

*Full Length Research Paper*

## Species composition and stand structure of secondary and plantation forests in a Kenyan rainforest

John Otuoma<sup>1,2\*</sup>, George Ouma<sup>1</sup>, David Okeyo<sup>3</sup> and Beatrice Anyango<sup>1</sup>

<sup>1</sup>Jaramogi Oginga Odinga University of Science and Technology, P. O. Box 210-40601 Bondo, Kenya.

<sup>2</sup>Kenya Forestry Research Institute, P. O. Box 20412-00200 Nairobi, Kenya.

<sup>3</sup>Maseno University, Private Bag, Maseno, Kenya.

Received 18 February, 2014; Accepted 26 May, 2014

Forest succession has been reported in forest plantations in tropical forests, but little is known about their successional dynamics because most studies have focused on succession in secondary forests. We assessed changes in species composition and stand structure in secondary and plantation forests in Kakamega rainforest in western Kenya. We used a nested experiment to collect data on tree species types, tree height and stem diameter at breast height from secondary forest stands, mixed indigenous plantations and indigenous and exotic monoculture plantations in three forest blocks. Data were analyzed for variation in species diversity, species similarity to the primary forest, stem density and basal area using analysis of variance in Genstat. The results indicated that species diversity and similarity to the primary forest were not different between secondary and plantation forests. However, successional species occupied all the canopy strata in secondary forests, but they occupied only the shrub and understorey layers of monoculture plantations, and the shrub, understorey and sub-canopy strata of mixed indigenous plantations. Mixed indigenous plantations had become nearly indistinguishable from secondary forests, but monoculture plantations maintained a plantation outlook. Old secondary forest had a significantly lower stem density than plantation forests, but their basal area was not significantly different. Middle-aged and young secondary forests had comparable stem density to plantation forests, but their basal area was significantly lower. The results confirmed that plantation forests are experiencing forest succession in tropical forests, their species composition and stand structure are comparable with secondary forests, but they differ in the emergence pattern of successional species and their distribution in forest canopy strata.

**Key words:** Secondary succession, plantation forests, tropical rainforest, species composition, stand structure.

### INTRODUCTION

Many tropical rainforests have been felled and thereafter converted to farmland, human settlement or pasture. Over time, as the farmlands, settlements and pasture are abandoned; these areas either regenerate naturally into secondary forests or are planted as plantation forests

(Chazdon et al., 2010; Omeja et al., 2012; Chua et al., 2013). The emerging forest stands are important as carbon sinks, biodiversity habitats, and sources of timber and non-wood forest products (Brown and Lugo, 1990; UNDP, 2000; FAO, 2010). Tremendous progress

\*Corresponding author. E-mail: [jmotuoma@yahoo.com](mailto:jmotuoma@yahoo.com)

Author(s) agree that this article remain permanently open access under the terms of the [Creative Commons Attribution License 4.0 International License](http://creativecommons.org/licenses/by/4.0/)

has been made to describe post-disturbance secondary forest succession in abandoned farmlands and pasture (Guariguata and Ostertag, 2001; Chazdon, 2003; Norden et al., 2009). However, little attention has been paid to changes in species composition and stand structure of plantation forests that are established in such abandoned sites (Fawig et al., 2009; Kanowski and Catterall, 2010). Studies in post-disturbance natural forest recovery have demonstrated that woody species emergence pattern during secondary forest succession is determined to a large extent by the light environment and longevity of the species involved (Montgomery and Chazdon, 2001; Pooter et al., 2005; Wright et al., 2010). For instance, the first 100 years of secondary forest succession have been described to comprise about three successional phases (Finegan, 1996; Pena-Claros, 2003; Capers et al., 2005; Norden et al., 2009; Bonner et al., 2013). The first phase has been described to comprise herbs, shrubs and climbers that emerge soon after site disturbance. The second successional phase is characterised by the emergence of early pioneer tree species, which dominate the site for between 10 and 30 years, depending on their life span. The third successional phase is dominated by long-lived pioneers, which emerge as early pioneers die off. The emergence of shade-tolerant species and other late successional species is thought to occur continuously during the establishment of both early pioneers and long-lived pioneer species (Finegan, 1996; Pena-Claros, 2003; Bonner et al., 2013).

A few studies have indicated that there is forest succession in plantation forests, particularly in tropical forests (Parrotta et al., 1997; Brockerhoff et al., 2008; Fawig et al., 2009). Some of the studies have suggested that such plantations may eventually convert to or facilitate the formation of secondary forests (Fawig et al., 2009). One of the tropical forests where forest succession has been reported in plantation forests is the Kakamega Rainforest in western Kenya (Fawig et al., 2009). The discovery of gold in this forest in 1923 led to commercial logging, which commenced in the early 1930s to clear up areas for gold mining (Tsingalia, 1990; Mitchell, 2004; Ouma et al., 2011). The situation necessitated the gazettement of the forest, which was done in 1933 (Glenday, 2006). By 1952, about 15 % of the closed canopy forest had been cleared (Schaab et al., 2010). Commercial logging intensified between 1952 and 1985 leading to a further decrease in the closed canopy forest cover by about 63 % (Wass, 1995; Althof, 2005; Schaab et al., 2010). Whereas some of the logged forest sites regenerated naturally into secondary forest, some were settled in by forest adjoining communities who provided labour for both mining and logging activities (Lung, 2009; Tsingalia and Kassily, 2009). Other logged sites were placed under agriculture and later abandoned, while others were planted with both indigenous and exotic species as plantation forests with a view of providing timber in the future. The plantation forests comprised mixed indigenous species, indigenous

