A 10-year evaluation of the functional basis for regeneration habitat preference of trees in an African evergreen forest

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ABSTRACT

The spatial distribution of tree juveniles in relation to light environments may reflect species differences in growth, survival, and functional traits and will shape the nature of forest regeneration. Long-term field experiments are important to evaluate this issue because of the potentially very long juvenile period in trees. Here, we combine a 10-year seedling survival–growth data with the results of community ordination and multivariate analyses of functional traits to ask how observed juvenile light guilds are related to species functional traits and seedling performance. We transplanted seedlings at a standardized height of 11 cm into the shaded understory and quantified their growth and survival for 10-years. Using the community-wide stem distribution data, we categorized 33 species including the focal 11 species to understory vs. gap/edge guilds. Then, we determined differences between the two guilds in seedling survival, growth, as well as seed size, adult height, and a series of leaf traits, including toughness and chemical traits (fiber, protein, phenolics, tannins, alkaloids, saponins). Among the 11 non-pioneer species whose seedlings were planted into the understory, there was no significant difference in 10-year survival between light guilds, but species in gap/edge guild tended to achieve greater height than species in the understory guild. The leaf chemical traits of 33 species did not differ between the two juvenile light guilds, but gap/edge species had smaller seeds, taller adults, and tougher leaves than understory species. We used logistic regression as a complementary approach to assess the extent to which plant traits varied between light guilds and the most parsimonious model based on AIC_c ranking included only leaf toughness and had an Akaike weight of 0.52. In addition, across the 11 species planted as seedlings, these traits were not significantly related to survivorship or growth over 10 years. A Principle Components Analysis illustrated associations among traits. We conclude that light guilds in terms of juvenile stem distribution could not be explained by long-term field performance of post-establishment seedlings alone. Earlier seedling stage or later sapling stage may be more important in differentiation of light guilds. For the species examined difference in growth rates could be linked to seed size and adult stature, but not to the adult leaf chemical traits considered. These results suggest the importance of examining ontogenetic shifts and relationships among functional traits for a better understanding of regeneration strategies of tropical trees.

1. Introduction

Canopy gaps create environmental heterogeneities, which in turn contribute to the maintenance of tree species diversity (Denslow, 1987; Brokaw and Busing, 2000; Wright, 2002; Obiri and Lawes, 2004). Historically, forest ecologists have recognized species differences in gap dependency based on observation of the relative abundance of stems in gaps vs. shaded understory (Shirley, 1943). While tree species are often classified into a few of juvenile light guilds, this is a continuum (Grubb, 1996; Poorter et al., 2005; Gilbert et al., 2006). At one end are pioneers that specialize on gaps for regeneration, growth, and reproduction, while at the other extreme are highly shade-tolerant species whose saplings are preferentially distributed in the shaded understory (Hubbell and Foster, 1986; Swaine and Whitmore, 1988; Dalling and Hubbell, 2002). However, most tree species have intermediate light

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requirements for regeneration (Augspurger, 1984; Wright et al., 2003). Furthermore, dispersal limitation and stochasticity may play an important role in determining which species arrive and persist in a given gap (Hubbell et al., 1999; Harms et al., 2000; Brokaw and Busing, 2000). Still, contrasting these groups is useful for determining suites of traits that vary in concert and for providing a mechanistic understanding of the apparent sorting of tree species along light gradients (Westoby and Wright, 2006). The next logical challenge to ecologists is to identify the functional traits that contribute to observed differences in light guilds of juveniles and adults among coexisting tree species (Poorter, 2007; Poorter et al., in review).

Spatial distributions of saplings along light gradients are shaped as a cumulative consequence of three life stages: seeds, young seedlings, and older established seedlings. A species' ability to colonize gaps is thought to be achieved by producing a large number of small seeds or maintaining these seeds in the soil seed bank (Dalling et al., 2002). Light requirements for germination and early seedling survival strongly constrain the spatial distribution of seedlings during the first stages of life and have lasting effects on sapling distributions (Augspurger, 1984; Pearson et al., 2002). Survival and growth of established seedlings further modify the distribution patterns of saplings relative to treefall gaps. Unfortunately, this last stage is the least well understood, as most existing comparative or community-wide studies of growth and survival are relatively short-term and limited to early seedling (Augspurger, 1984; Kitajima, 1994; Poorter, 1999; Gilbert et al., 2006) or sapling stages (e.g., with stems >2 m tall and 1 cm DBH, Hubbell and Foster, 1986; Poorter et al., 2003). There are few data on the critical transitional stage from seedlings to saplings. The short duration of many comparative studies is unfortunate, because recruitment of seedlings to saplings can take many years especially in the shaded understory where growth rates are extremely slow (Connell and Green, 2000; Osada and Takeda, 2003).

