ORIGINAL ARTICLE

bioTROPICA | ASSOCIATION FOR TROPICAL BIOLOGY AND CONSERVATION | WILEY

Responses of tropical tree seedlings in the forest–savanna boundary to combined effects of grass competition and fire

Hamza Issifu[1,2] | Philippine Vergeer[1] | George K. D. Ametsitsi[1,3] | Jelle Klijn[1] | Paolo Sartorelli[1] | Millicent Tanson[1] | Hypolite Bayor[4] | Vincent Logah[5] | Frank van Langevelde[6,7] | Elmar Veenendaal[1]

[1]Plant Ecology and Nature Conservation Group, Wageningen University, Wageningen, The Netherlands

[2]Department of Forestry and Forest Resources Management, University for Development Studies, Tamale, Ghana

[3]CSIR-Forestry Research Institute of Ghana, KNUST, Kumasi, Ghana

[4]Department of Horticulture, University for Development Studies, Tamale, Ghana

[5]Department of Crop and Soil Sciences, Kwame Nkrumah University of Science and Technology, Kumasi, Ghana

[6]Wildlife Ecology and Conservation Group, Wageningen University, Wageningen, The Netherlands

[7]School of Life Sciences, Westville Campus, University of KwaZulu-Natal, Durban, South Africa

Correspondence
Hamza Issifu, Plant Ecology and Nature Conservation Group, Wageningen University, 6700 AA Wageningen, The Netherlands.
Email: hamza.issifu@gmail.com

Abstract

Co-occurring tree functional types (TFTs) within forest–savanna transitions may differ in seedling responses to grass competition and fire in savannas. We performed a common garden experiment in the Guinea savanna of Ghana to test hypotheses related to competition effects on growth, allocation to root storage reserves, and subsequent survival responses to dry season fire for savanna-transitional TFT (i.e., species occurring both in forest and savanna) and forest TFT. The experiment included factorial combinations of TFT, comprising four species each of forest versus savanna-transitional trees, wet season grass competition (grass competition vs. grass no-grass competition), and dry season fire (burn vs. no-burn). Partly consistent with prediction, we found that grass competition suppressed tree seedling growth and caused a 17% reduction in root non-structural carbohydrates concentration [NSC] but had no effect on direct survival regardless of TFT at the end of the wet season. Post-fire survival averaged 6% for forest versus 91% for savanna-transitional TFTs across competition treatments. In contrast to our prediction on how grass competition influences post-fire seedling survival, a history of grass competition did not result in lower post-fire survival regardless of TFT, although plant mass, root mass fraction, and root [NSC] at the end of the dry season were lower for tree seedlings with a history of competition. Our results demonstrate that grass competition suppresses tree seedling growth and root storage reserves irrespective of TFT, and that competition alone (without fire) may not preclude the establishment of forest seedlings in savannas close to forests.

KEYWORDS
fire, forest trees, functional traits, herbaceous vegetation, root non-structural carbohydrates, savanna trees, seedling survival

1 | INTRODUCTION

The co-occurrence of distinct tree functional types (species typical of savanna, forest, or forest–savanna transitional formations) characterizes the zone of transition between forest and savanna across much of tropical Africa (Ametsitsi et al., 2020; Armani et al., 2018; Torello-Raventos et al., 2013; Veenendaal et al., 2015). Fire is generally considered a significant bottleneck for the establishment and subsequent survival and growth of forest tree seedlings in the savanna (Cardoso et al., 2016; Gignoux et al., 2009; Hoffmann et al., 2004) and seen as key factor in maintaining the typical mosaic appearance of the forest–savanna transition (Hopkins, 1974; Swaine et al., 1976; Van Langevelde et al., 2014). However, other factors may also play important roles directly, or indirectly by enhancing fire effects.

In tropical savannas, competition between tree seedlings and herbaceous vegetation may limit establishment success of forest tree seedlings through competition for water (February et al., 2013; Kulmatiski et al., 2010) or soil nutrients (Tomlinson et al., 2019; van der Waal et al., 2009) or for both soil resources and light (Barbosa et al., 2014; Holl, 1998; Vadigi & Ward, 2013). The suppression of tree seedling growth due to grass competition is often reported for savanna tree seedlings (Barbosa et al., 2014; February et al., 2013; Tomlinson et al., 2019; Vadigi & Ward, 2013; van der Waal et al., 2009). In very dry areas such as the Sudan or Sahel savannas, the presence of grass may again facilitate tree seedling establishment via the amelioration of microclimate (Anthelme & Michalet, 2009).

The chances of surviving drought and/or fire are generally greater for larger tree seedlings than smaller ones (Cardoso et al., 2016; Gignoux et al., 2016; Hoffmann et al., 2012) possibly due to differences in the amounts of stored carbohydrate reserves (Cardoso et al., 2016; Issifu et al., 2019). Thus, suppression of tree seedling growth in the wet season (as a result of grass competition) can decrease the chances of tree seedlings surviving fire in the dry season. Also, by slowing down seedling growth rates, grass competition may prolong how long it takes for tree seedlings to reach a "threshold of fire resistance" (Hoffmann et al., 2012), thereby affecting the dynamics between fire frequency and seedling recruitment into larger size classes.

Tree seedling–grass interactions which include forest tree species may differ from those that include savanna-transitional tree species as these tree functional types represent distinct strategies that maximize success in their respective forest and savanna environments (Boonman et al., 2019). If grass competition differentially affects tree functional types (e.g., by making forest species less successful than savanna-transitional species), then grass plays a more direct role (aside fuelling fire) in shaping the boundary between forest and savanna. Surprisingly, few studies have actually explored how, in forest–savanna transitions, humid savanna tree species common to both forest and savannas (henceforth, savanna-transitional species) may differ from forest tree species in the degree to which they invest in storage in roots and shoot growth in relation to environmental limitation by shading from grasses and fire (Boonman et al., 2019). There have been few studies exploring tropical forest tree–grass interactions, but these have focused on abandoned pastures and degraded lands within the forest biome (e.g., Celis & Jose, 2011; Hoffmann & Haridasan, 2008; Holl, 1998; Sun & Dickson, 1996) and not enough attention has been given to tree seedling–grass competition for forest–savanna transitional tree species.

Here, we test (1) if survival and growth responses to grass competition differ between forest and savanna-transitional tree functional types in savanna, and (2) if a history of grass competition influences post-fire tree seedling survival in the dry season for forest and savanna-transitional tree functional types. We hypothesize that (1) grass competition during the wet season decreases tree seedling growth, carbohydrate storage in roots, and seedling survival, with the effect being larger for the forest than the savanna-transitional tree functional types, and (2) a history of grass competition decreases the chances of tree seedlings surviving the dry season fire, with the effect being larger for the forest than the savanna-transitional tree functional types.

2 | METHODS

2.1 | Study site and species

The study was performed at the experimental garden on the Nyankpala Campus of the University for Development Studies, Ghana (9°24'52.0" N, 0°58'43.6" W). The site lies within the humid part of the Guinea savanna vegetation zone with an annual rainfall of ~1100 mm/year. The dry season from November to March follows the April–October wet season. Mean annual temperature is 28°C. The experimental garden is a former agricultural land with high herbaceous cover dominated by the two grass species: *Pennisetum pedicellatum* Trin. and *Andropogon pseudapricus* Stapf. The soil in the garden is sandy loam in texture with medium to coarse stones. Soils of the general study location are described as Plinthustalf, sandy over-clays skeletal phase and classified by FAO as Plinthic Lixisol (FAO, 2001; Serno & van de Weg, 1985).

Eight tree species were used in this study, classified a priori into species typical of forest (four species) or savanna-transition (four species) types (Table 1). Of the latter group, *Afzelia africana* is a transition/non-selective species (Ametsitsi et al., 2020) occurring both in savanna and in dry tropical forest. Seeds of the humid savanna and transitional tree species were collected in the forest–savanna transition zone at Kogyae Strict Nature Reserve (7°19'1.66'' N, 1°05'5.863'' W) while those of the forest tree species were collected from dry semi-deciduous forest near Abofour (7°19'1.66'' N, 1°05'5.863'' W) between December 2017 and February 2018. Seedlings were raised in a temporary nursery at the experimental site and transplanted into the experiment at ~8 weeks old in early April 2018.

