Diversity of woody species in forest, treefall gaps, and edge in Kibale National Park, Uganda

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Abstract

If specialization influences species presence, then high tropical tree and shrub diversity should correspond with high environmental heterogeneity. Such heterogeneity may be found among different successional communities (i.e., canopy types). We explore species associations in three forest-dominated canopy types, forest, gap, and edge, in Kibale National Park, Uganda and determine environmental, soil and light, differences among canopy types. To determine the strength of differences among forested canopy types, they are also compared to grasslands. Tree and shrub density and species richness using rarefaction analysis were determined based on data from 24 small plots (5 × 5 m) in all four canopy types and 16 large plots (10 × 50 m) in forest and grassland canopy types. Environmental variables were determined along 10 (20 m) transects in the four canopy types. Using analysis of variance and principal components analysis, we demonstrate that forest and gap environments had similar soils, but forest had lower light levels than gap. We also found that grassland and edge were more similar to one another than to forest and gap, but differed in a number of important biotic and abiotic factors controlling soil water availability (e.g., edge had higher root length density of small roots <2 mm diameter in the top 20 cm than grassland). Using principal components analysis to assess similarities in community composition, we demonstrate that gap and forest had indistinguishable communities and that edge was similar to but distinct from both communities. Complete species turnover only occurred between grassland and the three forested canopy types. Even though overall community composition was similar in the three forested canopy types, in analyses of individual species using randomization tests, many common species were most frequently found in only one canopy type; these patterns held across size classes. These results suggest that despite differences among environments, community composition was similar among forested canopy types, which are likely intergrading into one another. Interestingly, individual species are more frequently found in a single canopy type, indicating species specialization.

Introduction

Tropical rain forests are noted for their extraordinary species diversity (Connell 1978; Phillips et al. 1994; Wright 2002) with many such forests containing well over 100 tree species per ha, and as many as 283 species per ha (Phillips et al. 1994). These levels of diversity have spawned numerous studies examining what permits and maintains coexistence (Grubb 1977, 1996; Connell 1978;

Hubbell 1997; Brokaw and Busing 2000; Harms et al. 2001). A number of both deterministic and stochastic processes have been proposed to explain the maintenance of such high levels of diversity (Wright 2002).

Species specialization in landscapes that are heterogeneous over space and time is one suggested deterministic mechanisms allowing coexistence (Grubb 1977; Chesson and Huntly 1997; Clark et al. 1999; Wright 2002). Grubb (1977) argued that environmental heterogeneity might be particularly important at the regeneration stage. Species with different regeneration specializations may establish under different conditions but later share contiguous canopy positions as adults, thus increasing diversity (Wright 2002).

In the literature, specialization has found some measure of support (Grubb 1977; Wright 2002), but others have failed to find strong evidence of specialization (Hubbell and Foster 1986; Webb and Peart 2000; Harms et al. 2001). In a study in Panama, Harms et al. (2001) found some species to be differentially distributed across habitats (less than one-third), but most showed little affinity to a particular habitat, suggesting specialization is unlikely to be a mechanism maintaining high tropical tree diversity. Most of these studies defined habitats based on underlying environmental gradients (e.g., topography).

We explore the degree to which associations between species and canopy types (defined by the vegetation) may be occurring for trees and shrubs in Kibale National Park, Uganda. We examine differences at two levels: among several forested canopy types examining (α diversity); and between these forested canopy types and grassland canopy type (β diversity). The second level allows us to use grassland as an outgroup and examine how strong differences are among forested communities when compared to a dissimilar community.

To evaluate species distributions across canopy types varying environmentally, we take several approaches. First, we examine how environmental variables differ among canopy types. An understanding of underlying canopy type differences is helpful in understanding potential mechanisms influencing species distributions. Second, we examine whether tree and shrub community differences occur across canopy types. Communities that differ greatly from one another in species composition suggest strong species associations to particular canopy types. This approach is a coarse-grain examination of differences among canopy types. Third, we perform a fine-grain analysis to determine whether individual species show canopy type associations. If no associations are found, then relationships between species and environmental variables characteristic of those canopy types are unlikely to be determining species occurrences. It must be remembered that canopy type association does not necessarily mean canopy type specialization. Species presence in a canopy type may be due to historical patterns, biological interactions, current transient patterns (invasion into new territory), or specialization (Harms et al. 2001).

The first approach, to identify environmental differences among canopy types, involves examining environmental variables potentially influential in determining community composition. Burslem (1996) and Agyeman et al. (1999) found light to be an important factor affecting seedling growth in tropical forests. Other studies found water availability to be an important factor influencing forest composition (Swaine 1996; Bongers et al. 1999; Clark et al. 1999). These various environmental factors are likely not acting independently but are interacting with one another to influence species composition; this was indeed found in a study in Ghana in which seedling traits were associated with light and drought gradients (Agyeman et al. 1999). Because of these studies, we focus on environmental factors influencing light and soil moisture.

For the second coarse-grain approach, several studies have determined differences in overall community composition (Kappelle et al. 1995; Lieberman et al. 1995; Terborgh et al. 1996; Sheil 1999; de Carvalho et al. 2000). In South Africa, Kirkwood and Midgley (1999) distinguished tropical dry forest from evergreen forest communities using multivariate analyses. While in a Bornean forest, Webb and Peart (2000) found that multivariate analyses of species associations were able to distinguish the three physiographic forest types.

Various researchers have also investigated the third fine-grain approach, determining individual species specializations; these studies vary in spatial scale. Both a large-scale study in the Amazon in which species were examined over a 400 km^2 area

in different forest types (Pitman et al. 1999) and a small-scale study in Panama in which species were examined over 0.5 km² and classified in terms of their habitat associations and regeneration strategies (Hubbell and Foster 1986) found that most species were generalists. Only one in five species were associated with a specific habitat in the Amazon and one in 2.4 species were associated with a specific habitat in Panama. Despite large variation in the spatial scales of studies and types of environmental gradients considered, a number of studies found that generalists appeared to dominate communities [Swaine (1996) with 43% of species indifferent to habitat type; Webb and Peart (2000) with 57% of species indifferent; and Harms et al. (2001) with 25–49% of species indifferent, depending on the type of analysis]. As the majority of these studies define associations with environmental gradients, we may be more likely to find specialists if we focus on communities defined by their canopy type, which should also affect the light environment.

In this study, we investigated the importance of association in structuring species composition in three forested canopy types: closed canopy forest, forest treefall gap, forest/grassland edge, and compared them to grassland canopy type in Kibale National Park, Uganda. The gap and edge canopy types should be in dynamic association with closed canopy forest, as disturbance and successional processes occur over time. Gaps should be more similar to closed canopy forest as they are embedded in the forest matrix, whereas edge forms a boundary between forest and grassland and should have affinities to both canopy types. Both gap and edge though should create quite different microclimates to forest, even if these effects are ephemeral in space or time, and thus they may have their own suite of associated species. In this investigation, we wanted to characterize associations between canopy types and (1) environmental variables (i.e., soil bulk density, water content, root length density, field capacity, organic matter, particle size distribution, and pH; and light); (2) tree and shrub community composition; and (3) individual tree and shrub species distributions. We expected that differences in environmental conditions would lead to differences in individual species distributions and thus differences in overall community composition.

Materials and methods

Study site

Kibale National Park (766 km²; 0°13′–0°41′N and 30°19′–30°32′E) is located in western Uganda, 24 km east of the Rwenzori Mountains at an elevation of 1500 m. Between 1998 and 2000, a mean of 1760 mm of rain fell per year, annual mean daily maximum temperature was 23.1 °C, and minimum temperature was 15.1 °C. Two rainy seasons occur with peaks from April to May and September to October (Kamugisha 1993) although rain is well distributed throughout the year (Kingston 1967).

