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Variation in vegetation cover and seedling performance of tree species in a forest-savanna ecotone

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Research Article

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Abstract

Differential tree seedling recruitment across forest-savanna ecotones is poorly understood, but hypothesized to be influenced by vegetation cover and associated factors. In a 3-y-long field transplant experiment in the forest-savanna ecotone of Ghana, we assessed performance and root allocation of 864 seedlings for two forest (*Khaya ivorensis* and *Terminalia superba*) and two savanna (*Khaya senegalensis* and *Terminalia macroptera*) species in savanna woodland, closed-woodland and forest. Herbaceous vegetation biomass was significantly higher in savanna woodland (1.0 ± 0.4 kg m^{-2} vs 0.2 ± 0.1 kg m^{-2} in forest) and hence expected fire intensities, while some soil properties were improved in forest. Regardless, seedling survival declined significantly in the first-year dry-season for all species with huge declines for the forest species (50% vs 6% for *Khaya* and 16% vs 2% for *Terminalia*) by year 2. After 3 y, only savanna species survived in savanna woodland. However, best performance for savanna *Khaya* was in forest, but in savanna woodland for savanna *Terminalia* which also had the highest biomass fraction (0.8 ± 0.1 g g^{-1} vs 0.6 ± 0.1 g g^{-1} and 0.4 ± 0.1 g g^{-1}) and starch concentration ($27\% \pm 10\%$ vs $15\% \pm 7\%$ and $10\% \pm 4\%$) in roots relative to savanna and forest *Khaya* respectively. Our results demonstrate that tree cover variation has species-specific effects on tree seedling recruitment which is related to root storage functions.

Introduction

Forest-savanna ecotones characterized by a mosaic of forest patches within savanna environments represent a common feature of the landscape of West Africa (Hennenberg *et al.* 2005, McCook 1994). Across the tropics, observations of forest encroachment in savannas are on the rise (Bowman *et al.* 2001, Mitchard *et al.* 2009, Schwartz *et al.* 1996, Veenendaal *et al.* 2015), generally occurring at decadal timescales with rapid changes in vegetation cover and species composition (Cuni-Sanchez *et al.* 2016, Jeffery *et al.* 2014). Such vegetation transitions have important implications for ecosystem services and local livelihoods due to changes in composition, productivity, diversity and abundance of species (Mitchard *et al.* 2009, Poulter *et al.* 2014).

The process of forest advancement into savannas is still little understood, and the relative influences of fire (Higgins *et al.* 2007, Hoffmann *et al.* 2012a), edaphic and climatic factors (Bowman *et al.* 2015, Lloyd *et al.* 2015, Veenendaal *et al.* 2015, 2018) on the formation of closed-canopy vegetation have been highlighted in several studies. It is also recognized that vegetation (canopy) cover has important influences on fire behaviour and intensity, light and edaphic factors. As a result, tree seedling establishment success can be mediated by the extent of vegetation cover via fire suppression (Bowman 2000, Cardoso *et al.* 2016, Gignoux *et al.* 2009, Hoffmann *et al.* 2012a) or through amelioration of factors such as irradiance, soil moisture and soil fertility (Cuni-Sanchez *et al.* 2016, Ruggiero *et al.* 2002, Saiz *et al.* 2012, Veenendaal *et al.* 1996a, 1996b).

Forest species generally may lack the suite of traits that make savanna species successful in open pyrogenic savannas, while savanna species may be less successful in closed-canopy forests for the same reason and forest advancement in savanna may be facilitated in sites with higher woody canopy cover where low-light conditions constrain performance of savanna species (Armani *et al.* 2018, Bowman 2000, Cardoso *et al.* 2016, Hoffmann *et al.* 2004, Ruggiero *et al.* 2002). However, there is little empirical data on whether canopy closure facilitates the establishment of forest species and to what extent this limits survival and

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Table 1. Classification and biophysical limits of tree species used in this study. All species thrive within the Kogyae Strict Nature Reserve or in nearby semi-deciduous forest in Ghana. Sources of information: Hawthorne (1995), http://www.worldagroforestry.org/sites/treedbs/treedatabases.asp

Species	Family	Functional type	Guild	Distribution	Rainfall range (mm)
Khaya ivorensis (Desr.) A. Juss	Meliaceae	Forest	Non-pioneer light demander	Moist–dry forest	1600–2500
Khaya senegalensis (Desr) A. Juss	Meliaceae	Savanna	Moderately shade tolerant	Gallery forest	400–1750
Terminalia superba (Engl. & Diels)	Combretaceae	Forest	Pioneer	Moist–dry forest	1000–1800
Terminalia macroptera (Guill. & Perr.)	Combretaceae	Savanna	Open savanna	Moist open woodland	700–1500