2.2 | Study approach

The experiment consisted of two phases: a grass/no-grass competition treatment in the wet season, followed by a fire/no fire

TABLE 1 Functional classification of tree species used in the common garden experiment. Species information was obtained from Hawthorne (1995), Hall and Swaine (1976), Orwa et al. (2009)

Species	Family	Guild	Functional type
Khaya senegalensis (Desr.) A. Juss	Meliacaea	–	Savanna
Khaya anthotheca (Welw.) C.DC.	Meliacaea	Non-pioneer light demander	Forest
Khaya ivorensis (Desr.) A. Juss	Meliacaea	Non-pioneer light demander	Forest
Terminalia superba (Engl. & Diels)	Combretacae	Pioneer	Forest
Terminalia ivorensis A. Chev.	Combretacae	Pioneer	Forest
Pterocarpus erinaceous Poir.	Fabaceae	–	Savanna
Afzelia africana Sm. ex Pers.	Caesalpiniaceae	Non-pioneer light demander	Transitional
Daniella oliveri (Rolfe) Hutch. & Dalziel	Caesalpiniaceae	–	Savanna

FIGURE 1 Monthly rainfall, relative humidity, and temperature during the experimental period in Nyankpala within the Guinea savanna of Ghana. Weather data are from agro-meteorological station of the Savanna Agricultural Research Institute of Ghana, within 1 km of the experimental site. Various phases of the experiment are indicated with dotted vertical lines. Red vertical line indicates month (in the dry season) of the experimental burn
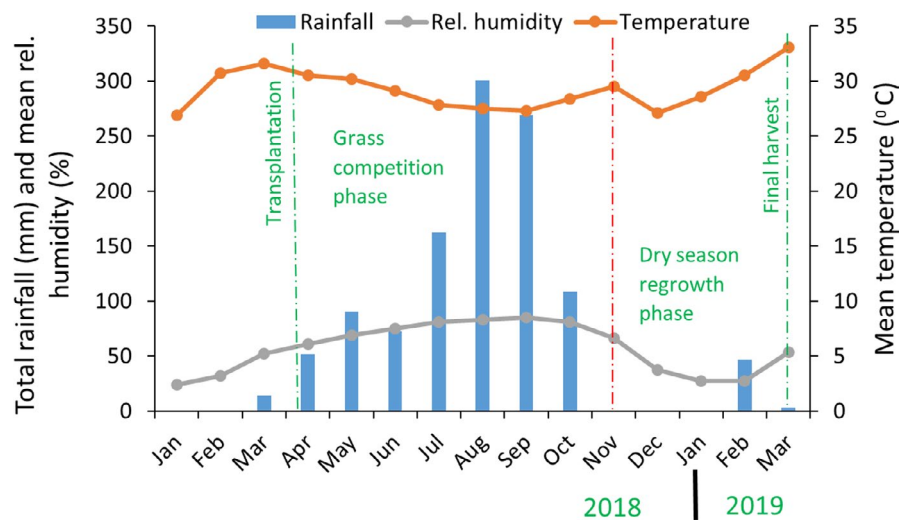
treatment in the dry season (Figure 1) in a full factorial design. Twelve 48 m^2 plots were established at the experimental site in early April, just before the onset of the wet season of 2018. All herbaceous vegetation was removed in six randomly chosen plots (i.e., control plots). Vegetation in the other six plots was left intact (i.e., grass competition plots). If necessary, tufts of *Pennisetum pedicellatum* Trin. and *Andropogon pseudapricus* Stapf were transplanted in the grass plots to ensure a homogeneous sward of herbaceous vegetation throughout. In each plot, four seedlings each of the eight species, except *Daniella oliveri*, were transplanted at a spacing of 0.7 m × 1.0 m within and between rows (respectively) of seedlings at the onset of the rainy season (April, 2018), with *D. oliveri* only present in three control and five competition plots because seedlings of this species were insufficient. We assigned seedlings at random to planting positions. In total, 360 seedlings were transplanted (12 plots × 7 species × 4 seedlings + 3 seedlings × 8 plots for *D. oliveri*). All plots received natural precipitation over the seven months of the wet season. No-grass (control) plots were kept free of grass by periodic weeding until October 2018, when the rains ended. At this point, we randomly selected six plots (three each for

grass and no-grass) for destructive harvest to measure the pre-fire plant performance. The remaining six plots were reserved for the fire (vs no-fire) treatments.

2.3 | The fire experiment

The percentage grass cover was estimated in three 1 × 1 m^2 quadrats randomly located per plot with standing grass biomass and the maximum height of the grass determined at the end of the rainy season. All six plots (three grass competition and three control plots) were first cleared of all existing vegetation and then prepared for burning with pre-prepared grass fuel to ensure uniformity in fuel (type, moisture content, and load) for plots to burn. Fuel used consisted of a mix of grasses, but mainly *Pennisetum pedicellatum* Trin. and *Andropogon pseudapricus* Stapf, harvested from the adjoining savanna and air-dried for two weeks.

We made fuel beds by covering each plot (entirely) with grass at a fuel load of 1 kg/m^2 of grass. Each plot was burnt separately. Burning took place, for all plots, between the hours of 15:00 and

17:00 hours in November 2018. Fire temperature in each plot was measured using a thermocouple thermometer (Hanna instruments), with the probe cable buried while the full length of the probe was sticking out. This probe position allowed for the most accurate ambient temperature in the presence of fire to be determined close to the seedling (Dayamba et al., 2010). After this, the plots were left untouched until being re-watered on February 1, 2019, to mimic early start of the wet season after four months of dry season. From then on, each seedling received 1.4 L/day of water for three weeks after which plants were harvested.

2.4 | Measurements on plants during the experiment

Three months after the start of the experiment, we measured seedling height and stem basal diameter for all seedlings in all plots. Census of live or dead was conducted for seedlings in all 12 plots at the end of the wet season, before the fire/no-fire treatment (November 2018). We defined dead plants as seedlings with dry (dead) aboveground parts (stem and leaves), which upon excavation also had dead roots. Excavation was done after visual inspection of the aboveground parts. We determined changes in seedling height and stem basal diameter using data from July 2018 and November 2018 for all 12 plots. Post-fire and/or dry season survival (henceforth, post-fire survival) was assessed in each plot (total of six plots) by counting the number of resprouting seedlings for each species.

2.5 | Plant biomass and trait measurements

We determined seedling start (dry) mass from five random seedlings (from the seedling pool) per species prior to transplantation. Pre-fire harvest (in November 2018) was done just before the fire treatment in November by carefully excavating all seedlings in six random plots (three grass and three control). Seedlings were separated into leaf, stem, and root parts before oven drying (at 70°C) to constant weight. Various plant traits (Table 2) were then derived based on data at this harvest. Leaf mass fraction (LMF) was calculated as leaf dry weight divided by total plant dry weight; stem mass fractions (SMF) as stem dry weight divided by total plant dry weight; root mass fraction (RMF) as root dry weight divided by total plant dry weight; specific stem length (SSL) as stem length divided by total plant dry weight; and specific rooting depth (SRD) as rooting depth divided by total root dry weight. We also calculated average seedling mass gain as the difference between start plant mass and mass at end of wet season harvest. RGR was calculated using ln-transformed final plant mass minus mean ln-transformed initial mass divided by the growth period (d = 32 weeks) following Hoffmann and Poorter (2002).

We did the final harvest in March 2019, 16 weeks into the post-fire regrowth phase (Figure 1). Prior to excavation, we watered all seedlings for four weeks (to ascertain mortality). Live seedlings were counted as those with (at least) live belowground buds. After oven drying, we determined the total mass of new shoot as new stem mass plus new leaf mass. Total plant mass was determined as mass of new shoot plus mass of root.

Roots of plants excavated in both harvests (November 2018 and March 2019) were analyzed for concentrations of simple carbohydrates (mainly sugars, hereafter referred to as "soluble sugars") and complex carbohydrates (mainly starch). We used the carbohydrate extraction protocol of Duranceau et al. (1999) adapted from Dubois et al. (1956). Soluble sugars were extracted in 80% ethanol samples, centrifuged, and separated in supernatant and pellet. Soluble sugars were determined in the supernatant and complex carbohydrates ("starch") after digestion of the pellet in 6 M HCL. Root non-structural carbohydrate (NSC) concentration was then estimated as the sum of soluble sugars and starch. Total NSC content in roots was estimated as (NSC concentration × root dry weight). For the November 2018 harvest, root samples of 6 seedlings × 2 grass treatments × 7 species (three savanna-transitional tree species and four forest tree species) were analyzed. At the March 2019 harvest, sufficient samples for root carbohydrate analysis were available only for the three savanna-transitional tree species, due to the very high mortality of the forest species.

2.6 | Environmental measurements

Data on precipitation, temperature, and relative humidity for the whole experimental period (Figure 1) were obtained from the Agro-meteorological station of Savanna Agricultural Research Institute Ghana (within 1 km of our experimental location). We measured soil moisture (vmc %) within the top 10 cm of the soil using a theta probe (Spectrum technologies Inc.) in mid-August (peak wet season of 2018) and then in November (one week into the dry season). Measurement in August was done at five random positions in all 12 plots (six each for competition and control) while the November measurement was done at every seedling position but in six plots (three each for competition and control). After the fire treatment, we sampled soil for chemical analysis. Sampling was done within the top 10 cm soil layer in nine plots, three each for fire following wet season grass competition, fire without wet season grass competition, and no-fire without wet season grass competition. We made composite samples from four locations within each plot. Soil exchangeable bases (Mg, Ca, K, Na) were analyzed following extraction with buffered 1.0 M ammonium acetate solution (NH_4OAC, pH = 7) (Thomas, 1982). Soil organic C and total N were determined using dry chemistry (Vario MACRO Cube). Soil available P was determined as phosphorus soluble in dilute acid fluoride (Okalebo et al., 1993) using double beam spectrophotometer (Biochrom Ltd.).