Soils

Underlying the study area are pre-Cambrian sedimentary rocks that have been strongly folded and metamorphosed (Struhsaker 1997). The ridges often contain crystalline quartzite with granites, gneisses, and amphibolites intruding; some of the hills are underlain by purplish low-grade schists and phyllites. Volcanic tuff from Pleistocene eruptions of the Ndale Volcanic Field 50 km to the south occurs in the park. Hilltops have shallow rocky soils or are covered with laterite caps (Struhsaker 1997), while hillslopes often have red sandy clay to 2 m in depth (Lang Brown and Harrop 1962). In the Lang Brown and Harrop (1962) study, they found grasslands have a build up of bases with forest soils being much more acidic and lower in organic matter. No detailed soil analyses for the Kibale soils exist. From a countrywide soil map, soils near Kanyawara have been described as ferralitic red soils that are mainly sandy clay loams (Kamugisha 1993), and another source suggests Andisol soils are dominant in the area (Jacob Aniku, personal communication).

Vegetation

Kibale consists of mature forest (57%), colonizing forest (19%), grassland (15%), woodland (4%), swamp (4%), and plantations of exotic trees (1.0%; Chapman and Lambert 2000). In the northern part of the park near the Kanyawara

field station where this study was conducted, the forest is medium altitude, moist evergreen, and the forest becomes medium altitude, moist semi-deciduous to the south (Langdale-Brown et al. 1964; Howard 1991). The northern section is classified as *Parinari* forest as climax with *Trema orientalis* as a typical secondary successional species and the southern section as *Cynometra-Celtis* forest with *Cynometra alexandrii* as climax on poor soils and *Celtis* spp. and *Chrysophyllum* spp. increasing on richer mixed forest sites (Langdale-Brown et al. 1964). The forest has also been characterized by timber managers (Kingston 1967) who documented that the northern timber-rich section is composed mainly of *Parinari excelsa*, *Carapa grandiflora*, *Olea capensis*, *Pouteria altissima*, *Strombosia scheffleri*, and *Newtonia buchanani*. The central section of the park is more mixed containing *P. excelsa*, *Celtis* spp., *Chrysophyllum* spp., *Diospyros abyssinica*, and *Markhamia lutea*. The southern section is characterized by *Pterygota mildbraedii*, *O. capensis*, *Celtis* spp., *Warburgia ugandensis*, and *D. abyssinica*, as well as mono-dominant stands of *Cynometra alexandrii*.

Grasslands consist primarily of *Pennisetum purpureum*, *Hyparrhenia* spp., or *Cymbopogon afronardus* depending upon location and characteristics such as past disturbance, soil type, and rainfall regime (Kingston 1967). Lang Brown and Harrop (1962) found *Flueggea virosa*, *Acanthus arborescens*, *Hoslundia opposita* and *Vernonia* spp. occur as scattered shrubs and *Erythrina abyssinica* and *Millettia dura* occur as occasional trees in this grass matrix. They also report that *M. dura* and *Olea capensis* are typical species of the forest/grassland edge. They found a band of *Acanthus* scrub surrounding the forest edge and that this *Acanthus* scrub grades into the grassland canopy type (see Lang Brown and Harrop 1962 for a graphical representation of the grassland, edge, forest matrix). We do not focus on this *Acanthus* scrub canopy type in this paper.

Forest history

Kibale was originally designated a Forest Reserve in 1932 and received the protected status of National Park in 1993 (Struhsaker 1997). Forestry compartment K30 near Kanyawara is a relatively undisturbed forest of 300 ha. Prior to 1970,

0.03–0.04 large stems/ha were removed by pit-sawyers; the impact on forest structure appears small (Skorupa and Kasenene 1984). Annual rate of natural treefalls is between 1 and 2% (Skorupa and Kasenene 1984), and mean gap size for K30 was estimated as 256 m^2 (range: 100–663 m^2; Kasenene 1987). No information exists on rates of canopy closure in treefall gaps. We do know that closure had not occurred in a series of natural gaps after 10 years. Kibale lacks aggressive colonizers found in other parts of the tropics (e.g., *Cercropia*, *Musanaga*, and *Macaranga*) and members of the Acanthaceae, especially *Acanthus arborescens*, are frequent colonizers of large-scale disturbance that can lead to arrested succession (Paul et al. in press). A series of logging gaps is still present 30 years after their creation.

Early records by Langdale-Brown et al. (1964) indicate two grass savanna areas in the northern section of Kibale and suggest that much of the grass savanna areas throughout Uganda are a result of repeated cultivation, grazing, and burning. These grass savanna areas have had a long tradition of being called grasslands (Lang Brown and Harrop 1962), and we will continue in this tradition. Grasslands are found on hilltops and hillslopes within the northern section of the park, including Kyenjura grassland (31.5 ha), which archaeological evidence suggests were formerly agricultural settlements (Kingston 1967). Human settlement declined in these areas during the early-1900s due to an increase in rinderpest that killed cattle (Kingston 1967), and no cattle grazing is currently occurring in the grasslands inside the park. Forest has begun to reestablish in some grasslands, perhaps due to their shape (e.g., facilitating seed dispersal) or isolation from disturbance, while the majority remains as grassland due to fire (Lang Brown and Harrop 1962; Kingston 1967), elephant activity (Wing and Buss 1970), and/or competitive dominance of grasses over trees (Kingston 1967).

No record of the frequency of fires in Kibale grasslands exists. Fires have likely burned Kyenjura grassland in the past; however, it has not burned since we began our study in 1998, and based on anecdotal evidence, they have not been burned for much longer. We focus on Kyenjura as it is one of the most isolated grasslands from human contact within Kibale, and thus we should be better able to separate natural successional

processes from human mediated processes (e.g., recent fire). Other grasslands in and near Kibale burn frequently and those close to human settlements burn annually, thus we were not able to replicate our grassland. and edge canopy types. Some fires, especially those within the park, may be intentionally set to facilitate animal poaching (Lang Brown and Harrop 1962). Vegetation in grasslands differs in response to fire (e.g., grass leaves burn and grass roots remain relatively undamaged; Lang Brown and Harrop 1962). Woody species fire adaptations range from having thick corky bark (*Erythrina abyssinica*), moist or leathery leaves (Acanthaceae and Compositae), and ability to resprout (*Millettia dura*); however, these traits are only found in a few species. Fires do not appear to burn into closed forest, and no evidence of fire damage is apparent in K30 or along the edge. The grassland forest matrix has been poorly studied and so little is known of the dynamics of the different edges, whether they are advancing or retreating.

Vegetation measures

From May 1998 to July 2000, we quantified tree and shrub species richness and individual density in 24 small plots (5 × 5 m) in each of four canopy types (closed canopy forest, treefall gaps, forest/grassland edge, and grassland). All size classes of shrubs and trees (newly germinated seedlings to trees) were counted. These plots were randomly located within each canopy type along the hilltops and hillslopes (forest and gap: K30 and Kyenjura forests, grassland and edge: Kyenjura grassland; Figure 1). Compartment K30 is located on two hills within the park (K30 upper camp and K30 lower camp), so eight forest and eight gap plots each were located along the two hilltops and hillslopes, as well as, a third set of forest and gap plots being placed in the forest adjacent to and downslope from Kyenjura grassland. To locate forest plots in K30, we randomly selected trail junctions and then randomly selected one of the four sections of forest radiating from that junction. Plots were then placed at least 5 m from any trails. All plots were in closed canopy forest with a minimum distance of 5 m from any gap edges (with gap edge defined as cleared of vegetation to within 2 m of the forest floor; Brokaw 1982). To locate forest plots in Kyenjura forest that lacked a network of trails, we randomly selected a distance between 10 and 60 m along the main trail and then randomly selected a distance between 10 and 60 m from the main trail for the plot. For gap plots, we located treefall gaps throughout the forests in which fallen trees had no fine branches and leaves remaining yet little decay had occurred on the main bole. Approximately 60 gaps were found that fit our requirements; we then randomly selected a subset of these gaps, placing plots in the center of the gap. Gap size was determined by measuring the longest axis and the second longest axis
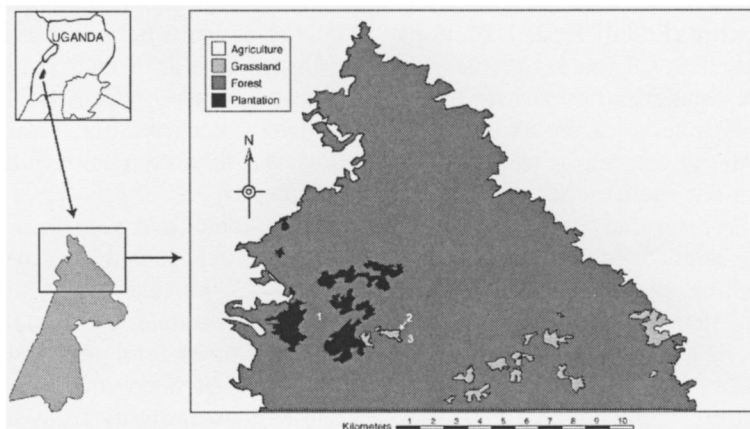