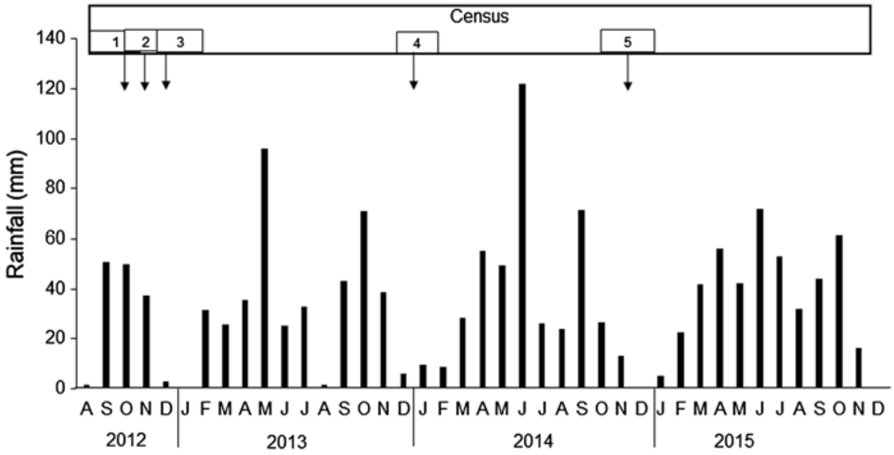

Figure 1. Mean monthly precipitation for Ejura, Ghana (nearest meteorological station to Kogyae Strict Nature Reserve ± KSNR) for the experimental period and beyond. Timing of all five censuses conducted are shown.

growth performance of savanna species across forest-savanna ecotones.

In this study, we investigated influences of vegetation type (with a focus on canopy cover levels being the main distinguishing factor) and its associated factors on seedling survival, growth and traits (i.e. root mass fraction and root starch concentration) in a field transplant experiment that lasted three growing seasons and two dry/fire seasons. We used two congeneric species pairs of forest and savanna species that are common to the forest-savanna ecotone or to nearby semi-deciduous forest in West Africa to test the following hypotheses: (1) The forest tree species have lower survival than their savanna congeners in savanna due to relatively lower root mass fraction and root starch content needed to survive dry periods and to resprout after fire. (2) Higher vegetation (canopy) cover, being associated with a lower fuel load and higher soil nutrient status, benefits mainly forest tree seedlings as savanna species are less competitive in deep shade.

Materials and methods

Study site

The field transplant experiment was carried out in Kogyae Strict Nature Reserve (KSNR) located in the forest-savanna transition zone of Ghana (7°19′1.661′′N, 1°05′5.863′′W). Climatically, the area has a bimodal rainfall pattern with major peaks occurring in May–June and September–October (Figure 1), with a mean annual rainfall of 1200–1300 mm. Four vegetation types are distinguished in the area: transitional forest, savanna, riparian woodland and boval vegetation (vegetation on flat iron pans) (Wildlife Department 1994), but plot selection for this study was done following the structural classification of Torello-Raventos *et al.* (2013) in woodland, closed woodland and forest vegetation patches. In the study site, tree cover has been stable or slowly increasing over the last 30 y (Janssen *et al.* 2018).

Species selection

We selected four tree species from two families and two genera. Each species pair in a genus comprised one forest and one savanna species (Table 1). Seeds of *Khaya ivorensis* and *Terminalia superba* were collected from a moist semi-deciduous forest (Bobiri Forest reserve, 6.678°N, 1.32°W), while those of *Khaya senegalensis* and *Terminalia macroptera* were collected within Kogyae Strict Nature Reserve itself. Seedlings were raised from seeds at the Forestry Research Institute of Ghana nursery in April 2012. At 3 mo old, seedlings were transported to the Kogyae Strict Nature reserve and allowed 7 d to recover from any transportation shock before transplanting.

Transplantation experiment

Thirty-six 10 × 10-m plots were randomly established under the three vegetation types differing in canopy closure; 12 each for cover classes typical for woodland, closed woodland and forest canopies (following Torello-Raventos *et al.* 2013) in three sites (blocks) that were about 750 m apart. In each plot, six seedlings each of the four species (Table 1) were assigned and planted in random positions in rows (1.4 m within and between rows of seedlings). A total of 864 seedlings were planted (i.e. 6 seedlings × 4 plots × 3 cover classes × 3 blocks × 4 species). Seedlings were transplanted in September 2012 at the beginning of the second rainy season (Figure 1). No additional watering was done and no fire protection was given during the experimental period.

Canopy cover of plots in the various vegetation patches was assessed using leaf area index (LAI) and canopy openness in October before the end of the rainy season (peak leaf cover). Additionally, we assessed absence/presence of C_4 grasses in the herb layer. LAI and canopy openness were obtained by analysing hemispheric photos, taken at 1 m above the ground in each plot with a fish-eye lens mounted on a Nikon E4500 camera. Images were then analysed with Gap Light Analyser software (Veenendaal *et al.* 2015). Mean percentage canopy openness and (LAI) ranged between 18.5–25% (1.7–2.0) for forest plots, 32–45% (0.7–1.0) for closed woodland plots and 60–73% (0.1–0.25) for (savanna) woodland plots. The herb layer in plots with highest LAI (forest plots) consisted mainly of C_3 species, while canopy cover was mainly provided by forest trees. In the closed woodlands tree cover was provided by a mix of different species with tree crowns not touching and C_4 grasses were present, while cover in woodlands was provided by savanna trees (Torello-Raventos *et al.* 2013).