In this paper we report growth and survival of experimentally planted seedlings in the understory over a 10-year period along with other selected functional traits for tree species in a moist-evergreen forest at Kibale National Park, Uganda. Our two main objectives are to explore (1) how species contrasting in stem distribution between understory vs. gap/edge differ in growth and survival in the understory during the seedling–sapling transition, and (2) what additional functional traits are associated with preferred regeneration habitats among tree species in Kibale. For functional traits, we examine seed size, maximum adult height, and adult leaf traits. These are traits often examined in recent analyses of functional traits encompassing multiple sites and species in the Neotropics (Wright et al., 2007; Poorter et al., in review). Our report is the first such analysis that we are aware of for a wet African forest to explore functional traits relationships with juvenile distribution, growth, and survival.

2. Materials and methods

2.1. Study site

This study was conducted in Kibale National Park in western Uganda (795 km^2; 0° 13′–0° 41′N and 30° 19′–30° 32′E; Chapman et al., 1997). Kibale is a mid-altitude moist-evergreen forest with a relatively species poor flora (68 tree species were identified in 4.8 ha of vegetation sampling; Chapman et al., 1997). The study was conducted at Kanyawara (∼1500 m elevation), which receives approximately 1719 mm of rainfall annually (1990–2006) that peaks during two rainy seasons and is well disperse throughout the year, falling on average 166 days per year. Because of this well dispersed rain, the forest floor rarely dries and wilting of

understory herbs is infrequent. The annual mean daily maximum temperature of 23.1 °C and minimum temperature of 15.1 °C. The soils of the region are dark gray to red sandy loams or sandy clays and the fertility of the soils range from fair to good (for details on soils see Struhsaker, 1997).

The forest is classified as transitional between lowland rain and montane forest with a canopy height averaging 25–30 m, and natural disturbances leading to treefall gaps are common (Howard, 1991). The forest is notable for its lack of aggressive colonizers (e.g., *Musanga* spp., *Cercropia* spp.) typical of other tropical regions, but other early successional species are present (e.g., *Albizia grandibracteata*, *Polyscias fulva*, *Trema orientalis*; Zanne and Chapman, 2005).

2.2. Species and assessment of habitat association type

The determination of light guild is difficult without long-term monitoring of growth and mortality of marked individuals. Hence, statistically significant bias of stem distribution to gaps vs. shaded understory (Welden et al., 1991), as well as expert opinions based on field observations (Mostacedo and Fredericksen, 1999), are still commonly used methods for assessing light guilds. Poorter et al. (2005) developed a method to assess juvenile light demand as continuous variable derived from logistic regression of crown-exposure index against individual height. The relationships of functional traits and juvenile vital rates achieve using this index is similar to their relationships with light guild classes based on expert opinions (Poorter and Kitajima, 2007). In this paper, we used two means of assessing species light guilds, one based on spatial bias of stem distribution to forest understory vs. gap/edge (Zanne and Chapman, 2005), and another based on expert opinion of how common seedlings and saplings were in the shaded understory.