Figure 1. Kibale National Park, Uganda and surrounding areas with agriculture, grasslands, forest, and plantations denoted. Study locations: 1 = K30 forest, 2 = Kyenjura grassland, 3 = Kyenjura forest. The map is based on 1996 data from the National Biomass Study, Forestry Department, Government of Uganda.

perpendicular to the first; gaps averaged 300 m^2 (range: 39–636 m^2).

We defined the forest/grassland edge as the end of the continuous forest canopy. Plots were placed such that 2.5 m extended toward the grassland and 2.5 m extended toward the forest. To locate plots along the edge, we randomly selected a distance between 10 and 60 m along the ~1 km length of edge. We then walked that distance to establish a plot. As the grasses were tall (up to approximately 4 m) and difficult to maneuver through, we were required to cut trails in the grassland to locate plots. We randomly selected locations between 50 and 100 m apart along the length and on either side of the main trail (620 m) through the grasslands. We then cut a 20 m trail perpendicular to the main trail, placing a plot at the end of the new trail. Furthermore, since few large trees and shrubs >2 m tall occurred in small plots (5 × 5 m), we sampled this larger size class of trees and shrubs using large plots (10 × 50 m) randomly located in forest and grassland canopy types (not gap and edge canopy types). The forest plots were located in K30 as in the smaller plots, but plots were placed to 5 m perpendicular to the trail edge on either side of the trail (for a total of 10 m) and 50 m along the length of the trail. Grassland plots were located in Kyenjura grasslands by randomly selecting eight locations between 50 and 100 m apart along the main trail. Trails were then cut to 40 m perpendicular from the trail. Secondary trails were cut at 20, 30, and 40 m from and running parallel to the main trail for 50 m, and these trails formed the edges of the 16 plots.

For species identification, we used species names found in recent literature (Polhill 1952; Hamilton 1991; Katende et al. 1995; Lwanga 1996). All shrubs and trees were categorized by growth form as shrub, treelet (sometimes growing as a shrub and sometimes growing as a tree), or tree. Determination of life form for each species was taken from the *Flora of Tropical East Africa* (Polhill 1952). Shrubs were defined as self-supporting woody plants branching near the ground and either having several stems from the base or a single stem but short in stature (<2 m), and trees were defined as woody plants with a single main stem and tall in stature (>2 m; Polhill 1952). We applied the definition of tree, treelet, and shrub consistently to all individuals encountered for a given species; we did not try to determine whether

individuals of a species in the treelet category were growing in the shrub or tree category.

Soil and light measures

We characterized each canopy type with respect to soil bulk density, soil gravimetric water content, estimated soil field capacity, soil particle size distribution, soil organic matter, soil pH, root length density separated for roots with diameters <2 and >2 mm, and photosynthetically active radiation. Ten randomly placed (with randomizations occurring as in the vegetation plots) 20 m transects were sampled in each canopy type. These transects were near to, but not at the same locations as, the vegetation plots. We took soil samples for soil and root measures by first clearing away litter and removing a 2 cm diameter core to 15 cm depth. In January 2000, 10 soil cores were taken approximately every 2 m along each transect; cores were combined within transects. Adjacent to the first five cores, we took five more cores of the same size for root sampling; root cores were combined within transects. From February to June 2000 (encompassing one wet and one dry season), five soil cores per transect were taken each month for water content measures. For bulk density, larger diameter cores (6.4 cm) were taken in June 2002 and treated similarly to the smaller diameter cores. Upon collection, soils were placed in paper bags and immediately placed into drying ovens after wet mass was recorded. Bulk density, gravimetric water content, and root separation were done in Uganda, but all further soil analyses were conducted at University of Florida. These soils were transported still in their paper bags. During storage and transportation to Florida, some changes may have occurred due to increased soil moisture; however, these changes should be consistent across all samples.

Soil wet and dry masses were measured; dry mass was determined after drying to constant mass at 105 °C. We calculated bulk density (BD = soil dry mass/volume; g cm^{-3}; Klute 1986) for June 2002 samples and gravimetric water content (WC = [wet mass−dry mass]/dry mass*100; %; Klute 1986) monthly from January to June 2000 samples. An estimate of field capacity was taken by saturating soils and draining them for 24 h at room temperature. Soils were weighed and then

dried to constant mass at 105 °C and reweighed. This method is only a relative estimate of field capacity as it was not measured *in situ* and much of the gross soil structure was lost.

Particle size distribution (% sand, silt, and clay) was determined by pipet method in which dry mass of sand and clay was determined for a soil sample after organic matter was removed (Klute 1986). Particle size distribution was measured for all forest, gap, and edge plots but only three grassland plots, as other grassland plots had high organic matter values that would have led to inaccurate measures of particle size distribution. Soil organic matter was determined by measuring loss on ignition in a muffle furnace at 550 °C for 24 h, and pH was measured on 3 g of soil in 3 ml distilled water (Page et al. 1982).

For root cores, roots were separated from soils by sieving samples through 2 μm and 250 mm mesh and extracting remaining roots; roots were preserved in ethanol for transportation to Florida. Root length densities (Lv, cm cm^{-3}) for small (<2 mm) and large (>2 mm) roots were determined by measuring total root length in a given volume of soil using GSRoot 4.0 Automated Root Length Measurement (PP Systems, Haverhill, Maine).

Photosynethically active radiation (PAR; μmol m^{-2} s^{-1}) was measured during dry (June) and wet (October) seasons with an LI250 light meter and an LI-190SA quantum sensor (Licor, Lincoln, NE) along 20 randomly placed transects (the 10 used in the soil analyses plus 10 additional transects) in the four canopy types. All measurements were taken between 1000 and 1400 h. Two light readings were taken at 5 cm above the ground at each of four locations approximately 5 m apart along each transect. Measurements were averaged per transect.

Analyses

When examining species richness, problems can occur if differences exist among samples in sampling effort or individual abundances; rarefaction analyses are particularly appropriate in these cases as species number is estimated on a per individual basis (Gotelli and Colwell 2001). As density varied among canopy types, rarefaction was used to assess species richness. Rarefaction analyses were run using programs written by Brzustowski (2002),

as described in Krebs (1989) and based on methods by Hurlbert (1971) and Simberloff (1972). Principal components analysis (PCA) was used to describe: (1) relationships among environmental variables in the forested and in all four canopy types and (2) ecological relationships among tree and shrub species in forested canopy types. We ran detrended correspondence analysis on the species abundances for all four canopy types (data not shown). The scores for the grasslands and forested canopy types were well separated with much less separation among the three forested canopy types. Based on these results, we chose to use PCA for comparisons of the three forested canopy types, as the difference between grassland and forested canopy types was less interesting than differences among the forested canopy types. Analyses were conducted with Canoco 4.5 (ter Braak and Smilauer 1999). For PCA, eigenvalues greater than 0.1 were considered strong axes explaining a large percentage of the variance in the data, and when scores or factor loadings were greater than 0.5 for a given axis, those variables were considered strongly related to that axis (Norusis 1994). Since the species abundance data were highly skewed with many plots with few individuals and a few plots with many individuals for each species, we transformed species data using ln (x + 1) transformations (Jongman et al. 1987).