Light availability to seedlings was measured using a PAR quantum sensor (Skye Instruments) by measuring light reaching the top canopy leaves of randomly selected seedlings in the grass and no-grass plots. Light measurements were done under overcast conditions between 11:30 hours and 12 hours. Monthly summaries of temperature, relative humidity, and rainfall before and after the

TABLE 2 Overview of functional traits analyzed in this study

Trait	Abbr. (units)	Relevance
Leaf dry weight	LDW (g)	Light capture/growth
Stem dry weight	SDW (g)	Height growth/light capture/avoiding fire top-kill
Root dry weight	RDW (g)	Belowground reserves/fire or drought survival
Leaf mass fraction	LMF (g g^{-1})	Investment in light capture, photosynthesis, and growth
Stem mass fraction	SMF (g g^{-1})	Investment in light capture and aboveground growth
Root mass fraction	RMF (g g^{-1})	Storage of reserves and/or belowground foraging
Plant height gain	PH (cm)	Indication of aboveground growth. Important for light competition or avoiding fire top-kill
Stem length	SL (cm)	Light capture/aboveground growth
Specific stem length	SSL (cm g^{-1})	Light foraging and growth, avoiding fire top-kill
Rooting depth	RD (cm)	Foraging for deeper soil moisture
Specific rooting depth	SRD (cm g^{-1})	Investment in water foraging at depth
Relative growth rate	RGR (g g^{-1} week^{-1})	Photosynthetic capacity, biomass accumulation
Plant mass gain	PDW (g)	Biomass accumulation, growth
Stem basal diameter	SBD (mm)	Thicker stem/root, protection of tissues from fire, indication of root size or plant growth
Root total non-structural carbohydrate concentration	[NSC] (%)	Allocation of carbon to roots. Indicates investment in post-disturbance recovery
Root total non-structural carbohydrate content	NSC content (g)	Total carbon available in roots storage. Indicates total reserves available to support post-disturbance recovery
Ratio of soluble sugars to starch	Sugars:Starch ratio	Concentration of soluble sugars indicates carbon available to support growth versus starch which is carbon put in storage

experimental fire are presented in Figure 1, and temperature, relative humidity, and wind speed on the day of burning were 30°C, 66%, and 0.88 km/hour, respectively.

2.7 | Statistical analysis

We analyzed all data in *R* (R Development Core Team, 2017) and used *ggplot2* (Wickham, 2009) for data visualization except Figure 1. Soil moisture content (MC) was tested for differences between grass and no-grass plots for August and November measurements separately using linear mixed-effects models (LMMs). This was achieved with the *lmer* function in *lme4* package (Bates et al., 2015) together with *lmerTest* package (Kuznetsova et al., 2015). In the LMMs, plot was included as a random factor. Soil chemical properties were analyzed (separately) for differences between grass and no-grass plots and between burnt and unburnt plots using linear models (LM). We tested

light intensity for differences between grass and no-grass plots using an LMM including plot and seedling position as random factors.

We tested growth-related traits (i.e., RGR, gains in total plant mass, height, and stem basal diameter), root non-structural carbohydrates (NSCs, both concentration and total reserves), ratio of soluble sugars to starch, and seedling morphology traits (LMF, SMF, RMF, RD, SRD, and SSL determined at the end of the competition phase) for fixed effects of tree functional type (TFT) × grass treatment. Plot was included as a random factor. Where necessary, traits (e.g., root NSC and SRD) were ln-transformed prior to analyses to meet assumptions of normality and residual variances. We estimated the effect size of competition for growth-related traits using Hedges' *g*, where a *g* of 1 indicates that the two treatment groups differ by 1 standard deviation, a *g* of 2 indicates a difference of 2 standard deviations, and so on (Hedges & Olkin, 1985). On whether effect sizes are "small" or "large", we used Cohen's rule-of-thumb interpretation as follows: a *g* of 0.2 is "small," 0.5 is "medium," and 0.8 is "large" (Cohen, 1977). In separate models

(for each TFT), we tested fixed effects of species × grass treatment including random plot effect. We separated significant species effects (or interaction effects) using Tukey's post hoc contrasts achieved with the *emmeans* package (Lenth et al., 2019).

We analyzed seedling survival in a generalized linear mixed model (GLMM) with the binary data using binomial error (with logit link function). For this, we used the *glmer* function in *lme4* package. We analyzed survival for fixed effects of TFT ×grass treatment and then for species ×grass treatment separately for each TFT, including random plot effect in each separate model. Post-fire seedling survival (also binary data) was analyzed in GLMMs to test competition and TFT effects, including random plot effect following the same procedure as described for survival due to grass competition. Within the forest TFT, we analyzed survival of *K. anthotheca* and *K. ivorensis* together (as there were no survivors of the two Terminalia species) for fixed effect of species × grass treatment, including random plot effect. Then, we tested post-fire growth among savanna-transitional species for species × grass treatment effect in an LMM that included random plot effect. Also, among the savanna-transition species, we assessed the relationship of post-fire survival to pre-fire seedling size (plant height) in a GLMM. Correlations among traits were performed separately for seedlings in grass and no-grass treatments using Pearson's product-moment.

3 | RESULTS

3.1 | Environmental variables

Total rainfall received within the wet season was 1053.8 mm with peak rainfall recorded in August (Figure 1). Soil moisture content (% vol.) varied between 26.4 ± 2.6% in August and 12.4 ± 2.2% in November. In both measurement months, soil moisture content was higher in the grass than no-grass treatment (Table 3). Grass dominated the herbaceous layer in the grass plots (>75% vs 5–12% cover

for herbs). Mass of herbaceous vegetation averaged 0.76 kg/m^2 ± 0.15 kg/m^2, with a maximum height of 2.26 m ± 0.29 m.

Light intensity recorded in grass plots averaged 10.9 ± 5.0%, which was lower ($F_{1, 33}$ = 467, p < 0.001) than intensity recorded in the no-grass plots at 90.5 ± 5.9% of full light levels. The amount of light reaching the seedling crowns varied between 75 and 100% of above canopy height, and correlated (β = −0.25, t = −2.80, df =14, p = 0.015) with seedling height in the no-grass treatment. In the grass treatment, the amount varied between 10% and 27%, but has no correlation (β = −0.015, t = −0.15, df =16, p = 0.886) with seedling height (Figure S1).

Height of the fuel bed made in the fire experiment averaged 0.23 ± 0.1 m, yielding a fuel bulk density of 1.1 kg/m^3. Mean moisture content of grass (calculated on a dry weight basis) used as fuel for the experimental burn was 3.0 ± 1.1%, and mean ambient temperature recorded in the presence of fire was 535 ± 157°C. Soil chemical properties of samples at the end of the experiment did not differ between grass treatments or between burnt and unburnt plots (Table S1).

3.2 | Tree seedling survival and growth during the wet season

Seedling survival proportion at the end of the wet season averaged 0.93 ± 0.14 across treatments (Table 4). There were no effects of tree functional type (TFT) or competition treatment or their interaction on tree seedling survival proportion at the end of the wet season (Table 5).

Relative growth rate (RGR) was lower for tree seedlings in competition (at 0.03 ± 0.03 g/g/week) compared to control at 0.06 ± 0.05 g/g/week across TFTs (Table 5; Figure 2a). TFT or its interaction with competition had no effect on seedling RGR (Table 5). As a result, Hedge's effect size estimated for competition effect on RGR was large, but similar, for both TFTs (g = −0.89). Plant mass gain was lower for seedlings in competition (1.14 ± 1.70 g) compared to control (6.20 ± 6.70 g) across TFTs (Table 5; Figure 2b). TFT or

TABLE 3 ANOVA from linear mixed-effects models on differences in soil moisture content between competition and no-competition (control) plots in August (peak wet season) and November (start of dry season) in a common garden in the humid Guinea savanna of Ghana

|	Mean (VMC % ± sd)				
	Grass	No-grass	*F*-value	df	*p*-value
August MC	28.2 ± 2.73	24.5 ± 2.81	10.1	1	0.009
November MC	13.2 ± 2.57	11.6 ± 1.84	17.3	1	0.015

TABLE 4 Seedling survival proportion (± standard deviation) at the end of the wet season (October 2018) and end of dry season (March 2019) in a common garden in the guinea savanna of Ghana. Statistical comparisons were done with binomial model (with logit link function) between tree functional types (TFT) and grass competition treatments. Significant (p < 0.05) effects from GLMM are indicated by different letters

	Wet season census		Dry season (post-fire) census	
	Grass	No-Grass	Grass	No-Grass
Forest TFT	0.91 ± 0.16	0.90 ± 0.16	0.02 ± 0.08[a]	0.08 ± 0.16[a]
Savanna-transitional TFT	0.96 ± 0.13	0.95 ± 0.10	0.89 ± 0.18[b]	0.92 ± 0.18[b]

TABLE 5 ANOVA Table from GLMM on seedling survival proportions and LMM on growth-related parameters measured at the end of the wet season. Detailed descriptions of (abbreviated) traits are found in Table 2

Source of variation	Seedling survival			RGR			Plant mass gain			Plant height gain		
	F	df	p-value	F	df	p-value	F	df	p-value	F	df	p-value
TFT	0.91	1	0.341	2.15	1, 148	0.145	0.38	1, 148	0.539	28.8	1, 307	<0.001
Grass	0.28	1	0.600	16.1	1, 4	0.014	8.71	1, 4	0.041	21.3	1, 10	<0.001
TFT × Grass	0.33	1	0.564	0.09	1, 148	0.770	0.12	1, 148	0.725	1.53	1, 307	0.217

