

Note and record

Limited dispersal into appropriate microhabitats likely explains recruitment failure in a chimpanzee-dependent tree species

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Introduction

Seed dispersal may be essential to (i) escape parent-proximity mortality; (ii) colonize new areas or (iii) reach favourable microsites (Schupp, 1993). Sensitivity of large-bodied animals to anthropogenic disturbance puts dependent large-seeded tree species at high risk of dispersal limitation (Cardoso da Silva & Tabarelli, 2000; Babweteera, Savill & Brown, 2007; McConkey *et al.*, 2012). Mechanisms responsible for recruitment failure following reduced dispersal vary (Babweteera & Brown, 2009; Coughlin *et al.*, 2014), and understanding them is essential for conservation.

Cordia millenii (Boraginaceae) is a shade-intolerant tree ~12 m tall (Keay, 1989; Chapman *et al.*, 1999; Babweteera, 2009; Mwavu & Witkowski, 2009), producing ovoid fruits with one moderately sized seed (~2.5–3.5 cm long, ~1.2–1.8 mm wide and weighing ~2.4 g; Keay, 1989; Dutton, Chapman & Moltchanova, 2014). It is found across tropical Africa and currently considered of minimal conservation concern (IUCN, 2015). Because chimpanzees (*Pan troglodytes*) are the only primates known to swallow and effectively disperse *C. millenii* seeds (Babweteera, 2009; Dutton, Chapman & Moltchanova, 2014), chimpanzee decline may adversely affect recruitment (Babweteera, 2009).

While monkeys (such as *Cercopithecus nictitans* at our site) consume *C. millenii* fruits, they do not swallow the seeds and are ineffective dispersers (Thia, 2014; Kelly Hutchinson pers. comm.). Furthermore, secondary dispersal by rodents (Nyiramana *et al.*, 2011; Jansen *et al.*, 2012) is unlikely because rodents do not remove seeds from the forest floor (Dutton, Chapman & Moltchanova, 2014; Thia, 2014).

Extremely low seedling recruitment at our study site, evinced by highly skewed adult-seedling ratios (Thia, 2014), led us to test two competing hypotheses: (i) establishment is dispersal limited versus (ii) herbivores depress survivorship. The former tests the necessity of seed dispersal, either to escape parent-proximity effects (Janzen, 1970; Connell, 1971) or into favourable microhabitats (Schupp, 1993; Dalling & Brown, 2009). The latter seeks to understand the contribution of herbivore-induced mortality on seedling establishment (Schupp, 1988; Hall, 2008).

Materials and Methods

Ngel Nyaki Forest Reserve (07°04'N 011°03'E) is situated on the Mambilla Plateau (between 1400 and 1600 masl) on the Nigerian–Cameroon border (Chapman & Chapman, 2001). Mean annual rainfall is 1,800 mm. The forest itself is a fragment approximately 5.5 km², threatened by hunting and cattle farming, although since 2004 (with the presence of the Nigerian Montane Forest Project) such threats are reducing. However, large mammal populations are declining (*e.g.* ungulates and primates) or been extirpated (elephants) since the 1970s (Chapman, Olson & Trumm, 2004). While the forest is floristically diverse and relatively intact compared to nonprotected forests on Mambilla (Chapman, Olson & Trumm, 2004), chimpanzee decline has raised concern for the persistence of dependent tree species (Beck & Chapman, 2008; Dutton, Chapman & Moltchanova, 2014).

We established transplant/exclusion experiments to separate effects of: (i) conspecific proximity; (ii) sunlight; and (iii) herbivores, on seedling survival. Seedlings sourced from a nearby forest remnant near the Kam

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Kam River (07°07'N 011°04'E) were transplanted to Ngel Nyaki Forest early in the week of 5 August 2013; dead seedlings were replaced until 19 August 2013, the start of the experiment. Forest remnants along the Kam Kam River are highly degraded, so although *C. millenii* seedlings were there, such habitat is not a sustainable forest.

Two treatments were within 50 m of the forest–grassland boundary (*i.e.* forest edge), representing forest understorey sites differing with respect to the presence ('Conspecific'; five sites; 120 seedlings) or absence ('Edge'; four sites; 96 seedlings) of adult *C. millenii*. A third treatment considered the ability of seedlings to establish in grassland bordering the forest ('Grassland'; four sites; 96 seedlings). Sites were >200 m apart and contained a pair of plots: one protected using a wood and wire-mesh cage (vertebrate exclusion), the other exposed. Sixteen seedlings per plot were planted in a 4 × 4 array (1 m²); half were randomly assigned for invertebrate protection (weekly placement of Yates Blitzem snail pellets around seedlings and Rambo pesticide spray during the dry season). Deaths were recorded as the day a plot was surveyed (mostly weekly). Data contained interval censoring and right censoring for 225 days.

Statistical analysis was conducted in R v3.1.0 (R Core Team 2014). The per cent of seedlings alive was modelled as a function of habitat (HABITAT), vertebrate exclusion (CAGE) and invertebrate exclusion (INVERTS), with time as a random variable (DAYS), in a split-plot ANOVA. We used 'survfit' in the R-package 'survival' (Therneau, 2015)

to conduct survival analyses considering both interval and right censoring.