To determine how species were associated with canopy types, we ran randomization tests using confidence intervals for common species in programs we wrote in R 1.6.2 (R Development Core Team 2002). Individuals were separated into three size classes in small plots (<0.5 m, 0.5–2 m, >2 m) and one size class in large plots (>2 m). Since many species were represented by only a few individuals (e.g., in small plots 40.4% of species had <10 individuals across all plots), only species with >15 individuals across all small or all large plots in a given size class were included in the analyses. This cut off allowed us to detect associations if they were present, as we did not have the power to test for relationships with fewer stems. This cut off was similar to that used by Hubbell and Foster (1986) who used a minimum of 10 stems per species to define the lower end of rare species. Forty-seven of 104 species in small plots and 52 of 97 species in large plots were common enough to examine their canopy type associations. We kept the natural structure of the data within

the plots to avoid any biases created by clumping of individuals of a species within a plot. To do this, we randomly reassigned plots to canopy types without replacement for 10,000 iterations. Significant species associations with a canopy type are reported if observed counts were more extreme than 95% of randomizations. With a significance level of 0.05, we would expect in the species canopy type associations that eight of the 40 species in the <0.5 m, six to seven of the 33 species in the 0.5–2 m, and six of the 30 species in the >2 m size classes in small plots and five to six of the 52 species in large plots would be falsely found associated with any given canopy type (either positively or negatively) by chance alone.

We chose to run Randomization tests with confidence intervals rather than Contingency table goodness-of-fit (GOF) tests and Randomization tests with deviation statistics (Σ(Randomized $-$ Expected)^2/Expected; from Webb and Peart 2000) using expected values (null model) determined by multiplying total number of a given species in all canopy types by proportion of individuals of all species for each canopy type (Webb and Peart 2000; Harms et al. 2001). Randomization tests with confidence intervals are more appropriate than GOF tests, as GOF tests assume that all individuals and plots are independent (Webb and Peart 2000; Harms et al. 2001). This assumption is violated, for example, if several individuals establish within a plot after the seeds were deposited in a single dispersal event. For our data, randomization tests with confidence intervals are also more appropriate than randomization tests with deviation statistics. Forest, gap, and edge canopy types had high numbers of individuals, but grassland canopy type had few individuals. Randomization tests with deviation statistics are strongly influenced by differences in total number of individuals among categories. As grassland had many fewer individuals than the three forested canopy types, randomization tests with deviation statistics were more appropriate for our data.

Results

Environment

Based on environmental characteristics, forest and gap canopy types were similar to one another, but differed from edge and grassland canopy types (Figure 2). Factors influencing soil water availability (% organic matter; % clay; field capacity; and mean, maximum, and minimum water contents) were significantly greater in grassland than in other canopy types (Figure 2). Percent sand and bulk density were greater in forest and gap than grassland and edge; root length density of small roots was greater in edge than in other canopy types. Roots <2 mm in diameter are the roots absorbing most of the water and nutrients in the soil, so their density may indicate the amount of belowground competition for resources. Light was greater in gap, edge, and grassland sites than in forest. No significant differences were found with respect to pH and root length density of large roots. The higher root length density of small roots in edge plots and a seedling experiment in which many seedlings appear to die from wilting in edge than any other canopy type (Zanne, unpublished data) suggest that edge is a more water-limited canopy type. In terms of soil color, dry soils are reddish brown in forest and gap, dusky red in edge, and reddish black in grasslands (Munsell Colour Company 1975). Wet soils are dusky red in forest and gaps, very dusky red in edge, and reddish black in grasslands.

In the PCA of environmental data with forested canopy types (forest, gap, and edge), most variance (67.3%) was explained by the first three axes, which all had eigenvalues >0.1 (Table 1); only the first two axes are plotted (Figure 3). Most factors were strongly related to Axis 1 with nine of 12 variables having factor loadings greater than 0.5 (Table 1, Figure 3a), root length densities of large roots and field capacity were strongly related to Axis 2, and % clay was strongly related to Axis 3. When canopy type transects were plotted along the first two axes, edge transects had more positive scores and forest and gap transects had more negative scores on Axis 1 (Figure 3b). Edge canopy types did not overlap with any other canopy type, but forest and gap canopy types completely overlapped with one another. When grassland plots were analyzed together with the forested canopy types, similar results were found with grassland plots having even larger scores along Axis 1 (data not shown).
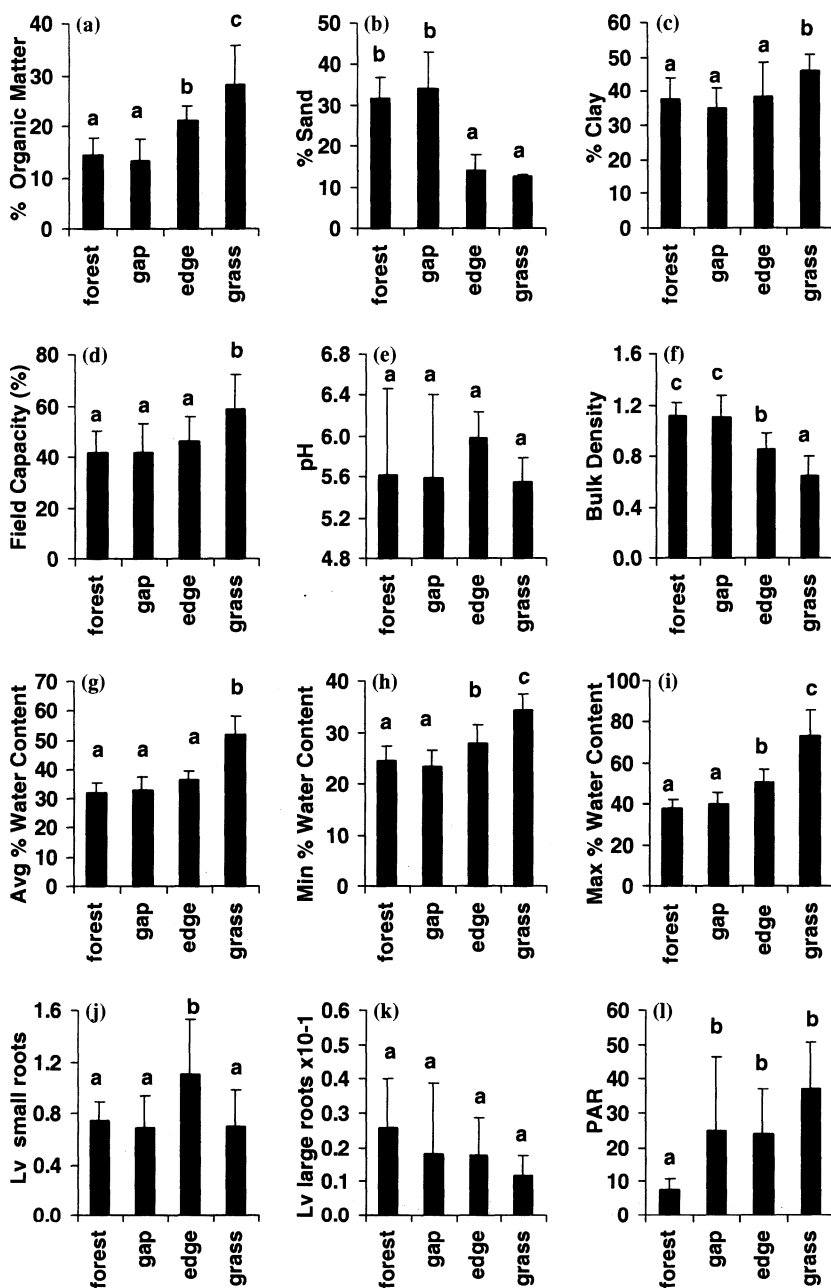
Figure 2. Means (± 1 SD) for environmental variables along 10 transects in four canopy types (forest, gap, grassland, edge) in Kibale National Park, Uganda. Differences among canopy types were determined using analysis of variance followed by Tukey Multiple Comparison procedures. Bars with different letters are statistically different at $p < 0.05$. (a) % Organic matter ($F = 20.1$, $p = < 0.001$). (b) % Sand ($F = 41.3$, $p = < 0.001$). (c) % Clay ($F = 4.3$, $p = 0.010$). (d) Field capacity (% water content; $F = 5.7, p = 0.003$). (e) pH ($F = 1.1, p = 0.353$). (f) Bulk density, g cm^{-3} ($F = 26.6, p = < 0.001$). (g) Mean water content (% dry mass; $F = 38.2, p = < 0.001$). (h) Minimum water content (% dry mass; $F = 9.7, p = < 0.001$). (i) Maximum water content (% dry mass; $F = 39.6, p = < 0.001$). (j) Root length density (Lv) for small roots, cm cm^{-3} (diameter <2 mm; $F = 4.5, p = 0.009$). (k) Root length density (Lv) for large roots, cm cm^{-3} (diameter >2 mm; $F = 1.7, p = 0.177$). (l) PAR, μmol m^{-2} s^{-1} ($F = 7.0$, $p = 0.001$).