FIGURE 2 Plant growth parameters in the wet season as influenced by grass competition among seedlings of forest and savanna-transitional (S-T) tree functional types in a common garden experiment in the Guinea savanna of Ghana. Letters compare TFTs and grass competition treatments. Different letters are significant at $p < 0.05$ from Tukey's pairwise comparisons following linear mixed-effects models
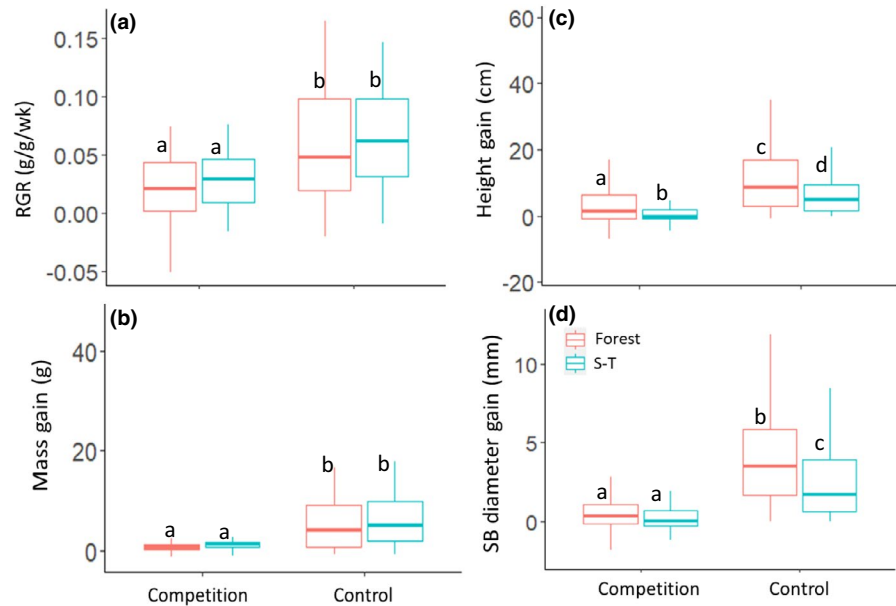
its interaction with competition had no effect on plant mass gain. Again, Hedge's effect sizes for competition effect on plant mass gain were large, but similar, for both TFTs ($g = -1.03$ for forest and -1.02 for savanna-transitional TFT).

Irrespective of TFT, plant height gain was lower for seedlings in competition (at 1.80 ± 5.46 cm) compared to control (at 9.9 ± 10.7 cm). Also, irrespective of grass treatment, seedling height gain was greater for forest (at 8.0 ± 10.9 cm) than savanna-transitional TFT (at 3.2 ± 6.4 cm, Table 5; Figure 2). Hedge's effect size estimated for competition effect on plant height gain was larger for the savanna-transitional TFT ($g = -1.26$ vs $g = -0.91$ for forest TFT). We found that stem basal diameter (SBD) differed greatly between both TFT and competition treatments, but there was also an interaction effect ($F_{1, 302} = 5.7$, $p = 0.017$) of TFT × grass competition treatment on SBD (Figure 2d). SBD increment was greater for forest TFT (at 4.2 ± 3.1 mm) than savanna-transitional TFT (at 2.7 ± 2.5 mm) seedlings without grass competition, but SBD increment did not differ between TFTs for seedlings with grass competition (Figure 2d). As a result, the effect of grass competition on SBD increment was larger for the forest TFT ($g = -1.56$) than the savanna-transitional TFT ($g = -0.95$).

We have included, as supplementary information, species-specific survival (Tables S2 and S3) and growth responses (Figure S2, Table S3) to competition for each tree functional type.

3.3 | Storage of non-structural carbohydrates in roots during the wet season

Non-structural carbohydrate concentration [NSC] in roots was lower ($F_{1, 80} = 196$, $p < 0.001$) for the forest (at $11.60 \pm 3.6\%$) than the savanna-transitional TFT (at $27.0 \pm 6.3\%$) irrespective of grass competition treatment (Figure 3a). Also, irrespective of TFT, root [NSC] was lower ($F_{1, 4} = 10.5$, $p = 0.033$) for seedlings in grass competition (at $17.3 \pm 5.4\%$) relative to control (at $20.8 \pm 4.5\%$). There was no effect of TFT ×competition treatment interaction on root [NSC]. Total root non-structural carbohydrates (total NSC reserves) were lower ($F_{1, 80} = 76.4$, $p < 0.001$) for the forest TFT (at 26.7 ± 31 g) than the savanna-transitional TFT (at 106 ± 77 g). Also, irrespective of TFT, total NSC reserves was lower ($F_{1, 4} = 40$, $p = 0.003$) for seedlings in competition (at 29.8 ± 28 g) relative to control (at 101 ± 80 g) (Figure 3b). There was no TFT × competition treatment interaction effect on total NSC reserves.

Ratio of soluble sugars to starch (sugars:starch ratio) in roots was higher ($F_{1, 83} = 43.2$, $p < 0.001$) for the forest TFT (2.9 ± 1.9) than the savanna-transitional TFT (0.83 ± 0.76) (Figure 3c). There was no effect of grass treatment at 2.1 ± 1.7 for competition compared to control at 1.8 ± 1.9. There was also no effect of species × grass treatment interaction on sugars:starch ratio.
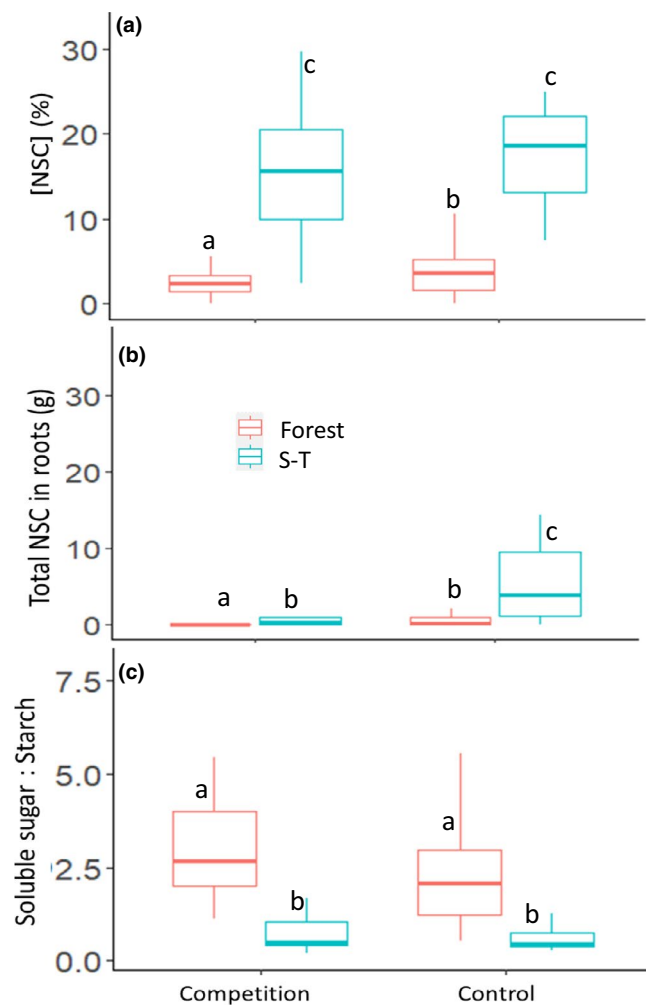
FIGURE 3 (a) Root non-structural carbohydrate concentration [NSC], (b) Root total non-structural carbohydrate content and (c) ratio of soluble sugars to starch in roots among seedlings of forest and savanna-transitional (S-T) tree functional types in grass competition versus control at the end of the wet season in a common garden experiment in the Guinea savanna of Ghana. Letters compare TFTs and grass competition treatments pairwise (Tukey's contrasts)

3.4 | Seedling morphology traits at the end of the wet season

Leaf mass fraction (LMF) averaged 0.19 ± 0.11 g/g for seedlings in competition, which was lower compared to control at 0.28 ± 0.14 g/g (Table 6, Figure S3a,d). There was a trend of higher (although at borderline significance) LMF for forest TFT (0.34 ± 0.12 g/g) than savanna-transitional TFT (0.23 ± 0.15 g/g) in control, but no apparent TFT difference in competition (Table 6). Forest tree seedlings had higher stem mass fraction (SMF) at 0.43 ± 0.10 g/g than savanna-transitional tree seedlings at 0.19 ± 0.09 g/g (Table 6; Figure S3b,e) irrespective of grass treatment. Also, savanna-transitional tree seedlings had higher RMF (at 0.62 ± 0.18) than forest (at 0.29 ± 0.10) tree seedlings irrespective of grass treatment (at 0.47 ± 0.21 g/g for control and 0.43 ± 0.22 g/g for grass treatment) (Table 6; Figure S3c,f).

TABLE 6 ANOVA tables from separate LMMs for seedling morphology traits. Detailed descriptions of (abbreviated) traits are found in Table 2

Source of variation	LMF			SMF			RMF			SSL			RD			SRD		
	F	df	p-value	F	df	p-value	F	df	p-value	F	df	p-value	F	df	p-value	F	df	p-value
TFT	15.0	1, 151	<0.001	286	1, 148	<0.001	197	1, 151	<0.001	8.93	1, 143	0.003	25.5	1, 142	<0.001	51.7	1, 143	<0.001
Grass	20.1	1, 151	<0.001	11.4	1, 4	0.025	2.20	1, 151	0.140	27.0	1, 4	0.006	2.74	1, 4	0.173	21.6	1, 4	0.009
TFT × Grass	3.70	1, 151	0.056	3.60	1, 148	0.059	0.04	1, 151	0.849	1.80	1, 143	0.182	0.39	1, 142	0.529	0.005	1, 143	0.944

We found that specific stem length (SSL) was higher for the savanna-transitional TFT (at 37.1 ± 24.0 cm/g) than the forest TFT (at 28.2 ± 19.8 cm/g) irrespective of grass treatment. SSL was also higher ($F_{1,\,4} = 27.0$, $p = 0.006$) in competition at 44.3 ± 22.1 cm/g compared to control at 21.2 ± 15.8 cm/g (Table 6; Figure S4a,e). Seedlings of the savanna-transitional TFT also had greater rooting depth (at 21.3 ± 6.7 cm) than the forest TFT (at 16.2 ± 6.1 cm) irrespective of competition treatment (Table 6; Figure S4c,g). Specific rooting depth (SRD) was higher for the forest TFT than savanna TFT irrespective of grass treatment (Table 6). Also, irrespective of TFT, SRD was higher in competition (at 29.8 ± 29.2 cm/g) than in control (at 16.8 ± 21.2 cm/g).