The statistical assessment of stem distribution described in detail by Zanne and Chapman (2005) is briefly summarized here. Trees and shrubs of all size classes were enumerated in 24 small plots (5 m × 5 m) in each of four habitats (closed canopy forest, treefall gaps, forest/grassland edge, and grassland; N = 96 plots). For gap plots, treefall gaps were located throughout the forest in which the crown of the fallen trees had no fine branches and leaves remaining, yet little decay of the bole had occurred. Gap size averaged 300 m^2 (range: 39–636 m^2). Since few large trees and shrubs >2 m tall occurred in small plots (5 m × 5 m), trees and shrubs of larger sizes were also sampled in large plots (10 m × 50 m) randomly located in forest and grassland habitats (not gap and edge habitats). To determine confidence intervals of stem counts in different habitat types, the data were randomized with a custom-written program in R 1.6.2 (R Development Core Team, 2002). The natural structure of the data within the plots was maintained by randomly reassigning plots to habitats without replacement for 10,000 iterations. Significant species associations with a habitat were reported if observed stem counts were more extreme than the 95% confidence limits. For 10 species not found in these habitat plots or found only rarely (Table 2), habitat associations were based on reports in Eggeling and Dale (1952), Polhill (1952), Hamilton (1991), Katende et al. (1995), and Lwanga (1996). For the analysis reported here, gap and edge associated species were combined as "gap/edge" species in contrast to "understory" species for more balanced sample size between groups.

Our second method of assessing juvenile light guilds is based on the abundance of seedlings and saplings in shaded understories (common, frequent, or rare in the understory). This relied on data of small individuals (height <0.5 m) in the plot data of Zanne and Chapman (2005) as well as published information (Eggeling and Dale, 1952; Polhill, 1952; Hamilton, 1991; Katende et al., 1995; Lwanga, 1996), and an independent assessment made by Peter Grubb based on his experiences with seedlings and sapling in

Table 1
The 10-year survival and mean height growth of seedlings transplanted at a common size of 11 cm along understory transects

	Stem distribution bias	Seedlings and saplings in shade	# Planted	Survival (%)	Growth (cm)
Balanites wilsoniana	Understory	Common	54	6	18
Chrysophyllum gorungosanum	**Understory**	Common	59	29	36
Uvariopsis congensis	**Understory**	Common	64	63	43
Symphonia globulifera	**Understory**	Common	11	27	55
Mimusops bagshawei	**Understory**	Common	57	30	57
Cordia millenii	Gap/edge	Common	13	40	55
Monodora myristica	**Gap/edge**	Often	22	50	37
Tabernaemontana sp.	**Gap/edge**	Often	9	33	71
Warbugia stuhlmanni	Gap/edge	Rare	16	50	66
Ficus exasperata	Gap/edge	Rare	27	7	144
Pseudospondias microcarpa	**Gap/edge**	Rare	64	55	178
Understory	Summary		49	31	42
Gap/edge	Summary		25	39	92
Common	Summary		43	33	44
Often	Summary		16	42	54
Rare	Summary		36	37	129

Species are grouped according to their preferred light guilds based on stem distributions and seedling and sapling abundance in shade (see Section 2). Bold letters for stem distribution bias indicate the species reported in Zanne and Chapman (2005).

Kibale (P. Grubb, personal communication). All 15 "understory" species are common as seedling and saplings in shade, whereas 9 of 18 "gap/edge" species are classified to be "common" in shade as seedlings (Table 2). This latter group corresponds to "partial shade-tolerant" species that can establish in shade, but strongly require gaps to reach maturity (Poorter and Kitajima, 2007). The remaining "gap/edge" species are observed only "often" or "rare" in shaded understories as seedlings and saplings, corresponding to pioneers or open swamp species (P. Grubb personal communication). While the analysis using the three guild groups yielded similar trends, the small number of species in each group limits the statistical power. Thus, we report only the results from comparing two guilds. Approximately the same number of species from each guild was used for seedling transplant experiment (Table 1). For examination of the relationships of seed mass, adult height, and leaf traits with light guilds, we included an additional 22 common tree species in Kibale, plus the 11 species used in the seedling experiment (Table 2).

2.3. Seedlings transplanted to forest understory

Seedlings were grown from seeds in a nursery under a semi-transparent roof. Seeds germinated on wet cloth towels were planted into individual pots (250 ml) in topsoil collected from the forest and seedlings were grown in the nursery (see Chapman and Chapman, 1996 for details). When seedlings were approximately 11 cm tall (2–3 months after germination), they were transplanted at 5 m intervals along 100–200 m transects (10 in total) that were separated from each other by approximately 100 m. The species available for planting on a specific date were randomly assigned to transect location, avoiding locations within 20 m of any canopy gaps on a transect. Seedlings were transported to the field in the pots they grew in and then bare-rooted seedlings were planted into holes dug in the soil and were watered on the day of planting only. Seedlings that died in the first month were replaced. Transplanting took place between October 1990 and May 1992 as nursery-grown seedlings became available, with most (70%) being transplanted during 1990–1991. As our objective was to study the survival and growth of established seedlings rather than very young seedlings, this experimental protocol circumvented the vulnerable emerging-seedling stage and allowed comparison of growth and survival across species. Plants were revisited opportunistically during the 10-year experiment to monitor survival, causes of death, and growth. Here, growth was assessed by height, and survival was assessed by %survival at the end of the study.