Data on seedling height and survival were taken for three seasons. Before the first dry season, three censuses were conducted at 1, 2 and 3 mo after transplantation, the third month being at the onset of the first dry season (December 2012) (Figure 1). Subsequent censuses were conducted only at the end of the consecutive growth seasons (December) of 2013 and 2014. The first dry season and its associated fires occurred 5 mo into the experiment (19 January and subsequent days in 2013). The plots also burnt in the second year (around 4 February 2014). The experiment ended in December 2014 at the end of the third wet season (Figure 1). Fire intensity was not measured separately in this experiment, but after each fire event we observed that the forest plots generally had been lightly touched by fire, whereas all plots in closed-woodland and woodland cover types burnt more heavily in both dry-season fires that occurred within the period of this study.

All surviving seedlings at the end of the experiment were carefully excavated. Seedling height, total plant dry weight and root mass fraction were determined. Immediately after harvest, samples were microwaved, in preparation for determination of root starch content, following a carbohydrate extraction protocol of Duranceau *et al.* (1999) adapted from Dubois *et al.* (1956). Root starch content was analysed for all species (except *Terminalia superba*, for which we had no adequate samples available).

Environmental factors

Soil moisture content of the top layer (0–60 mm) was determined with a theta probe (Delta-T Devices, Cambridge, UK). Five moisture measurements were made across all four plots of each vegetation type within a block (as all four plots laid fairly close to one another). This was done at the centre and at the outer corners of the plots. Measurements were done twice, at 7 wk (November 2012) and 13 wk (December 2012). We took five soil samples per vegetation type per block using a cylindrical auger at the centre and at the mid-distance to the four corners of the outer plots. Sampling was done at three depths (0–10 cm, 10–20 cm and 20–30 cm) and composites were formed from the replicates for each depth category and put in zip-lock plastic bags and later analysed for soil organic matter content (loss-on-ignition method; Ball 1964) and some biogeochemical properties. CEC, Mg, Ca, K analyses (Gilman 1979) were done using an Atomic Absorption spectrometer (VARIAN AA240FS, Varian Inc.). Total N and P were analysed according to Novozamsky *et al.* (1983) using the Segmented Flow Analyser (SKALAR SAN^{++} System) and P-Olsen was determined according to Olsen *et al.* (1954).

Data on fuel load and fuel composition as a proxy for fire intensity were taken from three random 1-m^2 quadrats per plot and averaged for each plot per vegetation type. In each plot, cover abundances of grasses and herbs were estimated. Also, dry weights of total herbaceous vegetation (i.e. including herbs and grasses) and litter were determined from sub-samples by cutting vegetation and collecting litter and weighing them after oven drying.

Daily rainfall data from August 2012 to December 2015 recorded in Ejura, the nearest meteorological station (25 km away from experimental site), were obtained from the Ghana Meteorological Agency. There were gaps in the data for some months (October 2012, November 2013 and June 2015). Mean monthly rainfall for months with missing data were estimated using records from the last 15 d of the month before and the first 15 d of the month after the reference month. For example, mean rainfall for October 2012 was estimated as mean of rainfall values from 16 September to 15 November 2012.

Statistical analyses

We used linear mixed-effects models (Zuur *et al.* 2009) to test for differences in soil moisture content of the top soil layer among vegetation types and measurement weeks (as fixed factors), including the interaction term of two fixed factors and a random block effect. Similarly, we tested fixed effects of vegetation type including a random block effect on organic matter content, litter mass, herbaceous vegetation biomass and cover abundances of herbaceous vegetation using linear mixed-effects models. Block was included as random factor in these analyses. Soil organic matter content was analysed for each soil depth separately. Also, cover abundance of grass and herbs were analysed separately. We checked for normality and homoscedasticity and applied natural log (ln), square root and arcsine transformations (Sokal & Rohlf 1995) on herbaceous vegetation biomass, litter mass and cover abundance proportions of grasses and herbs respectively. A multivariate analysis of variance (MANOVA) was used to test, for each soil layer, differences in soil chemical properties among vegetation types.

Survival data from each census (conducted at months 1, 2, 3, 15 and 27) were analysed separately to compare survival among species and vegetation types in generalized linear models (GLM) using binomial distribution with logit link function. Sidak correction was used for multiple comparisons.

Seedling heights recorded in years 1, 2 and 3, were tested for differences among years and vegetation types separately for each species in linear mixed-effects models. A random block effect was included in the models and Sidak correction was used for multiple comparisons. Also, for each species, a Kruskal–Wallis test (Sokal & Rohlf 1995) was used to determine if seedling height differed among years 1, 2 and 3. For *T. superba*, a Mann–Whitney U-test was used to compare height of years 1 and 2 as insufficient samples were available in year 3.

Data on total seedling dry weight, root mass fraction (RMF) and root starch concentration were analysed in separate linear mixed-effects models for each species to determine fixed effects of vegetation type. All analyses were done on SPSS version 23.0.