Table 1. Eigenvalues, cumulative % variance, and factor loadings for environmental variables along axes using PCA for 10 transects each in forested canopy types (forest, gap, and edge) in Kibale National Park, Uganda.

	Axis 1	Axis 2	Axis 3
Eigenvalue	0.43	0.14	0.10
Cumulative % variance	43.4	57.4	67.3
% Sand	**−0.90**	0.04	− 0.15
Maximum % water content	**0.88**	0.21	− 0.08
Mean % water content	**0.88**	− 0.05	− 0.19
% Organic matter	**0.85**	0.03	0.16
Minimum % water content	**0.71**	− 0.31	0.03
Bulk density (g cm^{-3})	**−0.69**	0.21	− 0.31
Root length density (< 2 mm; cm cm^{-3})	**0.64**	0.41	0.01
PAR (μmol m^{-2} s^{-1})	**0.51**	− 0.10	− 0.40
pH	**0.50**	− 0.44	− 0.23
Root length density (≥2 mm; cm cm^{-3})	− 0.05	**0.79**	0.11
Field capacity (%)	0.41	**0.69**	− 0.33
% Clay	0.23	0.10	**0.82**

Numbers in bold denote variables having strong scores (> 0.50) with a given axis.

Vegetation: community response

In small plots, density of shrubs was highest in grassland and species richness of shrubs was highest in grassland and edge canopy types (Table 2, Figure 4). Differences between forest and gap shrub species, as well as, grassland and edge shrub species became smaller as number of individuals increased, but these lines never crossed (Figure 4A). Density of treelets was highest in edge and species richness of treelets was highest in forest and gaps. Forest and gaps had similarly
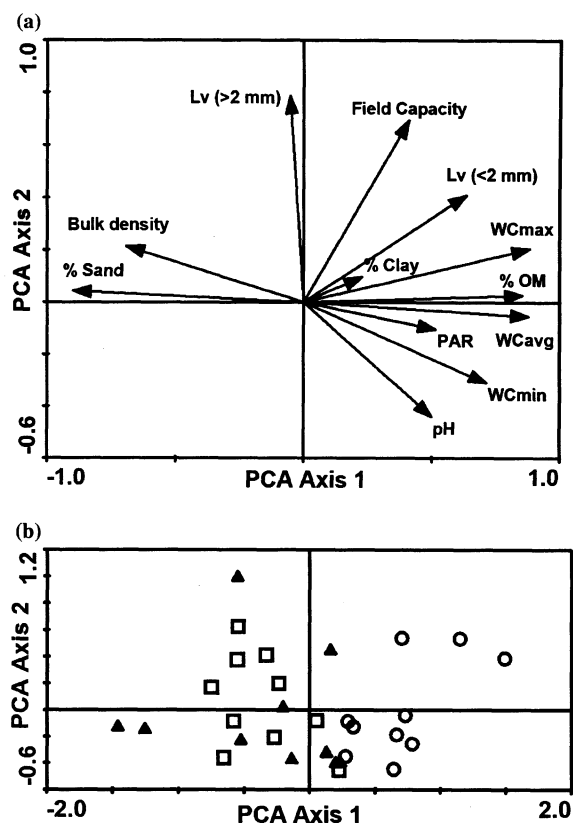
Figure 3. Ordination along Axes 1 and 2 using principal components analysis in 10 transects each in the forested canopy types (forest, gap, and edge) in Kibale National Park, Uganda. Environmental variable abbreviations are as follows: Lv (>2 mm) = root length density for roots >2 mm diameter, Lv (<2 mm) = root length density for roots <2 mm diameter, % OM = % organic matter, WCmax = maximum % water content, WCavg = mean % water content, WCmin = minimum % water content. (a) Environmental variables. (b) Canopy type transects with circles representing edge, triangles representing gap, and squares representing forest.

Table 2. Means (± 1 SD) for density and species richness using rarefaction in each canopy type by growth form (shrub, treelet, tree) for 24 small plots (5 × 5 m) in each of four canopy types (forest, gap, grassland, and edge).

		Individual #	Forest	Gap	Edge	Grass
Individuals/plot	Shrub		8.4[a] (7.1)	6.9[a] (3.9)	15.2[a] (19.4)	28.5[b] (26.6)
	Treelet		12.9[a] (7.6)	11.8[a] (7.8)	55.0[b] (41.2)	2.6[a] (3.9)
	Tree		139.8[a] (229.2)	102.3[a] (77.8)	82.1[a,b] (48.7)	7.9[b] (7.5)
Species/individual	Shrub	163	7.0[a] (0.1)	7.0[a] (0.1)	11.1[b] (0.7)	11.1[b] (1.0)
	Treelet	62	13.9[a] (1.4)	14.9[a] (1.5)	8.8[b] (1.6)	6.0[c] (0.0)
	Tree	190	21.2[a,b] (2.3)	25.2[a] (2.4)	19.9[b] (1.7)	13.0[c] (0.0)