2.4. Measurement of seed size, adult leaf traits, and adult stature

Seed size was estimated at the mean length of approximately 30 seeds per species, typically collected from five fruiting trees. The chemical and physical leaf characteristics of adult leaves were determined using leaves collected typically from three locations in the middle of adult crowns from one adult tree that was found in a habitat that was thought to represent the species preferred habitat (an analysis of interspecific variation in the chemical properties of leaves at this site can be found in Chapman et al., 2003). Although changes in light environment and ontogenetic shifts can cause changes in leaf traits, adult leaf traits and juvenile functional traits may be linked *via* life history correlations (Poorter, 2007; Wright et al., 2007). Leaves were dried, stored in sealed plastic bags, transported to North America, and ground in a Wiley mill to pass through a 1-mm mesh screen. Protein (estimated from nitrogen content), fiber (ADF), saponins, and presence/absence of alkaloids, and cyanogenic glycosides were determined following the procedures outlined in Chapman and Chapman (2002). Nitrogen was evaluated because of its importance to plants and because many herbivores select food bases on protein content. Fiber represents an important structural element of leaves and often serves to deter herbivore foraging. The secondary compounds that were selected are a small proportion of the great diversity of compounds plants use to defend their leaves. The selected compounds were those that have documented impact of herbivore foraging and that we were equipped to analyze (Chapman and Chapman, 2002). None of the study species had cyanogenic glycosides. Leaf fracture toughness, tannins, and total phenolic estimates were obtained from Dominy (2001). Maximum adult height data were derived from the literature (Eggeling and Dale, 1952; Polhill, 1952; Hamilton, 1991; Katende et al., 1995; Lwanga, 1996).

2.5. Statistical analysis

Our main objective was to compare growth, survival, and functional traits of species between light guilds. Ten-year survival and growth of seedlings, as well as functional traits, were compared between the two guilds with a two-tailed t-test with the degrees of freedom appropriately adjusted if the variances of the populations being compared were not equal. Survival and growth were correlated with functional traits.

Furthermore, to avoid type 1 error associated with multiple t-tests of the same hypothesis (i.e., difference between two light

Table 2

Functional traits (seed size, maximum adult height, and adult leaf traits) of 33 common tree species in Kibale National Park, Uganda, including 11 species used in the seedling transplanting experiment (marked with (*))