Results

Soil properties

Soil moisture content (SMC) of the top soil layer (0–60 mm) after 7 wk differed significantly ($F_{2,84} = 8.4$, $P < 0.001$) among vegetation types, higher in forest and closed-woodland (6.11% ± 1.71% and 6.25% ± 1.89% respectively) than savanna woodland at 4.25% ± 2.07%. We found that SMC had dropped to an average of 2.7% at 13 wk into the experiment (i.e. at the start of the dry season) ($F_{1,84} = 66.6$, $P < 0.001$). During the experimental period, all vegetation types showed a similar decline in moisture content and at the end of the experiment SMC was still lower in savanna

Table 2. Mean ± SD of soil properties in Kogyae Strict Nature Reserve, Ghana, taken at three depths. Each soil layer (depth) was statistically tested separately for differences among vegetation types (linear mixed-effects models for organic matter content and MANOVA for all chemical properties). Statistical differences ($P < 0.05$) are shown with letters only for parameters for which cover classes differed significantly

	0–10 cm layer			10–20 cm layer			30–40 cm layer		
	Woodland	Closed-woodland	Forest	Woodland	Closed-woodland	Forest	Woodland	Closed-woodland	Forest
pH-H20	7.09 ± 0.48^{a}	6.26 ± 0.38^{ab}	6.18 ± 0.13^{b}	6.81 ± 0.07^{a}	5.82 ± 0.41^{b}	6.05 ± 0.21^{b}	6.69 ± 0.23^{a}	5.79 ± 0.20^{b}	5.92 ± 0.37^{b}
P-Olsen (mg kg^{-1})	2.71 ± 0.61	3.59 ± 0.74	3.53 ± 0.77	1.75 ± 0.40	2.30 ± 0.96	2.00 ± 0.51	1.55 ± 0.75	1.70 ± 0.38	2.28 ± 0.06
N-total (mg kg^{-1})	497 ± 69.2^{a}	389 ± 49.8^{a}	805 ± 130^{b}	322 ± 8.22	251 ± 43.0	499 ± 233	221 ± 72.8	299 ± 194	272 ± 47.4
P-total (mg kg^{-1})	79.0 ± 9.35	73.5 ± 7.56	79.0 ± 5.91	62.2 ± 10.6	49.0 ± 5.24	56.8 ± 11.1	64.1 ± 15.4	63.0 ± 32.1	42.7 ± 7.17
CEC (cmol kg^{-1})	4.07 ± 0.57^{a}	0.22 ± 0.29^{b}	3.86 ± 1.52^{a}	1.97 ± 1.55	2.81 ± 4.87	1.76 ± 0.81	2.25 ± 3.27	0.56 ± 0.98	1.36 ± 1.81
K (cmol kg^{-1})	0.33 ± 0.05	1.45 ± 1.87	0.60 ± 0.41	0.29 ± 0.04	0.68 ± 0.43	0.37 ± 0.18	0.23 ± 0.07	3.50 ± 5.28	0.79 ± 1.05
Mg (cmol kg^{-1})	0.11 ± 0.14	0.44 ± 0.77	0.83 ± 0.34	–	0.61 ± 0.53	0.26 ± 0.28	–	0.50 ± 0.5	0.07 ± 0.1
Ca (cmol kg^{-1})	0.75 ± 1.30	0.35 ± 0.60	1.21 ± 0.39	0.53 ± 0.92	0.04 ± 0.08	0.29 ± 0.49	0.33 ± 0.57	0.53 ± 0.92	–
Organic matter (%)	1.69 ± 0.09^{a}	1.42 ± 0.16^{a}	2.76 ± 0.45^{b}	1.25 ± 0.23	1.09 ± 0.10	1.48 ± 0.44	1.19 ± 0.48	1.07 ± 0.16	1.14 ± 0.16

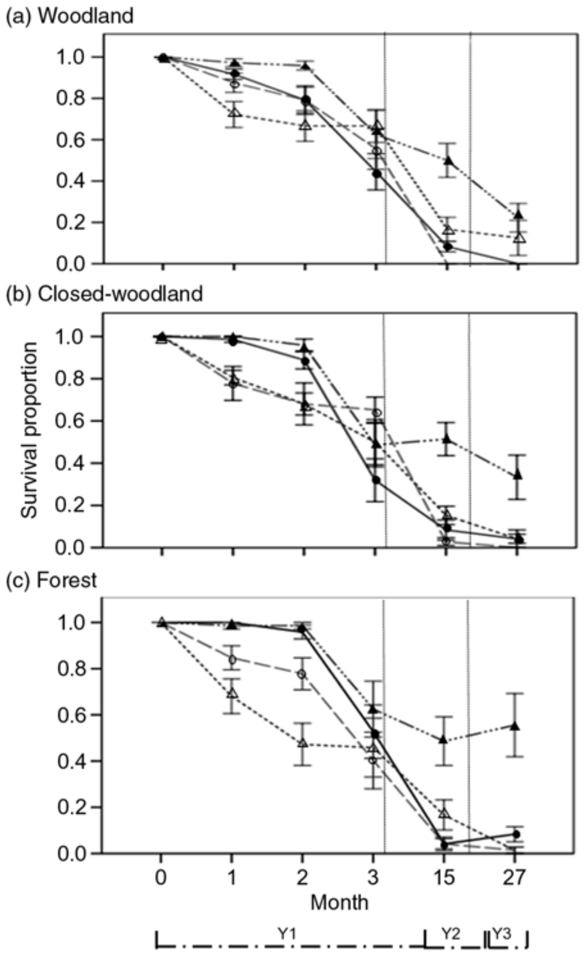

Figure 2. Proportion of surviving seedlings of *Khaya senegalensis* (filled-triangle), *Khaya ivorensis* (filled-circle), *Terminalia macroptera* (open triangle), *Terminalia superba* (open circle) at woodland cover (a), closed-woodland cover (b) and forest cover (c) in Kogyae Strict Nature Reserve, Ghana. Month corresponds to the month of transplantation, with month of transplanting = 0. Grey vertical lines indicate times when the dry season fires occurred. Error bars show ± 1 standard error of the mean.

woodland and closed woodland (1.95% ± 1.53% and 2.69% ± 1.89% respectively) than forest at 4.74% ± 2.2%.