monoculture species and exotic monoculture species, which were established between 1937 and 2005 (Lung and Schaab, 2006; KFS, 2010; Schaab et al., 2010). Mixed indigenous plantation forests comprised *Olea capensis* L., *Croton megalocarpus* Hutch., *Zanthoxylum gillettii* (De Wild.) Waterm. and *Prunus africana* (Hook.f.) Kalkm. (KFS, 2010). Indigenous monoculture plantations consisted of *Maesopsis eminii* Engl., *Zanthoxylum gillettii* and *Prunus africana*, while exotic monoculture plantations comprised *Pinus patula* Schlechtend. & Thonn., *Bischofia javanica* Blume and *Cupressus lusitanica* Mill. One common feature of these forest plantations is that they were planted at regular spacing of about 3 m between trees. The forest retained primary forest stands that were not subjected to commercial logging and were set aside as nature reserves. However, the nature reserves were exposed to selective logging by local communities between 1960s and early 1980s, which is estimated to have removed between 20 to 30% of the stems in the sub-canopy and main canopy layers (KEFRI, 2010). Thus, the nature reserves are presently commonly referred to as near-natural forest (but to avoid confusion with old-growth secondary forest, we refer to them in this paper as disturbed primary forest).

Following observations by Fawig et al. (2009) that plantation forests of this rainforest were undergoing forest succession and were therefore likely to convert to secondary forests in the future, we sought to examine the similarities and differences between plantation forests and secondary forests in this forest from a successional perspective. A clear understanding of the successional pathway in these plantation forests and its likely outcome is useful in providing insight on whether to change the prime function of some plantations from timber production to ecosystem functions, such as carbon sequestration and biodiversity conservation. It is also an important decision support tool for forest managers regarding the kind of plantations to establish in the future, how to manage them and the kind of logging operation to apply. Thus, with the disturbed primary forest serving as a control, we carried out a chronosequence study in this forest to understand changes in tree species composition and stand structure in secondary forest stands and plantation forests between 1930s and 2013. The objective of the study was to describe successional pathways of secondary and plantation forests with regard to (i) woody species diversity (ii) similarity in species composition, (iii) distribution of successional species in forest canopy strata, (iv) the fate of planted trees in the successional process, and (v) the stand structure of secondary and plantation forests.

## MATERIALS AND METHODS

### Study site

The study was carried out in Kibiri, Yala and Isecheno blocks of Kakamega Forest between April 2012 and December 2013. The

forest is a mid-elevation tropical rainforest – an eastern relic of the African equatorial rainforest (Kokwaro, 1988; Fawig et al., 2009). It is located in western Kenya between latitudes 0° 10' N and 0° 21' N and longitudes 34° 47' E and 34° 58' E at an elevation of 1,600 m above sea level (Fashing and Gathua, 2004; Musila et al., 2010). The area experiences a hot and wet climate characterised by a mean annual temperature of 25°C and an annual precipitation of 1,500 to 2,000 mm with a dry season between December and March (Otuoma et al., 2010). The forest is home to over 400 plant species (of which about 112 are tree species), 300 bird species and about seven endemic primate species (Kokwaro, 1988; Althof, 2005). The vegetation comprises a disturbed primary forest, secondary forests in different stages of succession, mixed indigenous forest plantations, indigenous and exotic forest plantations, and natural and man-made glades (Tsingalia and Kassily, 2009). Old-growth closed canopy natural forest stands are dominated by tree species such as *Funtumia africana* (Benth.) Stapf, *Antiaris toxicaria* Lesch., *Ficus exasperata* Vahl, *Croton megalocarpus* and *Celtis mildbradii* Engl. (Lung, 2009). The forest supports an adjoining human population of about 280,000 people who are distributed in surrounding farmlands and numerous isolated urban centres (Mutangah, 1996; KEFRI, 2010). The farmlands are fragmented into units measuring approximately 0.2 ha, each holding an average household of 8 to 12 people. Majority of these households are dependent on the forest to supplement their meagre agricultural produce. Some of the resources they obtain from the forest include fuel wood, timber, construction poles, medicine, fibre, pasture for livestock and indigenous fruits and vegetables (Althof, 2005; KEFRI, 2010).