Species	Stem distribution	Seedlings and saplings In shade	Seed Size (cm)	Adult height (m)	Fiber (%)	Protein (mg/g)	Saponins (mm)	Alkaloids P/A	Phenolics (%)	Tannins (%)	Toughness (J/m²)
Symphonia globulifera[*]	**Understory**	Common	7.05	40	30.6	11.2	14		0.5	1.7	580
Newtonia buchananii	**Understory**	Common	5.8	50	38.5	17.7	5	0	1.87	7.2	438
Balanites wilsoniana[*]	Understory	Common	4.77	35					0.67	0	892
Lovoa swynnertonii	Understory	Common	4.5	40	52.9	14.2	5	0	0.7	1	521
Strombosia scheffleri	**Understory**	Common	3.66	30	31.4	20.1	19	0	0.13	0	881
Rothmannia urcelliformis	**Understory**	Common	3.54	10	23.7	17.2	11	0	0.17	0	461
Cola gigantea	Understory	Common	2.85	50							
Chrysophyllum gorungosanum[*]	**Understory**	Common	2.45	45	38.8	17.1	14	0	2.08	5.7	1022
Mimusops bagshawei[*]	**Understory**	Common	1.54	40	41	10.6	3	0	2.89	6	1024
Pouteria altissima	**Understory**	Common	1.19	50	41.5	16.8	12	0	3.5	3.8	1165
Uvariopsis congensis[*]	**Understory**	Common	1.12	15	33.9	20.6	0.5	1	0.13	0	272
Blighia unijugata	**Understory**	Common	1.01	20	35.6	15	5	0	0.28	0	1720
Trilepisium madagascariense	**Understory**	Common	0.74	30	27.8	19	14	0	1.41	3.5	1508
Euadenia eminens	**Understory**	Common	0.67	20					0.07	0	267
Diospyros abyssinica	**Understory**	Common	0.44	30	27	21.1	2	1	2.26	0	489
Cordia millenii[*]	**Gap/edge**	Common	4.12	45	46.5	13	2	0			
Lepisanthes senegalensis	**Gap/edge**	Common	1.5	15	44.8	12.6	5	0	1.72	3.6	596
Antiaris toxicaria	**Gap/edge**	Common	0.73	45	38.3	27.2	10	0	1.87	3	726
Dovyalis macrocalyx	**Gap/edge**	Common	0.44	6	42.3	10.2	14	0			
Teclea nobilis	**Gap/edge**	Common	0.44	25	26.8	20.4	5	1	0.61	0	282
Coffea eugenoides	**Gap/edge**	Common	0.36	4					1.37	0	602
Celtis africana	**Gap/edge**	Common	0.24	30	14.8	23.7	5	0	0.41	0.5	292
Fagaropsis angolensis	**Gap/edge**	Common	0.21	30	11.5	24.8	10	1			
Pancovia sp. near *turbinata*	**Gap/edge**	Common		20	48.1	18.1	0	0	1.65	1.1	361
Monodora myristica[*]	**Gap/edge**	Often	2.62	30	37	13.9	16	0	0.33	0	1110
Tabernaemontana sp.[*]	**Gap/edge**	Often	0.75	15	33.2	24.7	15	0			
Cordia abyssinica	Gap/edge	Rare	1.92	15					0.33	0	462
Pseudospondias microcarpa[*]	**Gap/edge**	Rare	1.41	30	36.1	12.9	12	0	1.67	5.6	300
Warbugia stuhlmanni[*]	Gap/edge	Rare	0.75	40	37.9	12.1	15	1			
Trema orientalis	Gap/edge	Rare	0.1	15					0.8	0	245
Ficus exasperata[*]	Gap/edge	Rare	0.01	25	22.2	26.1	12	0	0.39	0.2	515
Neoboutonia macrocalyx	Gap/edge	Rare[**]	0.68	15	23.8	20.1	8	0			
Macaranga schweinfurthii	Gap/edge	Rare[**]	0.31	15	25.2	13.5	16	0	5.06	35.6	673
Understory	Summary		2.76	33.67	35.23	16.72	8.71	0.18	1.19	2.06	802.86
Gap/edge	Summary		0.98	23.33	32.57	18.22	9.67	0.20	1.35	4.13	513.67
Common	Summary		2.15	30.21	34.79	17.53	7.78	0.21	1.21	1.86	704.95
Often	Summary		1.69	22.50	35.10	19.30	15.50	0.00	0.33	0.00	1110.00
Rare	Summary		0.37	22.00	27.28	17.95	12.75	0.25	2.08	11.93	477.67

Species are sorted by stem distribution to understory vs. gap/edge (bold: reported in Zanne and Chapman, 2005), expert opinion on seedling and sapling abundance in shade, and seed size (large to small). Adult leaf chemistry is on a dry mass basis (fiber, protein), relative assay of a unit dry mass (mm of foam rise for saponin, % of gallic acid standard for phenolics, and % of quebracho tannin standard for tannin), or presence/absence (alkaloids; 1: present, 0: absent). Values are missing when not tested. (**) open swamp species.

guilds); presence/absence in shade was examined as a function of the various leaf traits using logistic regression. We used seven candidate models of leaf characters (starting with all variables and progressively removing the least significant variable) and ranked them according to Akaike's Information Criterion (AIC_c) adjusted for small sample size (Anderson et al., 2000). Akaike weights are standardized to a scale of 0–1 and give the approximate probability that a model "i" is the best model in the set of models considered. The 20 species in which all leaf traits were quantified were included in the models.