Soil organic matter in the top 10 cm was significantly higher in the forest compared with savanna woodland and closed-woodland sites ($F_{2,6} = 19.6$, $P = 0.002$). Interestingly, no significant differences between vegetation types were found for soil layers below 10 cm (Table 2). Significant differences between different vegetation types were also found for soil pH, total nitrogen and CEC ($F_{2,9} = 5.85$, $P = 0.039$; $F_{2,9} = 17.4$, $P = 0.003$; $F_{2,9} = 16.7$, $P = 0.004$ respectively), but again only in the upper 10 cm soil layer. Soil pH was lowest in forest and highest in woodland. Total nitrogen was higher in forest than in savanna woodland and closed-woodland. CEC was lowest in closed-woodland and similar between savanna woodland and forest. No significant vegetation type effect was found for levels of Ca, Mg, K, total P and P-Olsen (Table 2).

Herbaceous vegetation and litter

Total biomass of herbaceous vegetation (including grasses and herbs) differed among vegetation types ($F_{2,31} = 29.8$, $P < 0.001$). Biomass of herbaceous vegetation was 0.23 ± 0.12 kg m^{-2} in forest, lower than biomass in closed-woodland and savanna woodland which had similar biomass of 0.84 ± 0.25 kg m^{-2} and 0.99 ± 0.35 kg m^{-2} respectively. Similarly, litter mass differed significantly ($F_{2,31} = 23.3$, $P < 0.001$) among vegetation types being higher in forest (0.21 ± 0.11 kg m^{-2}) than closed-woodland (0.06 ± 0.05 kg m^{-2}) and savanna woodland (0.03 ± 0.05 kg m^{-2}).

Overall, grasses were more abundant ($F_{2,31} = 111$, $P < 0.001$) in savanna woodland (51.5% ± 8.8%) and closed-woodland (50.8% ± 8.7%) than forest at 15.4% ± 3.1%. Percentage cover of herbs was low overall (average of 3%) and did not differ significantly ($F_{2,33} = 1.68$, $P = 0.2$) among vegetation types.

Seedling survival

A few weeks (4–8 wk) into the experiment, both *Terminalia* species showed lower survival, relative to the *Khaya* species, in forest plots (Figure 2). Survival differences for *T. superba* versus *K. ivorensis* ($P = 0.02$) and *T. macroptera* versus *K. senegalensis* ($P < 0.001$)

Table 3. Binomial analysis (with logit link) of seedling survival of four tree species in three vegetation types in Kogyae Strict Nature Reserve, Ghana. Analyses were done separately for each census (month) and all factors included in the separate models are presented. Significant effects are indicated with asterisks and non-significant effects by 'ns'

Time (mo)	Main effects and interactions	df	Wald Chi-Square	P
1	Vegetation type	2	0.000100	1.0 ns
	Species	3	5.42	0.144 ns
	Vegetation type × Species	6	9.38	0.159 ns
2	Vegetation type	2	3.29	0.192 ns
	Species	3	68.6	<0.001*
	Vegetation type × Species	6	19.0	0.004*
3	Vegetation type	2	4.67	0.097 ns
	Species	3	10.7	0.013*
	Vegetation type × Species	6	21.5	0.001*
15	Vegetation type	2	0.000331	1.0 ns
	Species	3	97.4	<0.001*
	Vegetation type × Species	6	0.88	0.99 ns
27	Vegetation type	2	0.0000120	1.0 ns
	Species	3	34.4	<0.001*
	Vegetation type × Species	6	13.5	0.036*

Table 4. Pairwise comparisons (from Kruskal–Wallis test) of tree seedling height recorded in years 1, 2 and 3 at Kogyae Strict Nature Reserve, Ghana. Analyses were done for each species separately. For *Terminalia superba*, only years 1 and 2 are compared using Mann–Whitney U-test. Years for which median seedling height differed significantly (P < 0.05) are indicated with an asterisk

Species	Years compared pairwise	Test statistic	Standard error	P-value
Khaya senegalensis	2–1*	91.5	13.8	< 0.001
	2–3*	−139	15.3	< 0.001
	1–3*	−47.3	17.3	0.019
Khaya ivorensis	2–1*	136	9.70	< 0.001
	2–3*	−177	30.4	< 0.001
	1–3	−40.7	30.9	0.563
Terminalia macroptera	2–1*	109	10.4	< 0.001
	2–3*	−181	24.3	< 0.001
	1–3*	−71.4	25.3	0.014
Terminalia superba	2–1*	809	596	< 0.001

were revealed through pairwise comparisons (with Sidak correction). Generally, seedling survival remained high, particularly for the *Khaya* species and regardless of vegetation cover until 3 mo (i.e. onset of the first dry season). By this census, survival had considerably declined for all species (Figure 2). We found a significant species × vegetation cover interaction effect (Table 3), but differences among species were mainly between and not within vegetation cover type.