Correlations among growth and morphology traits are included in supplementary information (Table S5a,b for forest and savanna-transitional TFTs, respectively).

3.5 | Seedling survival, regrowth, and root [NSC] after the dry season fire

Proportion of seedlings that survived the dry season with fire (i.e., post-fire survival proportion) was lower ($F = 62.2$, $p < 0.001$) for the forest TFT (at 0.06 ± 0.12) than the savanna-transitional TFT (at 0.91 ± 0.18) across grass competition treatments (Table 4). There was no effect of competition and TFT × competition interaction was also not significant ($F = 0.33$, $p = 0.555$).

All plants were top-killed by the fire (and/or the dry season). We analyzed post-fire seedling regrowth only for the savanna-transitional TFT, as recovery was too low for the forest TFT at this stage. We observed that across all three savanna-transitional species, root mass constituted 97 ± 6.7% of total plant mass for seedlings harvested post-fire (Figure S5b), and was lower ($F_{2,\,58} = 32.7$, $p = 0.005$) for seedlings in prior competition (at 1.48 ± 1.07 g) than control (at 5.71 ± 3.61 g).
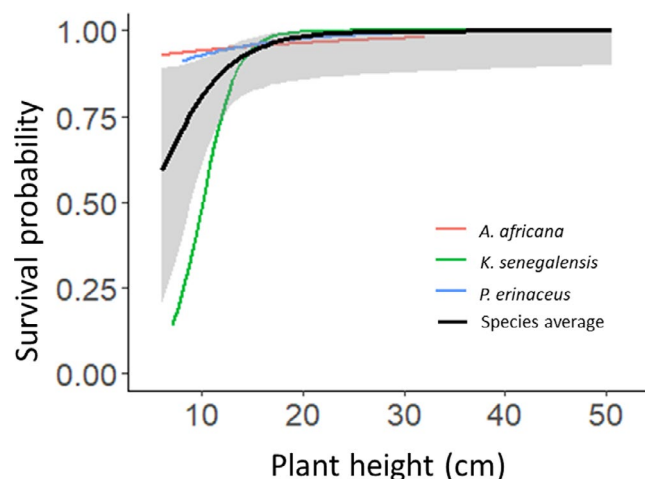

FIGURE 4 Dry season survival probability as predicted by wet season plant height (in a GLMM) for three savanna-transitional tree species (which survived the dry season with fire) in a common garden in the Guinea savanna of Ghana. Gray-shaded area is 95% confidence interval for species average (black curve)

Thus, new shoot mass post-fire averaged only 0.16 ± 0.4 g and did not differ between grass competition treatments. There was an interaction effect of species ×grass treatment ($F_{2,\,59} = 8.22$, $p < 0.001$) on post-fire total plant mass. Total plant mass at the end of the dry season was lower in prior competition relative to control for *K. senegalensis* and *P. erinaceus*, but not *A. africana* (Figure S5a).

Across all three savanna-transitional species analyzed for post-fire recovery, the chances of a seedling surviving fire were significantly related ($\beta = 0.27$, $z = 2.03$, $p = 0.043$) to pre-fire seedling height (Figure 4). Root non-structural carbohydrate concentration [NSC] was higher ($F_{2,\,26} = 14.5$, $p < 0.001$) for both *A. africana* (at 29.1 ± 10.5%) and *P. erinaceus* (at 21.1 ± 6.0%) than *K. senegalensis* (at 14.5 ± 4.3%) seedlings irrespective of prior competition treatment (Figure S6a). There was no effect of species ×grass treatment interaction on [NSC]. However, there was an effect ($F_{2,\,26} = 17.1$, $p < 0.001$) of species × grass treatment interaction on total NSC reserves, which was lower in the prior grass treatment relative to control for both *P. erinaceus* and *K. senegalensis*, but not *A. africana* (Figure S6b). *K. senegalensis* maintained a higher ($F_{2,\,26} = 6.1$, $p = 0.007$) soluble sugar to starch ratio (at 10.8 ± 13.7) than both *P. erinaceus* (at 0.57 ± 0.25) and *A. africana* (at 0.63 ± 0.40), irrespective of prior grass competition.

4 | DISCUSSION

In this study, we tested for competition effects on tree seedling performance and storage of carbohydrates during the wet season, and whether these effects were larger for the forest than savanna-transitional tree functional types. We also determined whether a history of wet season grass competition influenced the chances of tree seedlings surviving dry season fire, and whether such an effect was also dependent on tree functional type. Overall, we found differences in seedling performance and root carbohydrate reserves in the face of grass competition, which were related to differences in trait responses, mainly to shading by grasses, of the two tree functional types. Although we did not find evidence that a history of grass competition resulted in lower post-fire seedling survival, we observed that at the end of the dry season with fire, seedlings with a history of grass competition were smaller and had less carbohydrate reserves in roots. There was also a large difference in post-fire seedling survival between the two tree functional types. Here, we discuss these findings and their overall implications for the maintenance of the forest–savanna mosaic.

4.1 | Grass competition during the wet season decreases tree seedling growth and NSC storage similarly for forest and savanna-transitional tree functional types

We hypothesized that competition between tree seedlings and grasses reduces tree seedling growth, root non-structural

carbohydrates (NSC), and seedling survival. We also predicted greater adverse effect of competition for the forest than savanna-transitional tree functional type. The latter prediction was based on known differences in trait syndromes resulting from differences in selection pressures that shaped the evolution of forest and savanna species (Boonman et al., 2019; Oliveras & Malhi, 2016).

We found that all growth-related parameters were significantly lower in grass competition, consistent with prediction and in line with other studies reporting on growth suppression of savanna tree seedlings due to grass competition (Barbosa et al., 2014; Riginos, 2009; Sankaran et al., 2004; Scholes & Archer, 1997; Tomlinson et al., 2019). Differences in seedling growth rates are, in semi-arid to mesic savannas, mostly attributed to competition for soil moisture (February et al., 2013; Kulmatiski et al., 2010), soil nutrients (Riginos, 2009; Tomlinson et al., 2019; van der Waal et al., 2009), a combination of moisture and nutrients, or light (Barbosa et al., 2014; Holl, 1998; Vadigi & Ward, 2013). In our plots representing humid savannas, soil moisture content was unlikely to be the reason for the lower growth observed for tree seedlings in competition with grass because top-soil moisture content was generally high in all plots. Soil moisture was even slightly higher in competition plots and, therefore, likely sufficient for ample water uptake by tree seedlings (Veenendaal, Swaine, Agyeman, et al., 1996). Light intensity was, however, much lower in competition plots (Figure S1), where tree seedling growth was also lower, suggesting that light competition may present a stronger potential mechanism for tree seedling suppression in productive humid tall grass savannas. Relative light levels of 11% in the grass competition plots (while this was about 90% in control) indicate considerable shading of tree seedlings by grasses. Although some forest tree species (the shade bearers in this study) may still maintain considerable growth or even attain maximum growth (Agyeman et al., 1999; Veenendaal, Swaine, Lecha, et al., 1996), such relatively low light levels pose growth limitations to the forest pioneers (Veenendaal, Swaine, Lecha, et al., 1996) and the savanna-transitional species (Gignoux et al., 2016; Ratnam et al., 2011). The low light levels in competition plots also make competition for soil nutrients less likely because tree seedlings do not respond strongly to nutrient limitation in shaded environments (Tomlinson et al., 2012; Vadigi & Ward, 2013, but see Veenendaal, Swaine, Lecha, et al., 1996).

Also, consistent with prediction, grass competition decreased both the concentration and total reserves of tree seedling root non-structural carbohydrates (NSC), possibly reflecting lower photosynthetic carbon assimilation and storage by tree seedlings under tall grasses. Lower root mass of seedlings in competition explains the lower total NSC reserves in roots of seedlings in competition. These findings suggest that the strategy of tree seedlings was not to increase storage of resources in roots in the face shading by tall grasses, as might be the case when belowground competition is involved. Rather, seedlings attempted a more rapid growth response as indicated by a general pattern of higher (albeit non-significant in this study) ratio of soluble sugars to starch (Cruz, & Moreno, 2001; Liu et al., 2018) for seedlings in competition (Figure 3c).