Results and Discussion

Cordia millenii regenerates poorly in the disturbed Ngel Nyaki Forest. Our results provide strongest support for our first hypothesis: seedling establishment is dispersal limited. While seedlings in forested sites exhibited complete mortality, ~9% of grassland seedlings survived the study's duration. ANOVA (Table 1) demonstrated a significant habitat effect amongst sites ($P < 0.001$). Between plots, herbivore exclusion alone was nonsignificant, but a significant interaction (HABITAT * CAGE) between vertebrate exclusion and habitat ($P = 0.011$) suggests vertebrate herbivores might impact survival. Within plots, invertebrate exclusion (INVERTS) was nonsignificant. Habitats effects were confirmed in survival analyses ($P < 0.001$; Fig. 1).

The necessity of *C. millenii* to colonize well-lit microsites will have stark implications for its long-term persistence. Because *C. millenii* is disproportionally dependent on large-bodied vertebrates, like chimpanzees, for dispersal (Babweteera, 2009; Babweteera & Brown, 2009, 2010) loss of the already small local chimpanzee population will undoubtedly be highly detrimental. Indeed, recent genetic work on the Mambilla chimpanzees has highlighted the vulnerability of Ngel Nyaki's resident population (Knight, Chapman & Hale, 2015).

Table 1 ANOVA for repeated measures split-plot survival experiment. The percentage of surviving seedlings was modelled as function of HABITAT * CAGE * INVERTS, with DAYS (time) as a random variable. Error structure was plots nested within sites. Bold *P*-values indicate significance <0.05

	DF	SS	MS	F	P
Between sites					
HABITAT	2	271,362	135,681	32.44	<0.001
Residuals	10	41,820	4,182		
Between plots					
CAGE	1	114	114	0.188	0.674
HABITAT * CAGE	2	8,904	4,452	7.308	0.011
Residuals	10	6,092	609		
Within plots					
INVERTS	1	3	3	0.002	0.963
CAGE * INVERTS	1	2,201	2,201	1.654	0.199
HABITAT * INVERTS	2	285	142	0.107	0.899
HABITAT * CAGE * INVERTS	2	3,766	1,883	1.415	0.243
Residuals	1,008	1,341,223	1,331		

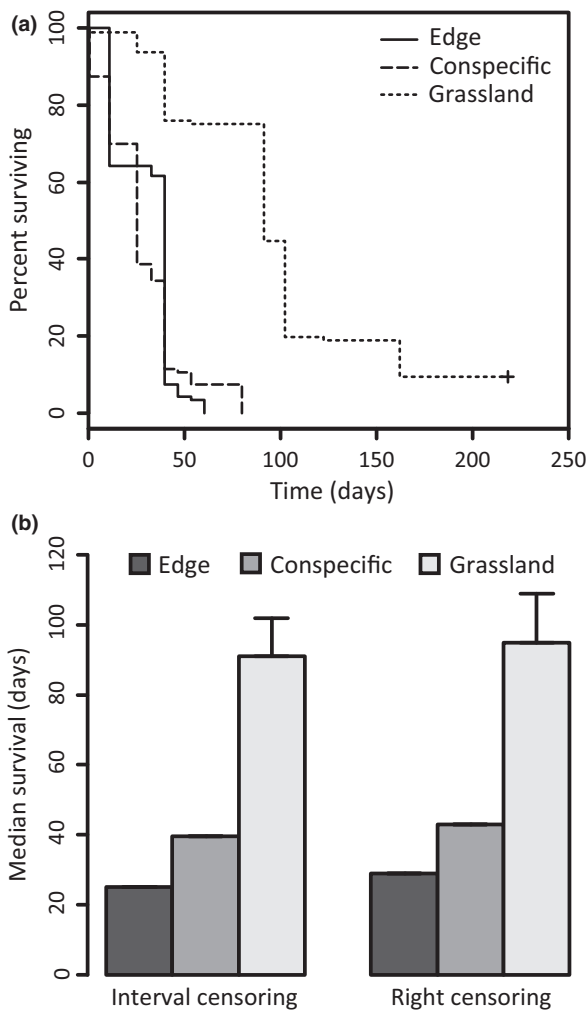


Fig 1 Results from the survival analyses. (a) The expected proportion of seedlings alive as a function of time and habitat, considering interval censoring. Seedlings across sites were pooled for each HABITAT treatment (Edge, Conspecific and Grassland). The '+' at the end of a line indicates the presence of seedlings surviving until the end of the study period (225 days). (b) Median survival times as a function of habitat and censoring method, with 95% confidence intervals.

Our study was able to separate the relative contribution of dispersal limitation and herbivore-induced mortality on seedling establishment, demonstrating the greatest survival benefits from dispersal into specific microhabitats. We suggest planting seedlings/seed in light gaps and along the forest–grassland boundary. This will aid in establishing a recruiting cohort and promote regeneration of *C. millenii*

at the forest periphery, which should attract large-bodied frugivores that will aid in forest edge regeneration.

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