At 15 mo, and after the first dry-season fire, significant survival differences were found among species (Table 3). Overall, 50% of all savanna *Khaya* was still alive versus 6% for its forest congener. We found a similar pattern in genus *Terminalia* with 16% survival for the savanna type versus 2% for its forest congener. Pairwise comparisons showed that survival of the savanna *Khaya* was significantly higher than all other species in all vegetation types. Savanna *Terminalia* also had a significantly higher survival than both forest species in savanna woodland. Between the two forest species, survival in savanna woodland and closed-woodland was higher for forest *Khaya* than forest *Terminalia*.

In the final census (27 mo on) after the second dry-season fire and third wet season (Figure 2), 12% of the total number of planted seedlings were still alive. There was a significant interaction effect of vegetation type and species (Table 3). None of the forest species was alive in savanna woodland where 20% survival for the savanna *Khaya* and 13% for savanna *Terminalia* were observed. Remarkably, higher survival was observed in forest (55%) and closed-woodland (33%) for the savanna *Khaya* as compared with 8% and 4% in the respective vegetation types for forest *Khaya*. The savanna *Terminalia* survived in very low numbers in closed-woodland (4%) and forest (1%). There were no seedlings of the forest *Terminalia* surviving in savanna woodland or closed-woodland and only 1% survived in forest (Figure 2).

Seedling growth

Seedling height was significantly lower in y 2 for all species relative to y 1 heights evidencing shoot loss (Table 4, Figure 3). We found that for the forest species in both genera, seedling height did not differ among vegetation cover types, but for both savanna species, differences between vegetation types were significant ($F_{2,107} = 5.32$, $P = 0.006$ for *Khaya* and $F_{2,33} = 3.27$, $P < 0.001$ for *Terminalia*). Savanna *Khaya* was taller in forest and closed-woodland than woodland while savanna *Terminalia* was taller in savanna woodland than closed-woodland and forest (Figure 3).

At the end of the third wet season, plant height was higher than recorded for y 2 for all species except forest *Terminalia* for which there were insufficient seedlings for comparison suggesting recovery from y 2 drought/fire. Also compared to y 1, both savanna species in y 3 were significantly taller, but forest *Khaya* in y 3 did not differ from y 1 height (Table 4), suggesting a higher cumulative shoot recovery of the savanna than forest species in this study.

Overall, plant dry weight of the savanna *Khaya* was 3.4 ± 1.9 g and did not differ significantly ($F_{2,80} = 0.20$, $P = 0.82$) among vegetation types as was the case for its forest congener ($F_{1,5} = 0.22$, $P = 0.67$) (Figure 4a). Seedlings of the savanna *Terminalia* did grow significantly larger in savanna woodland (16.0 ± 12.9 g; $F_{2,15} = 17.4$, $P < 0.001$) compared to closed-woodland and forest where seedlings weighed on average 1.9 ± 0.5 g. Unfortunately, for the forest *Terminalia*, biomass could not be analysed because not enough seedlings survived at final harvest (Figure 4a).

Biomass proportion and starch concentration in roots

We found that root mass fraction (RMF) significantly differed ($F_{2,77} = 4.88$, $P = 0.01$) among vegetation types for savanna *Khaya*, which was higher in savanna woodland at 0.71 ± 0.10 g g^{-1} and lowest in the forest at 0.61 ± 0.11 g g^{-1} (Figure 4b). RMF of the forest *Khaya* did not differ significantly ($F_{1,5} = 2.01$, $P = 0.22$) between closed-woodland and forest where it survived till the end (Figure 4b). Also for the savanna *Terminalia*, RMF did not differ significantly ($F_{1,10} = 1.14$, $P = 0.31$) between savanna woodland and closed-woodlands where it survived till the end.

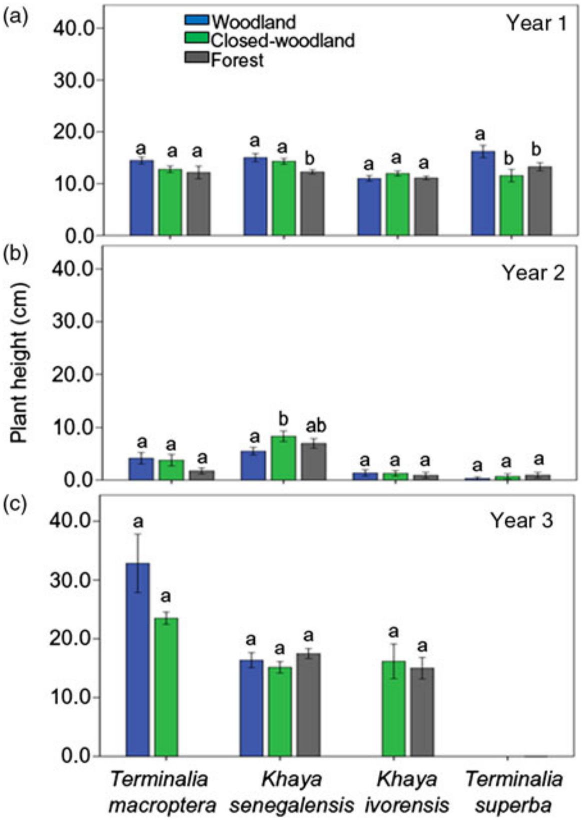

Figure 3. Mean seedling height of each species at three vegetation types for the three growing seasons in Kogyae Strict Nature Reserve, Ghana. In year 3, *Terminalia superba* was excluded due to too few numbers to allow for analysis. Also, there were insufficient samples of *Khaya ivorensis* and *Terminalia macroptera* for woodland and forest respectively. Statistical comparisons (with Sidak adjustment) are done among vegetation types for each species. Different letters indicate significant differences ($P < 0.05$). Error bars are ±1 SE of mean.