Differences among canopy types were determined using analysis of variance followed by Tukey Multiple Comparison procedure. Growth forms with different superscripts have different means at $p \leq 0.05$. Rarefaction results are presented at the minimum total number of individuals for any of the four canopy types for that growth form.
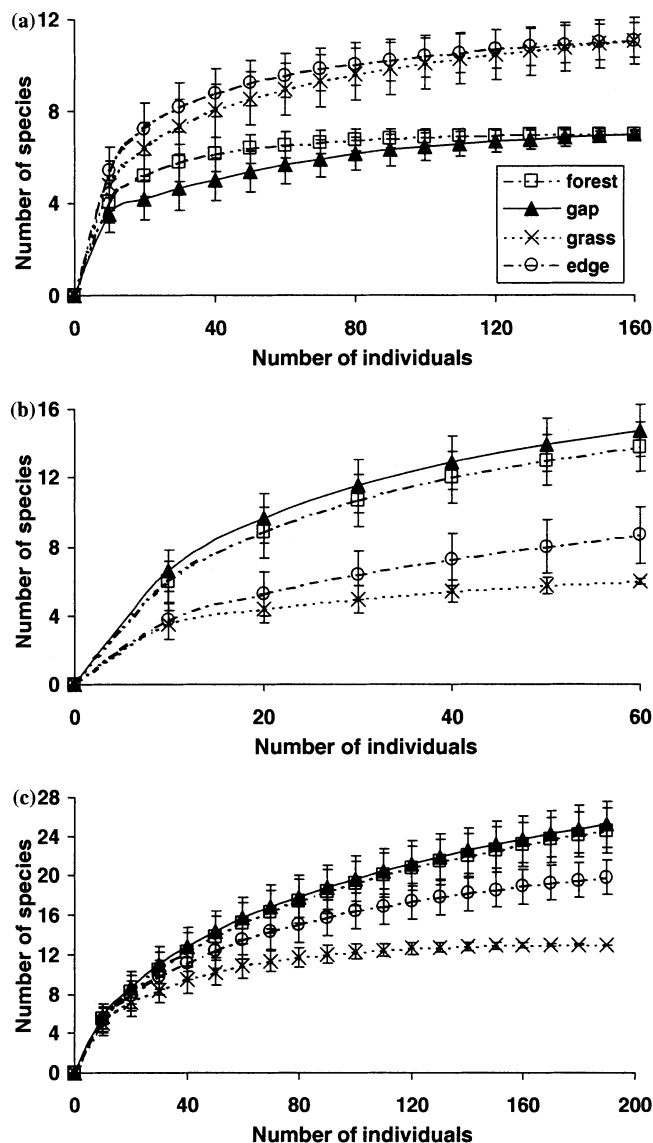
Figure 4. Number of species vs number of individuals using rarefaction for different growth forms (shrub, treelet, and tree) in all size classes in small (5 × 5 m) plots in four canopy types (forest, gap, grassland, and edge) in Kibale National Park, Uganda. (a) Shrubs, (b) Treelets, and (c) Trees. Error bars represent 1SD.

high tree species richness. Tree density was greatest in forest plots but was also highly variable. High density of forest trees was due to one plot that contained 1149 individuals of *Diospyros abyssinica*. When density for *D. abyssinica* in this plot was removed, no differences were found in density between forest, gap, and edge, but these canopy types had higher tree densities than grassland.

In large plots, forest, and grassland had similar shrub densities per plot (forest: 23.8 ± 18.4;

grassland: 24.5 ± 8.0), but forest had higher shrub species richness per individual (forest: 12.0 ± 0.0; grassland: 8.0 ± 0.2). Forest had higher density per plot and species richness per individual of treelets (forest individuals: 50.0 ± 22.3, forest species: 14.6 ± 1.6; grassland individuals: 3.2 ± 4.3, grassland species: 6.0 ± 0.0) and trees (forest individuals: 208.3 ± 51.4, forest species: 28.3 ± 2.3; grassland individuals: 6.9 ± 5.3, grassland species:

5.0 ± 0.0). When forest and grassland results are compared between small and large plots, treelet and tree densities and species richness were similar (the trend for treelet density was similar). Results for shrub density and species richness though differed between large and small plots with forest having more shrubs than grassland. These results may be due to more grassland shrubs being small in stature and thus not measured in large plots.

Principal components analysis of tree and shrub species abundances for small plots in forested canopy types (forest, gap, and edge) separated edge plots from forest and gap plots along Axis 1, but forest and gap plots were completely overlapping (Figure 5). Only Axis 1 explained a large percentage of variance (eigenvalue > 0.1). While forest and gap plots from Kyenjura were distinct from forest and gap plots from K30 upper camp and K30 lower camp along Axis 2 (an axis with an eigenvalue < 0.1), edge plots were more variable along Axis 1 than were all the forest and gap plots combined. Principal components analysis of tree and shrub species abundances for small plots using just forest and gap plots were unable to detect any strong axes (eigenvalue > 0.1) suggesting that the forest and gap communities are indeed indistinguishable. When grassland plots were analyzed together with the forested canopy types using detrended correspondence analysis, grassland

Figure 5. Plot ordination based on species along Axes 1 and 2 using PCA in 24 small plots (5 × 5 m) each in the forested canopy types (forest, gap, and edge) in Kibale National Park, Uganda (Axis 1: Eigenvalue = 0.10, % Variance = 9.7 %) with circles representing edge, triangles representing gap, and squares representing forest. Gray open symbols represent K30 lower camp, black filled symbols represent K30 upper camp, and black open symbols represent Kyenjura.

plots were quite different from the three forested canopy types (data not shown).

Vegetation: species associations

In small plots using randomization tests, 36 of 40 species <0.5 m tall, 31 of 33 species 0.5–2 m tall, and 29 of 30 species >2 m tall were significantly associated with a canopy type (Table 3). Positively associated species had on average 72.2% of their individuals in the <0.5 m size class in that canopy type (range: 45.2–100%), 49.1% of their individuals in the 0.5–2 m size class in that canopy type (range: 49.1–96.9%), and 75.3% of their individuals in the >2 m size class in that canopy type (range: 53.8–100%). Twenty-one of the 25 species with positive associations in more than one size class were positively associated with the same canopy type in the different size classes. One species (*Uvariopsis congensis*) had significant positive associations with one canopy type in the 0.5–2 m size class and two canopy types in the >2 m size class. Six species (*Albizia grandibracteata*, *Blighia* spp., *Dovyalis macrocalyx*, *Ficus asperifolia*, *Mimusops bagshawei*, *Teclea nobilis*) changed their significant positive canopy type associations among size classes. *Albizia grandibracteata* is most common in the edge at the smallest size class but grassland at larger size classes suggesting it germinates well with some cover but is able to persist in grassland perhaps where competition with other trees is lower. Similarly, *Blighia* spp. and *M. bagshawei* are more common in smaller size classes in gaps and the largest size class in forest suggesting these species may need gaps to germinate but are able to persist in closed canopy forest. The other three species are common among all the forested canopy types but alternate the canopy type in which they are most common for a given size class.

In randomization tests for species in large plots in grassland and forest, only three species (*Dombeya mukole*, *Millettia dura*, *Rinorea brachypetala*) were not significantly positively or negatively associated with any canopy type (Table 3). Species positively associated with a canopy type had on average 99.8% of their individuals in that canopy type (range: 95.1–100%). Four species were significantly positively associated with grassland in both large and small plots, and 27 species were
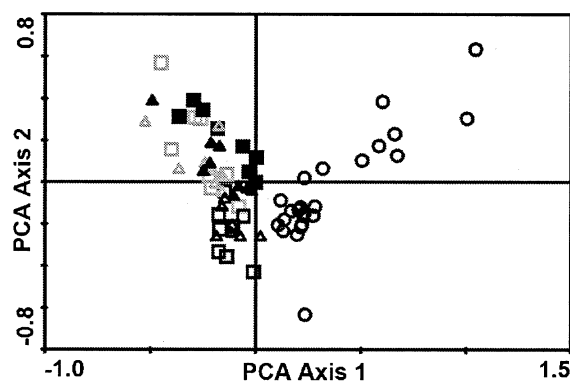
Table 3. Species, growth forms (shrub, treelet, and tree), and individual counts for all tree and shrub species with ≥ 15 total individuals in 24 small plots (5 × 5 m) each in four canopy types (forest, gap, grassland, and edge) and ≥ 15 total individuals in 16 large plots (10 × 50 m) each in two canopy types (forest and grassland).