Multivariate trait associations were examined using Principal Components Analyses (PCA) with varimax rotation and all variables were log transformed. As we did not have data for all variables for all species, a compromise between species number and variable inclusion was made; an analysis containing eight variables and 19 species was the best compromise allowing the most species and variables. Statistical analyses were done with SPSS 14.0 (SPSS Inc., Chicago, IL) and JMP v 3.0 (SAS Institute, Cary, NC).

3. Results

3.1. Seedling survival and growth in the understory

Over the 10 years, survivorship in the forest understory was extremely variable among regeneration strategies and species

(range 6–63%), averaging 35.5% (S.D. = 18.5%; Table 1). There were no differences in 10-year survival between understory vs. gap/edge species ($t = -0.712$, d.f. = 9, $p = 0.494$), or between species that were common vs. rare as seedlings in shade ($t = -0.561$, d.f. = 9, $p = 0.589$; Table 1). However, there was a tendency for gap/edge species to grow faster than understory species ($t = -2.094$, d.f. = 5.9, $p = 0.082$), as well as a trend for species whose seedlings were rare in shade to grow faster than those whose seedlings were commonly observed in shade ($t = -2.138$, d.f. = 3.3, $p = 0.114$). This latter result is particularly interesting, given that growth was measured for 10 years in the shaded understory, without any conspicuous gap-opening over these seedlings.

3.2. Seed size, adult stature, and leaf traits

Species classified as belonging to the edge/gap guild had significantly smaller seeds ($t = -3.00$, d.f. = 20.4, $p = 0.007$) and smaller maximum adult height ($t = 2.357$, d.f. = 31, $p = 0.025$) than understory species. In contrast, there was no difference between species common and those rare as juveniles in shade (seed size $t = 1.164$, d.f. = 30, $p = 0.253$; adult height $t = 0.729$, d.f. = 31, $p = 0.471$; Table 2).

Height growth of 11 species in the understory was only weakly and negatively correlated with seed size ($r = -0.50$, $p = 0.11$) and was not correlated with maximum adult height. Five species tested

Table 3
Eigenvalues and factor loadings for seed size, adult height, and leaf traits for the first four axes using Principal Components Analyses for 19 species for which all data were available

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	1.98	1.98	1.54	1.22
Cumulative % variance	24.7	49.4	68.7	83.9
Seed size (cm)	**0.85**	−0.22	0.13	0.14
Protein (mg g^{-1})	**−0.80**	−0.27	−0.18	0.38
Fiber (%)	**0.75**	0.19	−0.03	0.40
Phenolics (%)	−0.05	**0.95**	0.06	0.18
Tannins (%)	0.13	**0.93**	0.18	−0.01
Saponins (mm)	0.04	0.16	**0.90**	−0.03
Toughness (J m^{-2})	0.13	0.05	**0.79**	0.20
Maximum adult height (m)	0.11	0.14	0.17	**0.90**

Numbers in bold denote strong factor loadings (>0.50).

positive for alkaloids; three were gap/edge species, two were understory species, and four and one were common and rare as juveniles in shade, respectively. Seed size was weakly positively correlated with fiber ($r = 0.38$, $p = 0.059$) and negatively correlated with protein contents of adult leaves ($r = −0.39$, $p = 0.049$), which were negatively correlated with each other ($r = −0.55$, $p = 0.003$). However, no significant differences were found between light guilds in any of the chemical leaf characteristics (saponins, phenolics, tannins, $p > 0.4$ in all cases). Understory species though had tougher leaves than gap/edge species ($t = −2.41$, $p = 0.028$), as did species whose juveniles are common in shade relative to those whose juveniles are rare in shade ($t = −2.06$, $p = 0.052$).

We used logistic regression as a complementary approach to these t-tests to assess the extent to which plant traits varied between light guilds. This revealed a significant difference for toughness, but not for any other the other leaf characteristics (all chemical traits $p > 0.4$). The most parsimonious model based on AIC$_c$ ranking included only leaf toughness and had an Akaike weight of 0.52. No significant correlations were found between the leaf chemical traits and seedling survival or growth over 10 years in the understory.