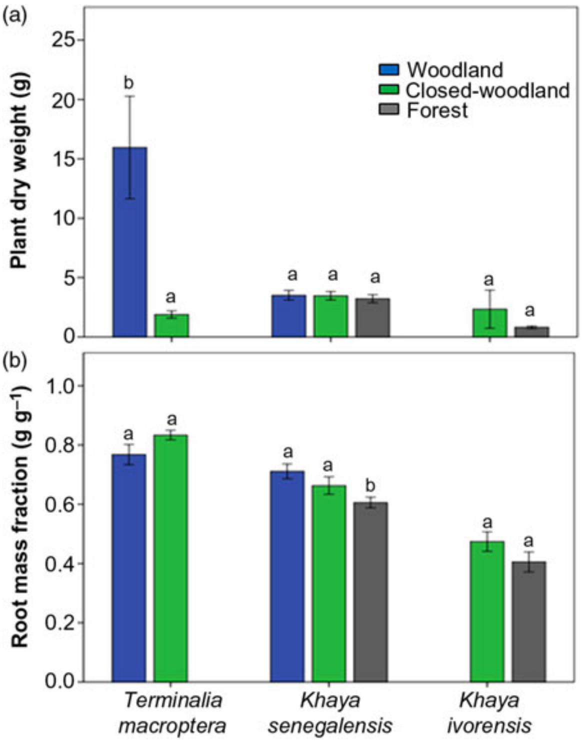

Figure 4. Mean seedling dry weight and root mass fraction for three species at three vegetation types in Kogyae Strict Nature Reserve, Ghana. Species are compared statistically among vegetation types, but not among species. Data not presented for *Terminalia superba* due to insufficient samples. Also, samples were insufficient for *Khaya ivorensis* and *Terminalia macroptera* in woodland and forest respectively. Different letters indicate significant differences ($P < 0.05$). Error bars are ±1 SE of mean.

Overall RMF (regardless of vegetation type) differed significantly ($F_{3,95} = 14.6$, $P < 0.001$) among species being highest in savanna *Terminalia* (mean = 0.79 ± 0.09 g g^{-1}) and lowest in forest *Khaya* (mean = 0.44 ± 0.07 g g^{-1}). RMF of savanna *Khaya* was intermediate (mean = 0.64 ± 0.13 g g^{-1}) between the two other species.

We found that root starch concentration differed significantly ($F_{2,27} = 19.1$, $P < 0.001$) among species and also among vegetation types ($F_{2,27} = 3.48$, $P = 0.045$). Pairwise comparisons revealed highest root starch concentration for seedlings in savanna woodland (21.6% ± 10.7%) and lowest in closed-woodland (13.8% ± 9.8%). Among species, savanna *Terminalia* stored the most starch in their roots (27.1% ± 9.6%) whereas forest *Khaya* stored the least (9.6% ± 3.9%) while savanna *Khaya* had intermediate root starch storage (14.9% ± 6.8%).

Discussion

Forest and savanna species occur predominantly in their respective non-pyrogenic and pyrogenic environments. Yet, widespread observations have been made of forest species encroaching savannas in many places across the globe (Bowman *et al.* 2001, Mitchard *et al.* 2009). Higher vegetation cover is hypothesized to increase establishment of forest species, but tests in forest-savanna ecotones produced mixed results (Bowman *et al.* 2001, Cardoso *et al.* 2016, Geiger *et al.* 2011, Gignoux *et al.* 2009, Hoffmann *et al.* 2004). Generally, higher canopy cover suppresses pyrogenic fuel loads (Hennenberg *et al.* 2006) and aids tree seedling survival as fire in open savanna vegetation induces high seedling mortality (Cardoso *et al.* 2016, Gignoux *et al.* 2009, Hoffmann *et al.* 2004). Here, we assessed survival and growth of seedlings of two congeneric pairs of forest and savanna trees over a period of 3 y (two dry/fire seasons) allowing for assessments at different moments in time and beyond one season in both forest and savanna environments. We assessed flammable material as an indication of fire intensity, soil characteristics as well as biomass fraction and starch concentration in roots in relation to different vegetation types (differing in extent of canopy closure).

The forest plots typically had higher soil moisture, organic matter and N content compared with the savanna woodland plots, which is in line with other studies (Fensham *et al.* 2003, Kellman 1985, Markham & Babbedge 1979) and which may be caused by the presence of increased cover and litter input by trees (Fensham *et al.* 2003, Kellman 1985). Higher N content could also be the result of fixation by trees and the nitrification of N (leftover after uptake by vegetation) could explain the lower pH found in forest plots (Ste-Marie & Pare 1999). These differences between forest and savanna woodlands were found in top (10 cm) soil only. Additionally, several other soil parameters measured such as P, K, Mg, Ca and CEC were similar in both environments. Thus, no firm conclusions can perhaps be drawn on whether soils differ markedly between forest and savanna patches in this ecotone. Nonetheless, higher top soil moisture content, organic matter and N may affect tree seedling growth and survival.

