey while the lower layers are more wet, yellowish and more rich in clay. Savanna soils were deep black cracking clays (Vertisol) in the lower slope, while at the margins soils had sandy topsoils, dry in the surface, and moist mottled greyish brown sub-soils. These soils, together with the presence of some indicator woody plants (e.g. *Ziziphus mauritiana*) correlated with the soil condition, show us that these soil types are seasonally waterlogged in the rainy season and suggest an edaphic origin of the savanna.

Additional bio-indicators

To help us to determine the origin of the savanna, we have chosen termites and birds as additional bio-indicators. We counted the termites in savanna and forest and we found a density respectively of 80 and 20 termites/ha, so in first analysis we could argue that the termites prefer mostly the open grasslands than the forest. If we look also at the soil texture we could argue that the termites prefer mostly the soil with high percentage of sand in the topsoil over a hydromorphic sub-soil and they clearly avoid pure clay soil. About birds, we have used simple observations to determine the presence/absence of typical and endemic grasslands birds. According to Pons & Wendenburg (2005), the presence of the regional endemic Madagascar cisticola (*Cisticola cherina*) and the endemic grey-headed lovebird (*Agapornis cana*) are strictly correlated to the savanna ecosystems indicating that the origin of the savanna is not so recent and not purely anthropogenic. The presence of other endemic not-strictly savanna species (forest-savanna edge species) such as Madagascar buttonquail (*Turnix nigricollis*) and Madagascar red fody (*Foudia madagascariensis*) also show that the transition between forest and savanna animal species (eco-tone) is not so recent. Unfortunately, we did not find the endemic Madagascar sandgrouse (*Pterocles personatus*), a very elusive bird, which is the most strictly-savanna species of the country, a clear bio-indicator of a more ancient origin of the Malagasy grasslands. However, we have noted the presence of helmeted guineafowl (*Numida meleagris*), introduced from Africa, in the savanna patch.

Forest woody plants and family

Berchemia discolor	Rhamnaceae
Adansonia rubrostipa	Bombacaceae
Astrotrichilia asetrotricha	Meliaceae
Baudouinia fluggeiformis	Cesalpinaceae
Bivinia jalberti	Flacurtiaceae
Breonia perrieri	Rubiaceae
Buxus madagascariensis	Buxaceae
Canthium sp.	Rubiaceae
Cedrelopsis grevei	Ptaeroxylaceae
Colubrina decipiens	Rhamnaceae
Commiphora arafy	Burseraceae
Commiphora guillaumini	Burseraceae
Cordyla madagascariensis	Fabaceae
Dalbergia trichocarpa	Fabaceae
Diospyros sp.	Ebenaceae
Fernandoa madagascariensis	Bignonaceae
Foetida asymetrica	Lecythidaceae
Girocarpus americanus	Hernandiaceae
Givotia madagascariensis	Euphorbiaceae
Grewia sp.	Tiliaceae
Hymenodiction decaryi	Rubiaceae
Hyperacunthus grevei	Rubiaceae
Neobeguea mahafaliensis	Meliaceae
Pandanus sp.	Pandanaceae
Phyllanthus argylodaphane	Euphorbiaceae
Phyllartron sp.	Bignoniaceae
Poupartia sylvatica	Anacardiaceae
Securinega perrieri	Euphorbiaceae
Securinega siyrigii	Euphorbiaceae
Stereospermum arcuatum	Bignoniaceae
Strychnos decussata	Loganiaceae
Strychnos henningsii	Loganiaceae
Zanthoxylum sp.	Rutaceae

