Agriculture, Ecosystems and Environment 199 (2015) 312–319

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

Effects of slash-and-burn practices on soil seed banks in secondary forest successions in Madagascar

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ARTICLE INFO

Article history:
Received 24 February 2014
Received in revised form 10 September 2014
Accepted 22 September 2014
Available online 24 October 2014

Keywords:
Agriculture
Regeneration
Highlands
Fallow age
Seed dispersal
Tillage
Tropical

ABSTRACT

Forest seed bank assessments are scarce in Madagascar and thus little is known about the relationships between the seed banks and vegetation dynamics on which secondary succession processes rely. The objective of this paper is to analyse the effects of slash-and-burn agriculture on soil seed banks and their dynamics along secondary forest successions. The aim of this work is to determine the effects of agricultural practices (cropping duration, tillage regime and fallow age) on seed bank density (SBD) and diversity (SBSR) during secondary succession periods (<25 years). Cropping duration was divided into three classes: (i) short (1–2 years), (ii) medium (3–5 years) and (iii) long (6–11 years). Tillage regime during crop successions was divided into three categories: (1) no tillage (only direct sowing is observed), (2) light tillage (after direct sowing, local shallow tillage is observed) and (3) heavy tillage (after direct sowing followed by light tillage practice, complete tillage practice is observed). Fifteen fallows subdivided into three regrowth age classes (2–6, 10–12 and 14–22 years) were surveyed. Fallow age is the main driver of SBD and SBSR: they increase with fallow age, regardless of cropping duration and tillage regime. SBD and SBSR recovery always occurs but is slower under long cropping duration (3–11 years) and heavy tillage regime because cropping duration helps to maintain a high level of wind-dispersed seeds during secondary succession and tillage regime contributes to reducing the proportion of viable seeds.

1. Introduction

The quality of the agroecological matrix following tropical forest conversion is now recognized as being crucially important for the maintenance of biodiversity (Perfecto and Vandermeer, 2010; Edwards et al., 2012; Estrada et al., 2012). In the tropics, agroecosystems and post-cultural secondary forests represent an important part of the remaining vegetation after forest conversion (Gardner et al., 2009; Perfecto and Vandermeer, 2010). However, most studies of biodiversity focus on primary forest fragments and ecosystems. Studies in agroecosystems and secondary forest successions consequently are needed to understand biodiversity changes and secondary forest dynamics (Gardner et al., 2009; Irwin et al., 2010; Carrière et al., 2013).

Secondary forest successions rely on remaining tree sprouts, seed rain from nearby fragment forests or isolated trees and the soil seed bank. The structure and diversity of secondary regrowths depend on the distance of seed sources and the ability of propagules to survive in the soil and then establish themselves following several cropping cycles (Carrière et al., 2002a,b; Guevara et al., 2004; Sandor and Chazdon, 2014).

Many soil seed bank assessments in the tropics focus on their ability to be a source of recruits (Wijdeven and Kuzee, 2000; Baider et al., 2001; Svenning and Wright, 2005; Vieira and Proctor, 2007; Castillo and Stevenson, 2010). Seed limitation restricts forest recovery (Wijdeven and Kuzee, 2000; Svenning and Wright, 2005; Vieira and Proctor, 2007), but low similarity between the seed bank and extant vegetation indicates that the seed bank probably contributes little to secondary forest regeneration (Saulei and Swaine, 1988; Dupuy and Chazdon, 1998; Alvarez-Aquino et al., 2005). Seed bank density tends to decrease along secondary succession stages while woody species (tree or shrub), which are scarce in early succession stages, become increasingly abundant during late succession stages (Vieira and Proctor, 2007; Baider et al., 2001; Saulei and Swaine, 1988). Seed banks are affected by grazing, timber harvesting and fire (Martins and Engel, 2007;

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http://dx.doi.org/10.1016/j.agee.2014.09.010
0167-8809/

Alvarez-Aquino et al., 2005). However, seed bank variations related to crop-fallow cycles and soil tillage are rarely studied in tropical areas (Chauhan et al., 2006). In temperate ecosystems, the effect of tillage and crop-fallow systems on the seed bank have been studied (Luzuriaga et al., 2005; Leon and Owen, 2006; Steckel et al., 2007), but mainly in the framework of weed management studies.

Secondary succession in the tropical forest of eastern Madagascar is well documented and shows that agricultural practices are the main drivers of secondary dynamics and have a combined effect on soil structure and seed bank (Pfund, 2000; Styger et al., 2007; Klanderud et al., 2010; Randriamalala et al., 2012). Species richness increases with fallow age (Klanderud et al., 2010) as observed elsewhere in the tropics. Randriamalala et al. (2012) showed that fallow vegetation recovery occurs regardless of plot agricultural history, although this recovery is faster under no tillage and short cropping duration and slower after long agricultural use. However, a reduction in fallow age and repeated vegetation burning may result in species-poor herbaceous vegetation dominated by fire adapted grass species like *Aristida* sp. (Styger et al., 2007).