Savanna woodland plots were characterized by higher biomass of herbaceous vegetation, while litter load was somewhat higher in closed-canopy forest cover (but only ~0.2 kg m^{-2}). This is the result of the higher canopy cover in forest excluding grasses, consistent with findings in other studies (Hennenberg *et al.* 2006, Hoffmann *et al.* 2012b). Faster and more intense fires have been observed for savanna than forests (Hennenberg *et al.* 2006, Hoffmann *et al.* 2012b) as a consequence of this difference in type and biomass of herbaceous vegetation.

Seedling survival

Survival in the first few weeks for both species in the genus *Terminalia* was lower in forest (at LAI of ~1.7–2.0) than in savanna, while species in genus *Khaya* were not affected. Clearly, both *Terminalia* species prefer higher light levels, at least in the first weeks after germination. The forest *Khaya* is a non-pioneer light demander (Hawthorne 1995) while its savanna congener is known to tolerate moderate shade (Kwesiga & Grace 1986). Three months into the first dry season, these apparent species differences were no longer observed and mortality had reached about half for nearly all individuals. Prior to this census (census 3) rainfall had declined from 37 mm in November to 3 mm in December (Figure 1). Thus, the high mortality of the initial establishment phase may suggest a similar response to dry season drought for all species and regardless of vegetation cover. It was in the second dry season that the reported differences between forest and savanna species (Hoffmann *et al.* 2004) became evident in both genera tested in this study. At this stage, seedlings had gone through the first dry and fire seasons and subsequent recovery. And thus fire- and drought-survival traits became more important explaining the greater survival of the savanna species.

At the end, the savanna *Khaya* had the most survivors in all vegetation types because it is both drought/fire tolerant and also moderately shade tolerant. None of the two forest species survived in woodlands where the highest biomass of flammable material was recorded. Except for the forest *Khaya* that had few surviving seedlings in closed-woodland, the forest species generally survived in forest, although in very low numbers. This suggests that the long dry seasons and associated fire events in this ecotone limits their colonization possibilities (Cardoso *et al.* 2016). Survival in savanna *Khaya* was similar to that of savanna *Terminalia* in savanna woodland, but markedly contrasting in closed-canopy forest and closed-woodland with intermediate canopy cover (although to a lesser extent), with canopy closure favouring savanna *Khaya* and more open environments favouring savanna *Terminalia*. Again, this is consistent with the natural distributions of the two species.

Seedling growth, biomass proportions and starch concentration in roots

Within the first growing season, seedlings tended to grow taller (significantly for two species) in woodlands than forest. Perhaps this represents an increased growth response to the increasing light availability (Veenendaal *et al.* 1996b) associated with increasing canopy openness from forest to savanna. By the second year, seedling height had greatly reduced for all species indicating shoot loss resulting from drought and/or fire of the first dry season. The difference in height between years 2 and 1 which was greater for the two forest species than their savanna congeners may be an indication of a greater adverse effect of the dry season on the forest species. At the end of year 3, seedlings were a lot taller (relative to year 1 heights) for both savanna species. By contrast, y 3 seedlings of the surviving forest tree *K. ivorensis* (mortality of forest *Terminalia* was 99% at this stage) were not taller than they were in year 1 suggesting a higher cumulative recovery and resprouting capacity for the savanna species than their forest congeners. This is consistent with our prediction and also reported in several other studies (Fensham *et al.* 2003, Gignoux *et al.* 2016, Okali & Dodoo 1973).

Vegetation cover type did not have profound effects on shoot loss and subsequent regrowth over the 3-y period except on savanna *Khaya* in year 2. This is inconsistent with our expectation because flammable material differed among vegetation types and should have influenced extent of stem die-back (top-kill) (Higgins *et al.* 2007). Perhaps this finding suggests that drought effect on stem die-back was stronger than the ameliorating influence of canopy cover. The fact that seedlings in closed-canopy forest also experience drought stress (Veenendaal *et al.* 1996a) lends support to this assertion. This may explain why patterns of forest development as well as mature trees of *Khaya senegalensis* appear to closely follow branching patterns of streams (http://www.worldagroforestry.org/sites/treedbs/treedatabases.asp). It may also explain the overall rather slow development of forest vegetation on savanna patches in Kogyae Strict Nature Reserve and elsewhere in the transition (Armani *et al.* 2018, Janssen *et al.* 2018).

At the end of the experiment, the savanna species outperformed the forest species in terms of attained biomass at harvest, allocation to roots and root starch concentration. This was consistent with our expectation as species from drier pyrogenic environments have been reported to have higher root mass fraction and carbohydrate reserves for overcoming drought and fire (Cardoso *et al.* 2016, Hoffmann *et al.* 2004, O'Brien *et al.* 2014, Tomlinson *et al.* 2012).

Overall, our results suggest that the possibilities for establishment of moist semi-deciduous forest species in the forest-savanna ecotone are particularly limited by the dry season and its associated pyrogenic environment. More interestingly, we demonstrate that savanna species also differ in their tolerance to canopy cover and open pyrogenic environments specifically related to root storage functions, thus contributing to a better understanding of differences in tree seedling recruitment between species across the forest-savanna ecotones.

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