In contrast to the second part of our prediction, we did not find evidence that competition effect was greater for forest compared to savanna-transitional tree functional type, particularly for seedling relative growth rates, mass gain, and root NSC. Competition effect on plant height was, however, higher for the savanna-transitional than forest tree functional type mainly because the former invested much less in height growth, particularly for seedlings in competition with grass, than the latter tree functional type. The forest tree functional type (mainly the species in genus Terminalia) on the other hand, invested more in height growth, with their height in competition being comparable with height attained by savanna-transitional seedlings without competition (Figure S2b,f). This differential investment in height growth reflects known differences in growth strategies between the forest tree functional type (which is more competitive for light on one hand) and savanna-transitional tree functional type (which is more competitive for belowground resources on the other hand) (Boonman et al., 2019; Hoffmann & Franco, 2003; Issifu et al., 2019). Rather, we found that responses to grass competition differed among species across tree functional types. *T. superba* and *T. ivorensis* (both forest species), and *K. senegalensis* and *P. erinaceus* (both savanna-transitional species) responded more strongly (with greater growth declines) to grass competition (Figure S2). Interestingly, species which did not show growth declines to competition; *K. ivorensis*, *K. anthotheca* (forest), and *A. africana*, *D. oliveri* (savanna-transitional species) were slow growing even in the absence of grass competition (Figure S2). The response of this latter group of species is in line with a conservative resource-use strategy (Boonman et al., 2019) and consistent with findings in greenhouse experiments (e.g., Tomlinson et al., 2019) that grass competition has a greater effect on faster-growing species. We thus conclude that grass competition prevents fast-growing species from attaining their full growth potential, but under competition, these species have a similar growth performance to slow-growing species.

We did not find evidence for direct competition effect on seedling survival, corroborating findings of Barbosa et al. (2014) and Vadigi and Ward (2013), but contrasting with other studies (e.gMidgley & Bond, 2001; van der Waal et al., 2009; Ward & Elser, 2011). These contrasting reports can be explained by the higher soil moisture in our plots as opposed to studies in drier savannas (e.g., Midgley & Bond, 2001; van der Waal et al., 2009). Both Barbosa et al. (2014) and Vadigi and Ward (2013) also explained their findings as the effects of a more favorable soil moisture distribution. Also, our plots were unlikely to be nutrient-limited, and the levels of plant-available nutrients found were similar for both competition and no-competition plots (Table S1). Light intensity differed between grass treatments, but the forest pioneers and savanna species, which survival should be affected by lower light, could survive the light intensities in grass competition plots (albeit with reduced growth as discussed earlier). These findings demonstrate that grass competition alone does not directly preclude the establishment of tree seedlings irrespective of tree functional type. Findings also explain why forest species are capable

of establishing in humid savannas (adjacent to forests) under fire exclusion (Charter & Key, 1960; Louppe et al., 1995; Veenendaal et al., 2015).

4.2 | Post-fire seedling survival differs between tree functional types, and a history of grass competition influences post-fire regrowth but not survival

We hypothesized that the suppression of tree seedling growth and storage of carbohydrates by grasses during the wet season reduces the chances of tree seedlings surviving the dry season fire. We predicted that any such adverse effect is greater for the forest than savanna-transitional tree functional types, again linked to trait differences between the two tree functional types. We found that the forest tree functional type was more strongly affected by fire, illustrated by a 15-fold lower survival after fire compared to the savanna-transitional tree functional type (Table 4). Our finding is in line with other studies across forest–savanna boundaries (Gignoux et al., 2009, 2016; Hoffmann et al., 2004, 2012; Issifu et al., 2019) and reflects higher sensitivity of forest tree seedlings to fire. The coupling of fire with the dry season possibly enhanced the effect of fire on forest tree seedlings observed in our study (Cardoso et al., 2016; Hoffmann et al., 2011). Differences in root allocation (and root carbohydrate reserves) prior to the fire event explain the lower post-fire seedling survival of the forest than savanna-transitional tree functional types (Cardoso et al., 2016; Hoffmann et al., 2004; Issifu et al., 2019).

Among savanna-transitional tree seedlings, the probability of a tree seedling surviving fire was related to its height at burning (Figure 4). Such a relationship among savanna juveniles is often attributed to the benefit of growing above flame height, although it may generally take several years before seedlings escape the fire trap (Higgins et al., 2000; Hoffmann et al., 2012; Issifu et al., 2019). It is likely that other strong correlates of seedling height such as root mass (Table S5a,b), and hence non-structural carbohydrate reserves, could explain the higher survival of taller individuals in line with other studies which report higher survival to be dependent on root allocation and carbohydrate storage (Hoffmann et al., 2004; Issifu et al., 2019). The savanna-transitional seedlings survived while nearly all seedlings of the forest tree functional type died. The few forest seedlings that survived the fire were from the Khaya genus (particularly *K. anthotheca*), which seedlings also had least growth during the wet season (Table S2; Figure S2). Thus, for some forest species, being more resource conservative (at least, until enough carbohydrate reserves have been built) ensures a higher survival during the dry season in the savanna, in line with the growth-survival trade-off hypothesis (Boonman et al., 2019; Wright et al., 2004).

We did not find that seedlings with a history of grass competition survived less after fire, which was partly inconsistent with our predictions. If the amount of stored carbohydrates influences post-fire resprout capacity (Hoffmann et al., 2004; Issifu et al., 2019), then reduced growth and carbohydrate storage during the wet season, as a result of grass competition, should lead to reduced post-fire seedling survival. However, this was not the outcome of our study, possibly because carbohydrate reserves in roots, although lower in competition, were still sufficient to guarantee resprouting after fire especially for the savanna-transitional seedlings. Gignoux et al. (2016) observed that savanna tree seedlings can still survive fire at very small sizes. A seedling height of slightly greater than 20 cm appears to guarantee complete post-fire survival for the savanna-transitional seedlings (Figure 4). For forest seedlings with a history of grass competition, we observed a fourfold lower survival after fire, but the interaction term of tree functional type × competition in our statistical model produced non-significant results, possibly due to too few survivors at the end for the forest tree functional type. The legacy effect of competition on tree functional type seedling survival after fire needs to be explored in further studies manipulating different fire intensities.

Although seedling sizes and the amounts of storage reserves prior to fire were apparently sufficient to guarantee survival after fire for the savanna-transitional seedlings, sizes attained (i.e., total plant mass) by seedlings at the end of the dry season (following the post-fire recovery phase) were smaller for seedlings with a history of grass competition. This adverse competition effect was mainly evident in root mass (Figure S5a,b), and therefore, in the total root carbohydrate reserves (Figure S6). Thus, an important outcome of grass competition in the savanna is that it reduces the rate (or extent) of regrowth of burnt tree seedlings and thus contributes to keeping tree recruits only as small plants in pyrogenic humid savannas (Freeman et al., 2017; Hoffmann et al., 2009).

4.3 | Seedling trait responses to grass competition suggest an important role for light competition during the wet season

We observed adjustments in some tree seedling biomass allocation and foraging traits in response to grass competition (Figure S4). Seedlings in grass plots (irrespective of tree functional type) had higher specific stem length (indicating thinner stems), which is often associated with shade avoidance (Schmitt et al., 1999). Seedlings also had higher specific rooting depth under competition, which is needed for foraging for deeper water (Tomlinson et al., 2012). However, seedlings in grass competition did not root more deeply compared to control. Thus, there was no evidence for (the nearly elusive) root niche separation for water uptake between roots of tree seedlings and grasses as proposed for drier savannas (Kulmatiski et al., 2010; Sankaran et al., 2004; Walter, 1971). Irrespective of grass treatment, seedlings of the savanna-transitional TFT rooted more deeply than forest seedlings, reflecting the need for species from dryer environments to forage more deeply for water compared to those from moister environments (Tilman, 1988).

We observed that patterns of larger investment in foraging traits were mainly by *T. superba* and *T. ivorensis*, which increased

investment in aboveground traits in competition to avoid shading, typical of forest pioneers (Veenendaal, Swaine, Lecha, et al., 1996). Both species had greater rooting depth, perhaps, only because they were bigger (Figure S4a). Their bigger sizes may also explain why specific rooting depth was lower in the absence of grass. Thicker roots, which also have additional storage function (Boonman et al., 2019; Issifu et al., 2019), tend to yield lower specific rooting depth values (Tomlinson et al., 2013). Among savanna-transitional species, specific stem length was higher for open-woodland species (*P. erinaceus* and *D. oliveri*) than closed-woodland types (*K. senegalensis* and *A. africana*) (Figure S4e) which suggests differences in shade tolerances even among savanna-transitional tree species (Issifu et al., 2019). Savanna-transitional seedlings increased root mass fraction in competition, but forest species did not. Forest pioneers in grass competition, instead, invested more in stems than leaves or roots in competition, also suggesting an attempt to escape shading at the expense of root allocation.

4.4 | Conclusion and overall implications for the maintenance of the forest–savanna mosaic

Our results show that grass competition suppresses tree seedling growth and root non-structural carbohydrate reserves during the wet season for both forest and savanna-transitional tree functional types, partly consistent with prediction. Contrary to prediction, a history of grass competition does not decrease post-fire tree seedling survival, but does decrease growth and storage of carbohydrates reserves in roots of surviving tree seedlings. Due to differences in fire survival traits, savanna-transitional tree seedlings survive fire far better than forest tree seedlings. Responses of tree seedling morphology traits to grass competition suggest shading by grasses is an important bottleneck to tree seedlings transitioning to bigger size classes.

