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Silvicultural disturbance has little impact on tree species diversity in a Central African moist forest

S. Gourlet-Fleury [a,*], D. Beina [b,c], A. Fayolle [d,e], D.-Y. Ouédraogo [a], F. Mortier [a], F. Bénédet [a], D. Closset-Kopp [c], G. Decocq [c]

[a] UPR BSEF, CIRAD, Campus International de Baillarguet, F-34398 Montpellier, France
[b] Université de Bangui – Cerphameta, BP 1450 Bangui, Central African Republic
[c] Université de Picardie Jules Verne, UR "Ecologie et Dynamique des Systèmes Anthropisés" (EDYSAN, FRE 3498 CNRS), 1 rue des Louvels, F-80037 Amiens, France
[d] Ministère des Eaux, Forêts, Chasse et Pêche, avenue du 19 janvier, BP 3314 Bangui, Central African Republic
[e] Agro Bio-Tech, Université de Liège, 2, Passage des Déportés, B-5030 Gembloux, Belgium

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ABSTRACT

Timber production is an important economic sector in most forested countries of Central Africa, where about 14 million hectares of lowland moist forests are now planned for management. This production is expected to be sustainable, but the actual impact of logging on biodiversity is still questioned.

To answer this question, we used a unique long-term controlled experiment implemented more than 20 years ago in an old-growth semi-deciduous moist forest of the Central African Republic (CAR). We tested whether (i) anthropogenic disturbances associated with silvicultural operations had an effect on the composition and diversity of tree communities, and (ii) there is a relationship between diversity and disturbance intensity in those forests.

For this, we botanically identified all trees $\geqslant$ 10 cm DBH in 28 1-ha plots where no treatment (controls), logging and logging + thinning operations were implemented 24 years ago and created a strong gradient of disturbance. We investigated the relationships between five diversity indices and a disturbance index calculated for each 1-ha plot, for all species and separately for three regeneration guilds.

We found a strong positive monotonic relationship between the intensity of disturbance and the percentage of pioneer species in the tree communities, which proved to be equally detrimental, in terms of relative abundance, to the non-pioneer light-demanding and the shade-bearing species.

Overall, disturbance appeared to have a weak monotonous negative effect on diversity, irrespective to the index considered. The diversity of shade-bearers slightly decreased along the disturbance gradient without significant decrease in species density; disturbance had no effect on non-pioneer light demanders, but a clear significant negative effect on the diversity of pioneers, with a significant decrease in species density. This negative effect was associated with the massive recruitment of the early-successional, fast-growing *Musanga cecropioides* R. Br. (Urticaceae), which rapidly preempted space and resources in the most disturbed plots. Despite this effect, disturbance did not significantly affect the local heterogeneity in species distribution.

These results suggest that the semi-deciduous moist forests of CAR are locally resilient to small-scale disturbances associated with silvicultural operations. This may be a consequence of the past anthropogenic and/or climatic disturbances, which have been stronger and more long-lasting than elsewhere within the tropical forest biome, and would have removed the most vulnerable species. Because logging intensity in these forests is usually low, we do not expect any direct major impact on tree species diversity, at least after the first felling cycle.

1. Introduction

Timber logging plays an important role in the economy of Central Africa. The formal forestry sector often represents the main sector able to generate direct and indirect employment as well as funding for infrastructure in still rural economies (Bayol et al., 2012). In the formal sector, logging occurs within concessions

* Corresponding author. Tel.: +33 (0)4 67 59 38 83; fax: +33 (0)4 67 59 37 33.
E-mail addresses: sylvie.gourlet-fleury@cirad.fr (S. Gourlet-Fleury), d_beina@yahoo.fr (D. Beina), adeline.fayolle@ulg.ac.be (A. Fayolle), dakis.ouedraogo@gmail.com (D.-Y. Ouédraogo), fabrice.benedet@cirad.fr (F. Bénédet), deborah.closset-kopp@u-picardie.fr (D. Closset-Kopp), guillaume.decocq@sa.u-picardie.fr (G. Decocq).

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granted to private companies within the permanent forest estate. An increasing part of these concessions is submitted to a management plan, made mandatory in all forest laws since the 1990s (Nasi et al., 2012). This has resulted in over 14 million ha of forests currently managed, out of 44 million ha of lowland moist forests allocated to timber logging in long-term concessions (Bayol et al., 2012).

Management plans implemented in Central Africa are supposed to be sustainable and thus to ensure "the production of a continuous flow of desired forest products and services without undue reduction of (the forest) inherent values" (ITTO, 2005). Whether timber can be sustainably produced has been a highly controversial topic (e.g. Bawa and Seidler, 1998; Rice et al., 1997, 1998; Zimmerman and Kormos, 2012, *vs* Fredericksen and Putz, 2003; Pearce et al., 2003; Putz et al., 2012), a central question being the potential negative impact of logging on tree species diversity. Three recent meta-analyses did evidence an overall negative impact of logging on tree species richness (Clark and Covey, 2012, Gibson et al., 2011, Putz et al., 2012) but this impact resulted from a high variety of logging situations (in terms of logging regime – frequency and intensity, initial state of forests, interaction with other types of disturbance) and hid a variety of results: in some reviewed cases, disturbance did increase species richness (e.g. Bobo et al., 2006; Swaine and Agyeman, 2008; van Andel, 2001).