Family	Species	Form	Small plots <0.5 m				Small plots 0.5–2 m				Small plots >2 m				Large plots >2 m	
			Forest	Gap	Edge	Grass	Forest	Gap	Edge	Grass	Forest	Gap	Edge	Grass	Forest	Grass
Euphorbiaceae	*Acalypha* spp. L.	Shrub	2	0	7	13	1	3	57	6	0	0	4	77	0	213
Acanthaceae	*Acanthus arborescens* Panzer	Shrub	0	2	4	61	0	0	19	93	0	2	13	24	4	77
Fabaceae	*Albizia grandibracteata* Taub.	Tree	0	2	34	21	0	1	31	40	0	5	8	0	41	0
Sapindaceae	*Allophylus dummeri* Baker f.	Tree	24	38	94	2	14	20	52	1	11	14	0	0	126	0
Moraceae	*Antiaris toxicaria* Lesch.	Tree									12				71	0
Sapindaceae	*Blighia* spp. Kon.	Tree	17	24	5	0	22	32	11	0	16	7	6	0	24	0
Rhizophoraceae	*Cassipourea ruwensorensis* Alston	Tree													25	0
Celtidaceae	*Celtis africana* Burm. f.	Tree	2	5	17	3	3	5	15	1	3	1	26	0	53	0
Celtidaceae	*Celtis durandii* Engl.	Tree	3	47	15	11									63	1
Celtidaceae	*Chaetachme aristata* Planch.	Treelet	3	14	13	0	4	5	8	0						
Sapotaceae	*Chrysophyllum* spp. L.	Tree													42	0
Rutaceae	*Clausena anisata* Hook. f., De Wild. & Staner	Treelet	24	24	754	0	4	8	46	0	1	3	32	0	31	0
Rubiaceae	*Coffea eugenioides* S. Moore	Shrub	2	9	7	0	9	17	6	0	12	10	0	0	205	0
Flacourtiaceae	*Dasylepis* sp. Oliver	Treelet	27	34	4	0	7	8	0	0					53	0
Ebenaceae	*Diospyros abyssinica* (Hiern) F. White	Tree	1572	750	511	4	41	15	76	0	13	16	18	1	192	0
Malvaceae	*Dombeya mukole* Sprague	Tree													18	0
Salicaceae	*Dovyalis macrocalyx* Warb	Shrub	35	32	74	4	18	35	14	2	7	7	8	0	65	31
Fabaceae	*Erythrina abyssinica* Lam.	Treelet													0	0
Capparidaceae	*Euadenia eminens* Hook. f.	Treelet													16	0
Rubiaceae	*Euclinia longiflora* Salisb.	Treelet													53	0
Rutaceae	*Fagaropsis angolensis* H. M. Gardner	Tree	8	13	8	0	3	3	12	0	9	9	1	0	69	1
Moraceae	*Ficus asperifolia* Miq.	Shrub	56	25	43	31	16	15	30	0	7	1	24	0		
Phyllanthaceae	*Flueggea virosa* (Willd.) Royle	Treelet	0	0	2	29					11	6	5	0		
Apocynaceae	*Funtumia africana* Stapf	Tree	38	25	17	26	14	5	7	1	16	4	3	0	91	0
Labiatae	*Hoslundia opposita* Vahl	Shrub	0	0	0	0					0	0	2	14	1	65
Bignoniaceae	*Kigelia africana* (Lam) Benth.	Tree	1	0	1	21	5	4	8	0						
Sapindaceae	*Lepisanthes senegalensis* (Poir.) Leenh.	Tree	31	54	18	0	8	25	5	0	5	21	0	0	89	0
Malvaceae	*Leptonychia mildbraedii* Engl.	Tree	8	5	2	0					10	6	0	0	78	0
Sapindaceae	*Lychnodiscus cerospermus* Radlk.	Tree													17	0
Bignoniaceae	*Markhamia lutea* K. Schum.	Tree													75	0
Celastraceae	*Maytenus gracilipes* (Welw. ex Oliv.) Exell	Shrub	6	0	9	0	7	0	9	0						
Celastraceae	*Maytenus undata* (Thunb.) Blakelock	Tree	2	3	17	0	0	2	16	0						
Fabaceae	*Milletia dura* Dunn	Treelet	0	0	9	6									7	27
Sapotaceae	*Mimusops bagshawei* S. Moore	Tree	66	74	0	0	12	25	2	0	15	7	0	0	160	0
Annonaceae	*Monodora myristica* Dun.	Tree	32	56	12	9	7	20	3	0					32	0
Fabaceae	*Newtonia buchananii* (Baker) Gilb. & Bout.	Tree					19	8	3	0					92	0
Oleaceae	*Olea capensis* L.	Tree	0	0	20	0										
Rubiaceae	*Oxyanthus speciosus* DC.	Treelet													91	0

Table 3. (Continued)

Family	Species	Form	Small plots <0.5 m				Small plots 0.5-2 m				Small plots >2 m				Large plots >2 m	
			Forest	Gap	Edge	Grass	Forest	Gap	Edge	Grass	Forest	Gap	Edge	Grass	Forest	Grass
Sapindaceae	*Pancovia turbinata* Radlk.	Tree	5	**29**	0	0	6	**28**	0	0	5	**16**	0	0	**230**	0
Thymelaeaceae	*Peddiea fischeri* Engl.	Treelet	2	2	**40**	0	0	3	*17*	0						
Apocynaceae	*Pleiocarpa pycnantha* Stapf	Tree													93	0
Sapotaceae	*Pouteria altissima* (A. Chev.) Baehn.	Tree													22	0
Anacardiaceae	*Pseudospondias microcarpa* Engl.	Tree													22	0
Rubiaceae	*Psychotria* spp. L.	Treelet	24	22	106	0	3	10	**40**	*1*	2	4	**38**	*1*	70	0
Malvaceae	*Pterygota mildbraedii* Engl.	Tree									9	4	5	0	92	0
Violaceae	*Rinorea brachypetala* Kuntze	Treelet													65	0
Rubiaceae	*Rothmannia* sp. Thunb.	Treelet									10	13	1	0		
Rubiaceae	*Rytigynia* sp. Blume	Shrub	1	1	**18**	0									18	0
Salicaceae	*Scolopia rhaniphylla* Gilg	Treelet	9	6	3	0									73	0
Olacaceae	*Strombosia scheffleri* Engl.	Tree													59	0
Loganiaceae	*Strychnos mitis* S. Moore	Tree	10	6	11	0	1	2	**21**	0	3	5	13	0	68	0
Guttiferae	*Symphonia globulifera* L.f.	Tree	14	1	1	0	**38**	6	1	0	15	4	0	0	45	0
Apocynaceae	*Tabernaemontana* spp. L.	Tree	27	**39**	7	0	13	14	7	0	14	7	20	0	42	0
Rubiaceae	*Tarenna pavettoides* Sim	Treelet	73	27	57	0	21	16	*31*	0					109	0
Rutaceae	*Teclea nobilis* Delile	Tree	51	**206**	56	0	**80**	50	*13*	0	40	40	31	0	**300**	0
Meliaceae	*Trichilia* spp. P. Br.	Tree					1	13	2	0	11	11	1	0	54	0
Moraceae	*Trilepisium madagascariense* D.C.	Tree	5	3	10	0					26	16	0	0	365	0
Meliaceae	*Turraea vogelioides* Bagshawe	Treelet														
Meliaceae	*Turraeanthus africana* Pellegrin	Tree													182	0
Annonaceae	*Uvariopsis congensis* Robyns & Ghesquiere	Tree	**556**	**442**	**459**	*0*	**211**	**106**	**113**	*0*	**59**	**60**	**26**	*0*	**513**	*0*
Compositae	*Vernonia* spp. Schreb.	Shrub	*0*	*0*	*0*	**212**	*0*	1	*0*	**31**	*0*	*0*	*0*	**20**	*0*	**72**
Monimiaceae	*Xymalos monospora* Baill.	Treelet													23	0

Results from randomization tests with 10,000 iterations for species abundances are indicated by italics for negative associations (associated significantly less than expected) and by bold for positive associations (associated significantly more than expected). Separate randomizations were run for individuals <0.5, 0.5-2, and >2 m in small plots and >2 m in large plots. If no individual counts appear for a species in a given size class, then that species had <15 individuals.

significantly positively associated with forest in large plots and also significantly positively associated with a forested canopy type (forest, gap, or edge) in small plots.