Forest seed bank assessments are scarce in Madagascar and thus little is known about the relationships between the seed dispersal, seed bank and vegetation dynamics on which secondary succession processes rely. This paper aims to fill this gap by analysing the effects of agricultural practices on seed bank density and diversity during secondary succession (<25 years), and discusses the influence of these two combined factors (agricultural practices and soil seed banks) on forest regeneration. Agricultural practices are characterised here by tillage regime, cropping duration, and fallow age. The soil seed bank is the viable seed pool in a 0–5 cm deep sample of soil.

2. Material and methods

2.1. Study site

The study was carried out in October 2007 at different points around Androy village (21°22′46″S; 47°18′34″E). These points fell within an approximately 6 km × 4 km area located on the north-western edge of the protected forested corridor between the national parks of Ranomafana and Andringitra. The study site was described in a previous paper (Randriamalala et al., 2012).

2.2. Study plot sampling

Fifteen formerly cultivated fallows, varying in size from 100 to 700 m^2, were chosen from the 89 plots studied by Randriamalala et al. (2012) according to their age and vegetation structure (young herbaceous regrowth: 2–6 years; middle age shrubby regrowth: 10–12 years; old shrubby or woody regrowth: 14–22 years, Table 1). All of the plots studied were on sloping hills and were part of the same, fine grain mosaic composed of mature forest, forested, shrubby and herbaceous fallows, and cultivated fields (Martin et al., 2012).

2.3. Soil seed bank sampling and vegetation study

Surface soil was collected with a drill (8 cm diameter, 5 cm deep) to estimate soil seed stock density and diversity. Ten repetitions per study plot were made randomly. Soil samples were stored in plastic bags for about 15 days at room temperature (25–30 °C) and under natural lightning, before being sieved through decreasing mesh sizes: 2 mm, 400 μm and 200 μm. Separated seeds were counted and identified using a low-power stereo microscope (2*x*) and voucher specimens collected previously (seed library from Picot et al., 2007 and the GEREM[1] research program, which carried out research on human–forest interaction in the study site in 2003–2006). They formed the seed stock, which is the total number of seeds that emerge from sieving. After sieving, germinated seeds were considered to be viable while the rest were tested with 1% triphenyl tetrazolium chloride (TZ test, 20–30 °C) over 48 h (Schmidt, 2000). This substance colors viable embryos red. The seed bank thus was formed by germinated and TZ test viable seeds. The difference between the seed stock (total seeds) and the seed bank (viable seeds) was made up of dead seeds, the amount of which characterised seed mortality. Many viable seeds were not identified; those belonging to Poaceae, Fabaceae, and Asteraceae were identified at the family level only. Poaceae and Asteraceae were considered to be wind-dispersed. The proportion of viable seeds from the seed stock then was calculated. The seed bank was characterized by the following: the total number of viable seed morphospecies, otherwise known as the seed bank species richness (SBSR); the number of viable seeds per sample, otherwise known as the seed bank number (SBN); the number of viable seeds per m^2, otherwise known as seed bank density (SBD); and the proportion of Poaceae and Asteraceae wind-dispersed seeds (%(Poa + Aster)). SBN and SBD were linked by the following relation: SBD = SBN/Sdr where Sdr (m^2) is the surface of the drill used to collect the soil samples (about 50.24×10^{-4} m^2).

Table 1
Proportion of viable seeds (%).

Factors		Number of plots	Over all seeds	Dispersal mode		*p* between dispersal modes
				Wind-dispersed seeds (Poa + Aster)	Other seeds	
FA	2–6	5	28a	32a	16a	>0.05
	10–12	4	49b	43a	52b	>0.05
	14–22	6	51b	45a	59b	<0.01
	p		0.001	>0.05	0.001	
TR	NTR	7	53a	53a	56a	>0.05
	LTR	4	44b	36b	56a	<0.01
	HTR	4	33b	30b	39a	>0.05
	p		0.001	0.001	>0.05	
CD	1–2	6	44a	30a	55a	<0.001
	3–5	4	66b	66b	65a	>0.05
	6–11	5	33c	29a	41b	>0.05
	p		<0.001	<0.001	0.022	

2.4. Agricultural practice variables

Interviews regarding the history of the fallow fields were conducted with the field owners and their relatives. The tillage regime (TR), cropping duration (CD) and fallow age (FA) were identified by recording the year-by-year history of each of the 15 fallow fields beginning with the first clearing of the mature forest. Three TR were defined: (1) no tillage (n = 7), (2) light tillage (n = 4) and (3) heavy tillage (n = 4). The no tillage regime consists of only direct sowing of maize and bean seeds (a simple hole) during the crop succession. For light tillage regime, after direct sowing, partial tillage with a spade immediately around the planting hole, called *kobokaka* (<10 cm depth, about 1 m radius around cassava cutting, which is the only crop planted with *kobokaka*; Randriamalala et al., 2012) is observed during crop succession. For heavy tillage regime, after direct sowing and light tillage practice,

[1] GEREM: management of rural landscapes and environment in Madagascar.