In a PCA of plant traits, seed size and fiber were positively and protein was negatively related to Axis 1 and phenolics and tannins were positively related to Axis 2 (Table 3). Axis 1 and Axis 2 explain an equal proportion (24.7%) of total variance, while Axis 3 explains an additional 19.8%. Saponins and leaf toughness were positively related to Axis 3 and adult height was positively related to Axis 4. None of the axes were correlated to seedling growth or survival, which could be due to limited statistical power from low sample sizes.

4. Discussion

Overall, the two light guilds based on stem distribution bias to understory vs. gap/edge differed only in three key functional traits. Surprisingly, understory-survival of post-establishment seedlings during 10 years showed no obvious relationship with light guilds in shade. However, there was a tendency for gap/edge species to grow faster than understory species in the shaded understory. Similarly, 33 species did not show difference in relation to light guilds with respect to leaf chemical traits (fiber, protein, phenolics, tannins, alkaloids, saponins), except that gap/edge species had smaller seeds, shorter adults, and less tough leaves compared to understory species. However, these traits were not significantly related to survivorship or growth of seedlings transplanted to the understory.

Several aspects specific to this study may have contributed to some of these unpredicted results. First, these seedlings were transplanted at the post-establishment stage (2–3 months after

germination) at a common height of 11 cm, and any seedlings that died within the first month were replaced. It is possible that mortality during and immediately after germination (Augspurger, 1984; Swaine and Whitmore, 1988), rather than mortality at the post-establishment phase, is the important discriminating factor for seedling establishment in shade vs. gap/edge. Also, classification of species into just two light guilds is too simple for assessment of regeneration light requirements. Unfortunately, the number of individuals and samples included in our analysis restrict use of continuous index for light demands, such as the average crown-exposure index at a given height (Poorter et al., 2005; Poorter, 2007) or one based on the growth and survival of sufficient number of individuals (Gilbert et al., 2006).

The finding of greater height growth for seedlings of gap/edge species than understory species, especially those rarely found in shade as juveniles, is in agreement with other results from studies of the early seedling stage (Kitajima, 1994; Dalling et al., 1999; Poorter, 1999; Walters and Reich, 1999). This suggests that species-specific traits that enhance growth rates, such as high specific leaf area and biomass allocation to shoot extension, may be the main determinants of height growth across light gradients (Kitajima, 1996; Walters and Reich, 1999; Poorter, 2001; Poorter et al., 2003). Although some suggest that this tendency (i.e., slower growth for more shade-tolerant species) disappear after early seed-reserve dependent period (Sack and Grubb, 2001, 2003), we found that cumulative height growth over 10 years was continuously greater in shade for gap/edge species than understory species.

Seed size is considered an important correlate of life history and shade tolerance (Pearson et al., 2002; Rose and Poorter, 2003; Moles and Westoby, 2004). In agreement with this, mean seed size was greater for the understory guild than for in gap/edge guild in Kibale. In a separate experiment addressing early seedling growth and survival of 24 tree and shrub species in Kibale, Zanne (2003) found a positive correlation between seed mass and survival, but not between seed mass and growth rates for young seedlings, regardless of whether seedlings were planted in the understory, gaps, edges, or grasslands. However, in our study seed size was not significantly correlated with post-establishment survival and growth during the 10-year period. One likely explanation is that seed size advantage disappears with time (Sack and Grubb, 2001, 2003; Moles and Westoby, 2004). Also, 11 species may insufficient to detect seed size relationship with survival, growth, and adult height. Among four functional traits (seed mass, wood density, specific leaf area, and maximum adult height), seed mass is the best correlate of diameter growth rates and survival rates of stems >10 cm in a data set including over 200 species of neotropical tree species from five sites (Poorter et al., in review). In the same data set, seed size is positively correlated with adult height consistently across sites (Wright et al., 2007). The relationship of seed size with adult height may be triangular, however; short species are constrained from having large seeds, while tall species may have large or small seeds (Grubb et al., 2005). In future research consideration should be made of the fact that, unlike tropical forests of many other regions, African forests still have abundant large bodied seed dispersers, such as elephants (Loxodonta africana) and chimpanzees (Pan troglodytes).