Savanna woody plants and family

Acridocarpus excelsus	Malpighiaceae
Albizia sp.	Fabaceae
Antidesma madagascariensis	Euphorbiaceae
Cordia myxa	Boraginaceae
Eugenia sp.	Myrtaceae
Hyphaene coriacea	Palmaceae
Mimosa delicatula	Fabaceae
Mimosa sp.	Fabaceae
Poupartia birrea	Anacardiaceae
Tamarindus indica	Fabaceae
Vitex sp.	Lamiaceae
Ziziphus mauritiana	Rhamnaceae
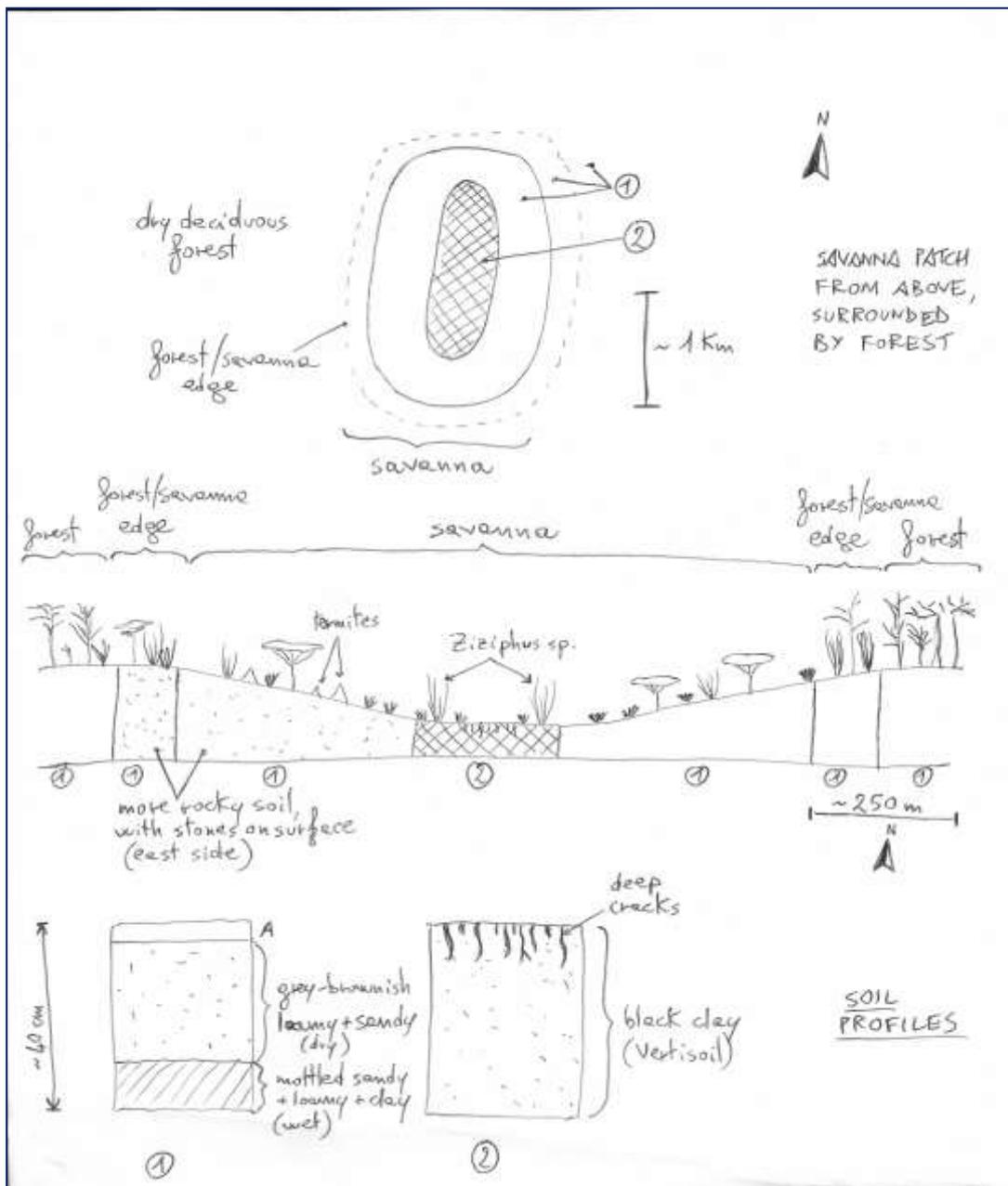
Figure 9. Soil patterns of savanna.
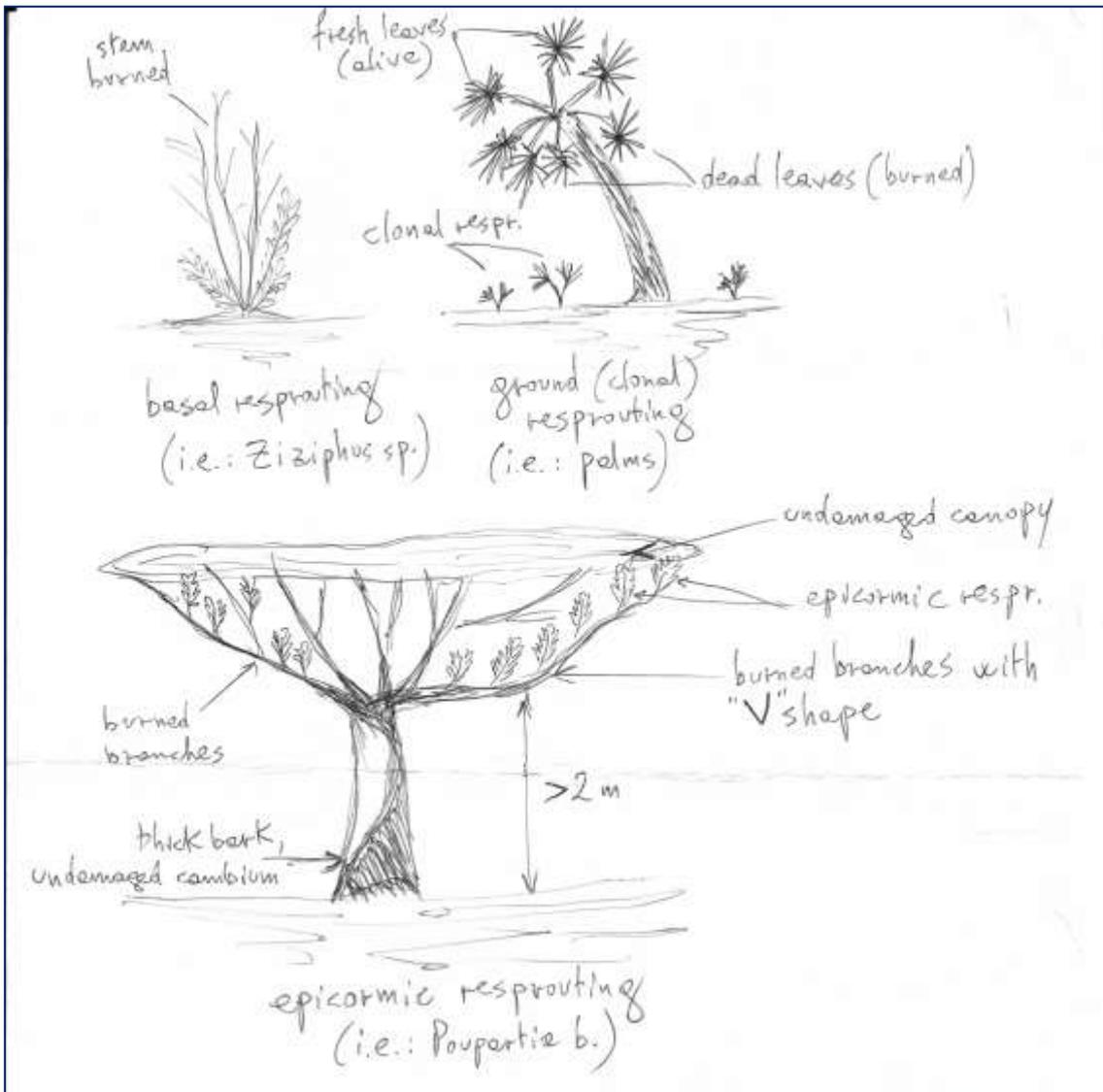
Figure 10. Re-sprouting response of savanna woody plants.