Overall, these findings have important implications for the maintenance of the forest–savanna mosaic. Regardless of tree functional type, poor growth performance and a lower allocation to root storage represent the fate of tree seedlings in tall grass savanna. This is particularly true for savanna patches within the forest–savanna mosaic, where biomass and cover abundances of herbaceous vegetation are high (Ametsitsi et al., 2020; Issifu et al., 2019; Torello-Raventos et al., 2013). By constituting a demographic bottleneck (Freeman et al., 2017), grass competition contributes to keeping savanna patches open and thereby creating a positive feedback loop that allows for the dominance of grasses (Van Langevelde et al., 2003). Fire tolerance traits (e.g., higher root mass fraction and root NSC) make savanna-transitional tree seedlings more likely, compared to forest tree seedlings, to persist in savanna patches (Issifu et al., 2019). Our findings also show that grass competition alone (without fire) does not preclude the establishment of seedlings of forest tree species in the savanna. Instances of forest seedling recruitment in savanna have often been suggested to result from an abatement of fire (Gignoux et al., 2016; Oliveras &

Malhi, 2016, Mitchard & Flintrop, 2013), but grass competition enhances this effect of fire.

DISCLOSURE STATEMENT

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.prr4xgxkz (Issifu et al., 2021).

ORCID

Hamza Issifu 🔟 https://orcid.org/0000-0003-4466-6157
Vincent Logah 🔟 https://orcid.org/0000-0002-8349-7600

REFERENCES

Agyeman, V. K., Swaine, M. D., & Thompson, J. (1999). Responses of tropical forest tree seedlings to irradiance and the derivation of a light response index. *Journal of Ecology*, *87*, 815–827.

Ametsitsi, G. K. D., van Langevelde, F., Logah, V., Janssen, T., Medina-Vega, J. A., Issifu, H., Ollivier, L., den Hartogh, K., Adjei-Gyapong, T., Adu-Bredu, S., Lloyd, J., & Veenendaal, E. M. (2020). Fixed or mixed? Variation in tree functional types and vegetation structure in a forest-savanna ecotone in West Africa. *Journal of Tropical Ecology*, *36*(4), 133–149. https://doi.org/10.1017/S0266467420000085

Anthelme, F., & Michalet, R. (2009). Grass-to-tree facilitation in an arid grazed environment. *Basic and Applied Ecology*, *10*, 437–446.

Armani, M., Van Langevelde, F., Tomlinson, K. W., Adu-Bredu, S., Djagbletey, G. D., & Veenendaal, E. M. (2018). Compositional patterns of overstorey and understorey woody communities in a forest–savanna boundary in Ghana. *Plant Ecology & Diversity*, *11*, 451–463.

Barbosa, E. R. M., van Langevelde, F., Tomlinson, K. W., Carvalheiro, L. G., Kirkman, K., de Bie, S., & Prins, H. H. T. (2014). Tree species from different functional groups respond differently to environmental changes during establishment. *Oecologia*, *174*, 1345–1357. https://doi.org/10.1007/s00442-013-2853-y

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48. https://doi.org/10.18637/jss.v067.i01

Boonman, C. C., van Langevelde, F., Oliveras, I., Couédon, J., Luijken, N., Martini, D., & Veenendaal, E. M. (2019). On the importance of root traits in seedlings of tropical tree species. *New Phytologist*, *227*(1), 156–167. https://doi.org/10.1111/nph.16370

Cardoso, A. W., Medina-Vega, J. A., Malhi, Y., Adu-Bredu, S., Ametsitsi, G. K. D., Djagbletey, G., Van Langevelde, F., Veenendaal, E., & Oliveras, I. (2016). Winners and losers: tropical forest tree seedling survival across a West African forest-savanna transition. *Ecology and Evolution*, *6*, 3417–3429.

Celis, G., & Jose, S. (2011). Restoring abandoned pasture land with native tree species in Costa Rica: Effects of exotic grass competition and light. *Forest Ecology and Management*, 261, 1598–1604.

Charter, J., & Keay, R. (1960). Assessment of the Olokemeji fire-control experiment (investigation 254) 28 years after institution. *Information Bulletin Forestry Department Nigeria New Series*, 3, 1–32.

Cohen, J. (1977). *Statistical power analysis for the behavioral sciences*. Routledge.

Cruz, A., & Moreno, J. M. (2001). Seasonal course of total non-structural carbohydrates in the lignotuberous Mediterranean-type shrub *Erica australis*. *Oecologia*, 128, 343–350.

Dayamba, S. D., Savadogo, P., Zida, D., Sawadogo, L., Tiveau, D., & Oden, P. C. (2010). Fire temperature and residence time during dry season burning in a Sudanian savanna-woodland of West Africa with implication for seed germination. *Journal of Forestry Research*, 21, 445–450. https://doi.org/10.1007/s11676-010-0095-y

Dubois, M., Gilles, K. A., Hamilton, J. K., Rebers, P. T., & Smith, F. (1956). Colorimetric method for determination of sugars and related substances. *Analytical Chemistry*, 28, 350–356.

Duranceau, M., Ghashghaie, J., Badeck, F., Deleens, E., & Cornic, G. (1999). $\delta^{13}C$ of CO_2 respired in the dark in relation to $\delta^{13}C$ of leaf carbohydrates in *Phaseolus vulgaris* L. under progressive drought. *Plant Cell & Environment*, 22, 515–523.

FAO (Food and Agriculture Organization of the United Nations) (2001). *Soil fertility management in support of food security in Sub-Saharan Africa*. FAO.

February, E. C., Higgins, S. I., Bond, W. J., & Swemmer, L. (2013). Influence of competition and rainfall manipulation on the growth responses of savanna trees and grasses. *Ecology*, 94, 1155–1164. https://doi.org/10.1890/12-0540.1

Freeman, M. E., Vesk, P. A., Murphy, B. P., Cook, G. D., Richards, A. E., & Williams, R. J. (2017). Defining the fire trap: Extension of the persistence equilibrium model in mesic savannas. *Austral Ecology*, 42, 890–899.

Gignoux, J., Konate, S., Lahoreau, G., Le Roux, X., & Simioni, G. (2016). Allocation strategies of savanna and forest tree seedlings in response to fire and shading: outcomes of a field experiment. *Scientific Reports*, 6, 38838. https://doi.org/10.1038/srep38838

Gignoux, J., Lahoreau, G., Julliard, R., & Barot, S. (2009). Establishment and early persistence of tree seedlings in an annually burned savanna. *Journal of Ecology*, 97, 484–495.

Hall, J. B., & Swaine, M. D. (1976). Classification and ecology of closed canopy forest in Ghana. *Journal of Ecology*, 64, 913–951.

Hawthorne, W. D. (1995). *Ecological profiles of Ghanaian forest trees* (p. 345). Oxford Forestry Institute.

Hedges, L. V., & Olkin, I. (1985). *Statistical methods for meta-analysis*. Academic Press.

Higgins, S. I., Bond, W. J., & Trollope, W. S. W. (2000). Fire, resprouting and variability: A recipe for grass-tree coexistence in savanna. *Journal of Ecology*, 88, 213–229. https://doi.org/10.1046/j.1365-2745.2000.00435.x

Hoffmann, W. A., Adasme, R., Haridasan, M., Carvalho, M. T., Geiger, E. L., Pereira, M. A. B., Gotsch, S. G., & Franco, A. C. (2009). Tree top-kill, not mortality, governs the dynamics of alternate stable states at savanna-forest boundaries under frequent fire in central Brazil. *Ecology*, 90, 1326–1337.

Hoffmann, W. A., & Franco, A. C. (2003). Comparative growth analysis of tropical forest and savanna woody plants using phylogenetically independent contrasts. *Journal of Ecology*, 91, 475–484.

Hoffmann, W. A., Geiger, E. L., Gotsch, S. G., Rossatto, D. R., Silva, L. C. R., Lau, O. L., Haridasan, M., & Franco, A. C. (2012). Ecological threshold of savanna-forest boundary: How plant traits, resources, and fire govern the distribution of tropical biomes. *Ecology Letters*, 111, 1461–2248.

Hoffmann, W. A., & Haridasan, M. (2008). The invasive grass, *Melinis minutiflora*, inhibits tree regeneration in a Neotropical savanna. *Austral Ecology*, 33, 29–36.

Hoffmann, W. A., Jaconis, S. Y., Mckinley, K. L., Geiger, E. L., Gotsch, S. G., & Franco, A. C. (2011). Fuels or microclimate? Understanding the drivers of fire feedbacks at savanna–forest boundaries. *Austral Ecology*. https://doi.org/10.1111/j.1442-9993.2011.02324.x

Hoffmann, W. A., Orthen, B., & Franco, A. C. (2004). Constraints to seedling success of savanna and forest trees across the savanna-forest boundary. *Oecologia*, 140, 252–260.

Hoffmann, W. A., & Poorter, H. (2002). Avoiding bias in calculation of relative growth rate. *Annals of Botany*, 80, 37–42.

Holl, D. K. (1998). Effects of above- and below-ground competition of shrubs and grass on *Calophyllum brasiliense* (Camb.) seedling growth in abandoned tropical pasture. *Forest Ecology and Management*, 109, 187–195.

Hopkins, B. (1974). *Forest and savanna* (2nd ed.). Heinemann.