Because adult height should be positively correlated with adult light environment (Thomas and Bazzaz, 1999), it is a surrogate for adult light niche that can be compared to juvenile light niche (Poorter, 2007). In a Bolivian moist forest, average crown-exposure index for 2 m tall samplings was greater for species with taller adults, suggesting that species more light demanding as adults tend to also be more light demanding as juveniles (Poorter, 2007). In contrast, among 33 species in our study, mean adult height was

significantly higher for understory than gap/edge species. In the Bolivian site and Kibale, there is a wide variation in adult height within understory guild. However, the upper canopy layer is dominated by more pioneer species in the Bolivian site than in Kibale, perhaps reflecting difference in historical disturbance regime and seasonality. In the evergreen forest of Kibale, treefall gaps tend to be small and filled by horizontal expansion of canopy species rather than by pioneers (Zanne and Chapman, 2005).

Other studies have shown that adult leaf traits, such as specific leaf area (=leaf area per unit leaf mass), nitrogen contents, and photosynthetic rates, are significantly correlated not only with adult light environment (Thomas and Bazzaz, 1999, in SE Asian forest), but even more strongly so with juvenile light environment (Poorter, 2007; in a seasonal Bolivian forest). Our study did not examine specific leaf area, but protein content (i.e., nitrogen) which should be positively correlated with photosynthetic rates, was unrelated to adult height. In a closer examination, however, the five highest protein content values, indicative of high photosynthetic rates per unit leaf mass, all belong to species in the gap/edge guild (Table 2).

Poorter (2007) found that adult leaf traits were more strongly constrained by juvenile light niche than by the adult light niche. In contrast, the only adult leaf trait that differed between the two light guilds in Kibale was fracture toughness. Indeed, this may reflect selection for greater leaf toughness in seedlings of shade-tolerant species. Alvarez-Clare and Kitajima (2007) found that seedling leaves have greater fracture toughness for shade-tolerant species in a Panamanian forest. Zanne (2003) studied young seedlings in Kibale and found that percent leaf herbivory was negatively related to cotyledon toughness, which is related to leaf turnover. Furthermore, understory species had lower leaf herbivory than open-associated species across different planting habitats, and seedlings growing in forest had lower leaf herbivory than seedlings growing in gaps. In contrast to toughness, chemical defense traits, including phenolics and tannins that are known to be correlated with juvenile light demands elsewhere (Coley, 1983; Kurokawa et al., 2004), were uncorrelated with juvenile light demands or adult height in this study. Although we expected possible relationships between adult leaf characteristics and juvenile functional traits, such relationships may be weak if leaf traits change with size, ontogeny, and light environments that the species experience as adults (Osada et al., 2002; Poorter et al., 2005). However, for the Neotropical trees studied by Dominy et al. (2003), adult canopy leaves and understory sapling leaves showed significant correlation for phenolics ($r = 0.76$, $p < 0.0001$, $N = 28$ spp.), but only weak and non-significant correlations for tannins ($r = 0.53$), proteins ($r = 0.43$), and fracture toughness of leaf lamina ($r = 0.43$).

5. Conclusions

In conclusion, post-establishment seedlings of understory and gap/edge guilds in Kibale showed only weak difference in height growth, but not in survival in shade over 10 years. The equally high survival of post-establishment seedlings of species in understory and gap/edge guilds may indicate that their difference in stem distributions along light gradients may be created at an earlier regeneration stage. Alternatively, gaps may be the more forbidding condition, i.e., light guilds may reflect species difference in growth rate and survival in gaps and forest edges, rather than species differences in survival and growth in shade. The tendency of gap/edge species to grow taller in shade may reflect strong selection for rapid height growth to be competitive in gap/edge environments. Of the functional traits we examined, seed size, adult height, and leaf toughness differed between understory and gap/edge guilds in

the expected directions. Of these, only seed size was correlated with seedling height growth in shade (negative correlation). Kibale differed from Asian and Neotropical forests in terms of adult height relationship with juvenile guilds and functional traits, perhaps reflecting differences in historical disturbance regimes and regeneration strategy of dominant trees. Constraints of statistical power limited our analysis to contrasts between two broad guilds based on overall stem distribution patterns. Regeneration strategies clearly need to be considered in a broader ecological context (i.e., beyond understory and gap specialists) and the extent to which ontogenetic shifts influence light niches and coexistence needs to be closely evaluated.

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