Discussion

We examined the importance of canopy type associations in influencing plant distributions using several approaches. These canopy types are dynamic with both edge and gap canopy types shifting to and from forest understory canopy type. We found environmental differences among all canopy types, but the three forested canopy types had similar tree and shrub communities. As expected, forest and gap were more similar to one another than either was to edge, as gaps are bounded only by forest whereas edge is bounded by two canopy types, forest and grassland. Despite these similarities, individual species were most frequently found in a single canopy type, and these patterns held across size classes.

Environmental conditions

We examined how canopy types vary in terms of their environment and found the three forested canopy types differed in a number of ways, and all differed from grassland. Forest and gaps were most similar with only light distinguishing them. This difference may be critical since light has been shown to be one of the most influential factors determining forest tree growth (Burslem 1996; Agyeman et al. 1999), and researchers have found differences among tropical trees in their abilities to establish in high or low light (Swaine and Whitmore 1988). Forest and gap canopy types differed in most environmental variables from edge and grassland canopy types, while edge and grassland canopy types differed from one another in many environmental factors affecting water availability. Again, the similarities between forest and gap were expected as more rapid turnover between these two canopy types is expected than between forest and edge.

Edge appeared to have the lowest availability of water of all four canopy types. Water availability also influences forest composition (Swaine 1996; Bongers et al. 1999; Clark et al. 1999). In Ghana,

light and drought gradients were both important determinants of species growth (Agyeman et al. 1999). Our results suggest that strong environmental differences exist among all three forested canopy types. Thus species could be assembling based upon specific sets of environmental conditions found in these canopy types.

Canopy type variation

From the multivariate vegetation analysis, it is clear that while forest and gap plots from Kyenjura differed somewhat from forest and gap plots from K30, these differences were small in comparison to differences between forest and gap canopy types vs edge canopy type. Furthermore, both forest and gap plots had similar species richness and individual density across locations, and where differences were found among locations, these differences occurred between the two K30 locations. These results suggest that differences between canopy types are greater than within canopy types from different locations.

As we were unable to obtain grasslands and edges with disturbance regimes comparable to Kyenjura, we are unable to make similar comparisons to the forest and gap plots. But, Kyenjura grassland and edge results are supported by two separate studies. In the first study, six grasslands (including Kyenjura grassland) were surveyed within Kibale along a 12 km trail in which all trees (>2 m) were recorded in 20 plots (40 × 50 m; Zanne and Chapman 2001). Tree density in grasslands was low (trees: 1.35 per 100 m^2). Furthermore, only 15 species occurred in the 40,000 m^2 grassland area surveyed. In the second study, eight small plots (5 × 5 m) were randomly located in grassland and edge canopy types in a grassland along the park boundary (Kyamugarra) near to agricultural plots and several kilometers from Kyenjura (Zanne, unpublished data). This grassland is known to burn annually. Species overlap between Kyenjura and Kyamugarra grassland and edge plots was considerable (46.0%), with more novel species being found in the Kyenjura grassland and edge plots. The latter result is likely related to the greater frequency of burning and lower access to seed trees in Kyamugarra. Species only found in Kyamugarra grassland and edge plots tended to be early

colonizers of disturbed sites. Species richness per plot was comparable between the two studies but individual density per plot was higher in Kyamugarra grassland; the high density was due to extremely high seedling densities of a few species in two plots.

Coarse-grained community analyses

We examined canopy type community differences corresponding to potential environmental differences we had identified. As expected, the grassland tree and shrub community was very different from the other three canopy types' communities, with grassland being most similar to edge. Thus this coarse-grain approach reinforces the distinction between the forested and grassland communities. Studies by Williams-Linera et al. (1998) in Mexico and Oosterhoorn and Kappelle (2000) in Costa Rica, also found that forest edge and interior communities varied greatly in species composition.

Within the forested plots, composition was less divergent. We found differences in species composition between edge plots and the other two forested plots (gap and forest). Despite differences in light availability, forest and gap plots were almost completely overlapping in species PCA ordination plots, suggesting that species are able to germinate in gaps and persist in the forest (and *vice versa*). Several other studies found forest and gap species composition to be similar and suggest that gaps are mainly comprised of advanced regeneration of species typically found also in the forest (Uhl et al. 1988; Raich and Christensen 1989; de Carvalho et al. 2000; Webb and Peart 2000; Schnitzer and Carson 2001). We expected edge canopy type to share equal affinity with both forest and grassland canopy types. Instead, edge community had much greater affinity to forest and gap communities. These results may be due to greater woody density occurring in the forest part of edge plots vs grassland part of edge plots.

Fine-grained analysis of individual species associations

Despite similarities in community structure, we found many common species in small plots had associations with a canopy type. These results are not surprising for grassland plots as their community was quite different in the coarse grain approach. But, strong positive associations were found with all of the forested canopy types, and the same associations were often found across size classes. Furthermore, many species in small plots were negatively associated with at least one canopy type suggesting that canopy type is less suitable for establishment and/or growth of that species.

These results are uncharacteristic, as researchers at other tropical sites, in both Paleo and Neotropics at a variety of spatial scales, have found most species to be generalists (Hubbell and Foster 1986; Swaine 1996; Pitman et al. 1999; Webb and Peart 2000; Harms et al. 2001; but see Svenning 1999). Also, Webb and Peart (2000) found species in smaller size classes to have broader distributions than in larger size classes, suggesting that associations should be strongest at later stages. We found though that canopy type associations were similar across size classes, suggesting that canopy type associations begin at juvenile stages and are maintained as the plants grow. These other studies predominantly defined their different locations based on underlying environmental gradients and thus our canopy types may be more different in their overall environment than theirs, leading to greater associations overall and in juveniles in our study.

A seemingly surprising finding from this study is complete species overlap between forest and gap and high species overlap between edge and forest/gap at the community scale, yet individual species associations with particular canopy types for many common species. Such differences can be attributed to differences between analyses. The community analysis represents all interactions among species both common and rare; it is the sum of many individual species parts, including both their presence and abundance. The individual species analysis, on the other hand, is a representation of presence and abundance of a single species with higher and lower densities potentially indicating association with or avoidance of that canopy type. Thus, when present, that species is contributing to the overall community, but may be found there less than expected in individual-species canopy type associations.

Conclusion

Strong associations of individual species with particular canopy types suggest that canopy type specialization may be occurring in this community leading to both high β diversity found between the forested canopy types and grassland and high α diversity found among the forested canopy types. Strong environmental differences were also found among the forested canopy types with forest being most light-limited and edge most water-limited. These environmental differences are strong candidates for determinants of species distributions. Furthermore, the strong similarities we found, both vegetative and environmental, between forest and gap canopy types suggest that strong distinctions between these two communities are unmerited. As also suggested by Webb and Peart (2000), these communities appear to be comprised of the same suite of shade-tolerant species with individual species perhaps differing in light tolerance and thus specializing to one of the two canopy types but still able to grow in the other canopy type. Forest and gap are two extremes of a continuum that regularly show interchange over both space and time. The relationship between forest and edge is less clear. These canopy types are also likely dynamic communities forming ends of a continuum; however, the timeframe of turnover is likely slower than that between forest and gap, as it is dependent on the influences of forest processes, as well as, grassland processes, which are regularly exposed to much larger disturbances (e.g., fire and elephants).

Acknowledgments

Appendix

For additional information on species, growth forms (shrub, treelet, and tree), and individual counts for all tree and shrub species, readers can access additional online material for this article via the SpringerLink website. (www.SpringerLink.com)

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