Disturbances associated with logging do not necessarily have a negative impact on diversity. In mature forests, logging create gaps which, when large enough, can be colonized by tree species requiring more light than the species previously settled in the canopy. When a forest has long remained undisturbed and is dominated by slow growing late successional species, large and medium-sized gaps created by logging and post-logging treatments might increase diversity (e.g. monodominant *Cynometra* forests in Uganda, Plumptre, 1996) while, conversely, small natural gaps in forests dominated by early and mid-successional species might have limited effect, or tend to reduce diversity (e.g. secondary forests in Panama, Hubbell et al., 1999; Sheil and Burslem, 2003). According to the intermediate disturbance hypothesis (IDH), diversity is expected to be the greatest at intermediate intensity or frequency of disturbance, as well as at intermediate time since the last disturbance, when there is a balance between late successional shade-bearing competitors and early successional light-demanding colonizers (Connell, 1978; Mackey and Currie, 2001; Sheil and Burslem, 2003). The IDH has been supported by empirical studies in tropical forests (time since major disturbance in moist forests of Uganda, Sheil, 2001, intensity effect in moist forests of French Guiana, Molino and Sabatier, 2001, intensity and frequency effects in wet to dry forests of Ghana, Bongers et al., 2009) but not systematically (Hubbell et al., 1999; Sheil and Burslem, 2003).

Studies reporting the impacts of logging on tree species diversity in tropical moist forests are scarce (Clark and Covey, 2012, Gibson et al., 2011, Putz et al., 2012 and references therein) and they are even scarcer for Africa. Moreover, most of these studies used observational, rather than experimental designs. This may hamper unambiguous comparison of forest communities' response to disturbance as the latter is usually not definitely dated and well-characterized, and may be due to multiple confounding factors. Given the importance of logging in Central Africa, and the unsolved debate about its potentially negative impact on tree species diversity, there is an urgent need for the results of long term experiments in old growth forests of the region.

In this study, we used a unique data set from a long-term controlled experiment, which was implemented more than 20 years ago – a near complete felling cycle – in a previously undisturbed semi-deciduous moist forest of the Central African Republic (CAR). We examined patterns of tree species diversity in 28 1-ha plots of the M'Baïki Experimental Station where silvicultural treatments (logging, logging + thinning) were added to natural gap dynamics to create a strong gradient of disturbance intensity. The experimental design at M'Baïki is similar to that used by Molino and Sabatier (2001) in French Guiana, and the forest type compares to the "moist forests" of Bongers et al. (2009) in Ghana.

Our first goal was to examine whether anthropogenic disturbances associated with the silvicultural operations still affect the tree species composition in terms of regeneration guilds. We hypothesized an increased importance of the most light-demanding, early successional tree species to the detriment of the most shade-bearing, late successional species in response to the increased light levels beneath the canopy. Our second goal was to make profit from the disturbance gradient to examine whether there is a relationship between diversity and disturbance intensity in those forests, in order to identify possible unsustainable levels of logging and thinning. For this, we used a variety of diversity indices accounting for species richness, species evenness and combinations thereof. We expected (i) some diversity indices like species richness to peak at an intermediate position along the gradient, as observed by Molino and Sabatier (2001) and, to a lesser extent, by Bongers et al. (2009); (ii) different shapes of the disturbance-diversity relationship among the regeneration guilds, as previously reported by Bongers et al. (2009). More specifically, we expected a monotonic increase of species diversity – due to both increased richness and evenness – with increasing disturbance in pioneer and light-demanding species, and a concomitant monotonic decrease of diversity in shade-bearing tree species.

2. Materials and methods

2.1. Study site

The M'Baïki Experimental Station (3°90′N, 17°93′E) is located in the Lobaye Province, Central African Republic (CAR), 110 km southwest to Bangui. The climate is humid tropical with a 3 to 4-months dry season (November/December–February, with less than 50 mm precipitation). The average annual rainfall is 1738 mm (1982–2007 period), the mean temperature is 24.9 °C (1981–1989 period) (meteorological station of Boukoko, A. Ougou, pers. comm.). The plots are located within a 10 km radius on a large plateau (500–600 m a.s.l) and the topography is generally flat. The Precambrian geological substrate is covered with a mix of schists, sandstones and quartzites (Ceccato et al., 1992). The alteration of the parent material led to deep, locally gravelly, red ferralitic soils, corresponding to acrisols in the WRB soil classification (IUSS Working Group WRB, 2006). The vegetation is a semi-deciduous moist forest of the Guineo–Congolian type (White, 1983). The canopy is dominated by species from the Malvaceae, Meliaceae, Ulmaceae, and Sapotaceae plant families (Boulvert, 1986).

2.2. Experimental design

Ten 4-ha permanent plots were established in 1982 in an old-growth forest to monitor the effects of silvicultural treatments (Bedel et al., 1998). Each 4-ha plot is composed of four 1-ha subplots, inside which all trees with a DBH $\geqslant$ 10 cm were individually marked, geo-referenced, and botanically identified. The plots have been annually monitored since 1982, with all standing trees $\geqslant$ 10 cm DBH recorded. Between 1984 and 1985, seven 4-ha plots were selectively logged, while three 4-ha plots were kept untouched to act as controls. During logging operations, trees from 16 timber species with a DBH $\geqslant$ 80 cm were harvested (2–7 stems per hectare). Between 1986 and 1987, four of these seven logged plots were additionally thinned to increase light availability in the understory and promote tree regeneration. Thinning consisted