Issifu, H., Ametsitsi, G. K. D., de Vries, L. J., Djagbletey, G. D., Adu-Bredu, S., Vergeer, P., van Langevelde, F., & Veenendaal, E. (2019). Variation in vegetation cover and seedling performance of tree species in a forest-savanna ecotone. *Journal of Tropical Ecology*, 35, 74–82. https://doi.org/10.1017/S0266467418000469

Issifu, H., Vergeer, P., Ametsitsi, G. K. D., Klijn, J., Sartorelli, P., Tanson, M., Bayor, H., Logah, V., van Langevelde, F., & Veenendaal, E. (2021). Data from: Responses of tropical tree seedlings in the forest-savanna boundary to combined effects of grass competition and fire. *Dryad Digital Repository*. https://doi.org/10.5061/dryad.prr4xgxkz

Kulmatiski, A., Beard, K. H., Verweij, R. J. T., & February, E. C. (2010). A depth-controlled tracer technique measures vertical, horizontal and temporal patterns of water use by trees and grasses in a subtropical savanna. *New Phytologist*, 188, 199–209. https://doi.org/10.1111/j.1469-8137.2010.03338.x

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2015). lmerTest Package: tests in linear mixed effects models. *Journal of Statistical Software*, 82, 1–26.

Lenth, R., Singmann, H., Love, J., Buerkner, P., & Herve, M. (2019). *Estimated Marginal Means, aka Least-Squares Means*. R package version 1.4. https://CRAN.R-project.org/package=emmeans

Liu, W., Su, J., Li, S., Lang, S., & Huang, X. (2018). Non-structural carbohydrates regulated by season and species in the subtropical monsoon broadleaved evergreen forest of Yunnan Province, China. *Scientific Reports*, 8, 1083. https://doi.org/10.1038/s41598-018-19271-8

Louppe, D., Oattara, N., & Coulibaly, A. (1995). The effects of brush fires on vegetation: the Aubreville fire plots after 60 years. *Commonwealth Forestry Review*, 74, 288–292.

Mitchard, E. T. A., & Flintrop, C. M. (2013). Woody encroachment and forest degradation in sub-Saharan Africa's woodlands and savannas 1982–2006. *Phil Trans R Soc B*, 368, 20120406. https://doi.org/10.1098/rstb.2012.0406

Midgley, J. J., & Bond, W. J. (2001). A synthesis of the demography of African acacias. *Journal of Tropical Ecology*, 17, 871–886.

Okalebo, J., Gathua, K., & Woomer, P. (1993). *Laboratory methods of soil and plant analysis: A working manual* (p. 88). Tropical Soil Biology and Fertility Programme.

Oliveras, I., & Malhi, Y. (2016). Many shades of green: the dynamic tropical forest–savannah transition zones. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371, 20150308. https://doi.org/10.1098/rstb.2015.0308

Orwa, C., Mutua, A., Kindt, R., Jamnadass, R., & Simons, A. (2009). *Agroforestry Database: a tree reference and selection guide*, version 4.0.

R Development Core Team (2017). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Ratnam, J., Bond, W. J., Fensham, R. J., Hoffmann, W. A., Archibald, S., Lehmann, E. R., Anderson, M. T., Higgins, S. I., & Sankaran, M. (2011). When is a 'forest' a savanna, and why does it matter? *Global Ecology and Biogeography*, 20, 653–660.

Riginos, C. (2009). Grass competition suppresses savanna tree growth across multiple demographic stages. *Ecology*, 90, 335–340.

Sankaran, M., Ratnam, J., & Hanan, N. P. (2004). Tree–grass coexistence in savannas revisited – insights from an examination of assumptions and mechanisms invoked in existing models. *Ecology Letters*, 7(480), 490. https://doi.org/10.1111/j.1461-0248.2004.00596.x

Schmitt, J., Dudley, S. A., & Pigliucci, M. (1999). Manipulative approaches to testing adaptive plasticity: phytochrome-mediated shade-avoidance responses in plants. *American Naturalist*, 154, S43–S54.

Scholes, R. J., & Archer, S. R. (1997). Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics*, 28, 517–544.

Serno, G., & van de Weg, R. F. (1985). *A preliminary assessment of the (available) existing soil information of Nyankpala Agricultural Experiment Station (Tamale, Northern Ghana)* (p. 82). Soil Survey Institute (STIBOKA).

Sun, D., & Dickson, G. R. (1996). The competition effect of *Brachiaria decumbens* on the early growth of direct-seeded trees of *Alphitonia petriei* in Tropical North Australia. *Biotropica*, 28, 272–276.

Swaine, M. D., Hall, J. B., & Lock, J. M. (1976). The forest-savanna boundary in west-central Ghana. *Ghana Journal of Science*, 16, 35–52.

Thomas, G. W. (1982). Exchangeable cations. In A. L. Page, R. H. Miller, & D. R. Keaney (Eds.), *Methods of soil analysis*. Number 9, Part 2. American Society of Agron.

Tilman, D. (1988). *Plant strategies and the dynamics and structure of plant communities*. Princeton University Press.

Tomlinson, K. W., Poorter, L., Sterck, F. J., Borghetti, F., Ward, D., de Bie, S., & van Langevelde, F. (2013). Leaf adaptations of evergreen and deciduous trees of semi-arid and humid savannas on three continents. *Journal of Ecology*, 101, 430–440. https://doi.org/10.1111/1365-2745.12056

Tomlinson, K. W., Sterck, F. J., Barbosa, E. R. M., de Bie, S., Prins, H. H. T., & van Langevelde, F. (2019). Seedling growth of savanna tree species from three continents under grass competition and nutrient limitation in a greenhouse experiment. *Journal of Ecology*, 107, 1051–1066. https://doi.org/10.1111/1365-2745.13085

Tomlinson, K. W., Sterck, F. J., Bongers, F., da Silva, D. A., Barbosa, E. R. M., Ward, D., Bakker, F. T., van Kaauwen, M. P. W., Prins, H. H. T., de Bie, S., & van Langevelde, F. (2012). Biomass partitioning and root morphology of savanna trees across a water gradient. *Journal of Ecology*, 100, 1113–1121.

Torello-Raventos, M., Feldpausch, T. R., Veenendaal, E., Schrodt, F., Saiz, G., Domingues, T. F., Djagbletey, G., Ford, A., Kemp, J., Marimon, B. S., Hur Marimon Junior, B., Lenza, E., Ratter, J. A., Maracahipes, L., Sasaki, D., Sonké, B., Zapfack, L., Taedoumg, H., Villarroel, D., … Lloyd, J. (2013). On the delineation of tropical vegetation types with an emphasis on forest/savanna transitions. *Plant Ecology & Diversity*, 6, 101–137.

Vadigi, S., & Ward, D. (2013). Shade, nutrients, and grass competition are important for tree sapling establishment in a humid savanna. *Ecosphere*, 4, 1–27. https://doi.org/10.1890/ES13-00239.1

Van der Waal, C., de Kroon, H., de Boer, W. F., Heitkönig, I. M. A., Skidmore, A. K., de Knegt, H. J., van Langevelde, F., van Wieren, S. E., Grant, R. C., Page, B. R., Slotow, R., Kohi, E. M., Mwakiwa, E., & Prins, H. H. T. (2009). Water and nutrients alter herbaceous competitive effects on tree seedlings in a semi-arid savanna. *Journal of Ecology*, 97, 430–439. https://doi.org/10.1111/j.1365-2745.2009.01498.x

Van Langevelde, F., de Groot, C., Groen, T. A., Heitkönig, I. M. A., & Gaigher, I. (2014). Effect of patches of woody vegetation on the role of fire in tropical grasslands and savannas. *International Journal of Wildland Fire*, 23, 410–416.

Van Langevelde, F., Van De Vijver, C. A. D. M., Kumar, L., Van De Koppel, J., De Ridder, N., Van Andel, J., Skidmore, A. K., Hearne, J. W., Stroosnijder, L., Bond, W. J., Prins, H. H. T., & Rietkerk, M. (2003). Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology*, 84, 337–350.

Veenendaal, E. M., Swaine, M. D., Agyeman, V. K., Blay, D., Abebrese, I. K., & Mullins, C. E. (1996). Differences in plant and soil water relations in and around a forest gap in West Africa during the dry season may influence seedling establishment and survival. *Journal of Ecology*, 84, 83–90.

Veenendaal, E. M., Swaine, M. D., Lecha, R. T., Walsh, M. F., Abebrese, I. K., & Owusu-Afriyie, K. (1996). Responses of West African forest tree seedlings to irradiance and soil fertility. *Functional Ecology*, 10, 501–511.

Veenendaal, E. M., Torello-Raventos, M., Feldpausch, T. R., Domingues, T. F., Gerard, F., Schrodt, F., Saiz, G., Quesada, C. A., Djagbletey, G., Ford, A., Kemp, J., Marimon, B. S., Marimon-Junior, B. H., Lenza, E., Ratter, J. A., Maracahipes, L., Sasaki, D., Sonké, B., Zapfack, L., … Lloyd, J. (2015). Structural, physiognomic and above-ground biomass variation in savanna-forest transition zones on three continents– how different are co-occurring savanna and forest formations? *Biogeosciences*, 12, 2927–2951.

Walter, H. (1971). *Ecology of tropical and sub-tropical vegetation*. Oliver and Boyd.

Ward, D., & Esler, K. J. (2011). What are the effects of substrate and grass removal on recruitment of *Acacia mellifera* seedlings in a semi-arid environment? *Plant Ecology*, 212, 245–250.

Wickham, H. (2009). *ggplot2: Elegant graphics for data analysis*. Springer-Verlag.

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., … Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, 428, 821–827.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.