### Study design

The study design followed the understanding that data were collected from three forest blocks, which were managed as distinct entities within the same forest ecosystem. The forest blocks comprised nine different forest vegetation types, which were the treatments in the study. The forest vegetation types were disturbed primary forest, old-growth secondary forest, middle-aged secondary forest, young secondary forest, mixed indigenous plantation, *Maesopsis eminii* indigenous monoculture plantation, and *Bischofia javanica*, *Cupressus lusitanica* and *Pinus patula* exotic monoculture plantations. They were treated as sub-blocks nested within each of the three forest blocks. The forest vegetation types were delineated from forest compartment registers (KFS, 2010) and geo-referenced with the aid of existing base maps (Schaab et al., 2010) in Geovis remote sensing software (FAO, 2003). The computer generated maps were validated through field assessment. Data were collected from the sub-blocks using a variable area technique, which ensured that trees of different stem sizes were assessed in transects of different sizes to enhance the probability of obtaining tree data in equal proportions (NAFORMA, 2010; Nath et al., 2010). The sampling unit comprised a concentric sample plot of 30 m radius with stratified sub-plots of 15 m, 10 m, 5 m and 2 m radius from the center of the sampling unit. The sub-plots were nested within sample plots, which were also nested within the nine sub-blocks. The observational unit of the study was an individual tree. The study employed a nested experimental design (Kuehl, 2000; Onwuegbuzie and Leech, 2007).

### Data collection

Stratified random sampling was employed to collect data on tree species types, tree height and stem diameter at breast height (DBH) from the sub-blocks (Gregoire and Valentine, 2007; Coe, 2008). Sample plots were randomly located in sub-blocks, but tree assessment was stratified on the basis of stem DBH. The 30 m

radius plot was used to measure the height and DBH of trees > 50 cm DBH. The 15 m radius sub-plot was used to measure the height and DBH of trees of 20.1 - 50 cm DBH. The 10 m radius sub-plot was used to measure the height and DBH of trees of 10.1 - 20 cm DBH. The 5 m radius sub-plot was used to measure the height and DBH of trees of 5.1 - 10 cm DBH; while the 2 m radius plot was used to measure the height and DBH of saplings ≥ 1.3 m in height, but with less than 5 cm DBH. Tree species were identified by their botanic names. Data on tree species were collected with the assistance of a plant taxonomist. Tree species that could not be identified in the field had their specimens collected and taken to the National Museums of Kenya herbarium for identification using previous collections. Data on tree DBH were obtained by measuring tree diameter in centimeters at 1.3 m above the ground using a diameter tape. The DBH of trees with a buttress was measured above the buttress. Tree height was measured in meters using a clinometer. Information on the age of disturbed sites, causes of disturbance and post-disturbance land use was obtained from forest compartment registers at the Kenya Forest Service office in Kakamega Forest (KFS, 2010). The information was corroborated through witness accounts by elderly members of forest adjoining communities who worked as casual labourers during commercial logging or forest plantation establishment.

### Data analysis

Tree species diversity was described using Shannon diversity index (Pena-Claros, 2003; Magurran, 2004; Newton, 2007). Tree species similarity to the disturbed primary forest was calculated using Jaccard's similarity index (Chandrasekharan and Rajagopalan, 1989; Real and Vargas, 1996; Chao et al., 2005). Variations in species diversity and similarity indices were analyzed using analysis of variance in Genstat at 5 % significance level (Buysse et al., 2004; VSN International, 2013).

Data on stem density, tree height and basal area among forest vegetation types were analyzed using analysis of variance in Genstat at 5% significance level (Sokal and Rohlf, 2012; VSN International, 2013) to determine possible variations between secondary and plantation forests. In situations where statistical significance was recorded, means were separated using the Ryan-Einot-Gabriel-Welsch Multiple Range Test (REGWQ) at 5% significance level (Krull and Craft, 2009; Sokal and Rohlf, 2012; Holt et al., 2013). Regression analyses were used to determine the relationship between tree species richness and stand age (Sykes, 1993).

## RESULTS

### Species composition

A total of 4,261 trees representing 85 woody species, 75 genera and 34 families were identified from an area of 36.82 ha. Seven woody species could not be identified. Among families, Euphorbiaceae and Moraceae had the highest number of species with each representing 10.6% of all the tree species. Rubiaceae and Sapotaceae had the second largest number of species with each accounting for 7.1 % of the woody species. Rutaceae and Ulmaceae tied for the third position with 5.9 % of the tree species. Approximately 54% of the tree species were represented in the main forest canopy, 62% were located in the sub-canopy, while 55% and 66 % were located in the understorey and shrub canopy layers, respectively.

**Table 1.** Floristic composition and species diversity of different forest vegetation types in Kakamega Forest in western Kenya.

Vegetation type	Families	Tree species		
		Maximum recorded	Mean per ha	Shannon diversity index
<i>Bischofia</i> plantation	10	17	10.7 ± 0.3 <sup>ab</sup>	2.5 ± 0.5 <sup>a</sup>
<i>Cupressus</i> plantation	9	16	10.0 ± 1.5 <sup>ab</sup>	4.8 ± 0.7 <sup>ab</sup>
Disturbed primary forest	18	51	32.7 ± 2.0 <sup>a</sup>	10.9 ± 2.2 <sup>abc</sup>
Middle-aged secondary forest	18	47	25.7 ± 5.4 <sup>a</sup>	12.3 ± 3.0 <sup>bc</sup>
<i>Maesopsis</i> plantation	14	38	20.3 ± 3.8 <sup>a</sup>	8.3 ± 1.6 <sup>abc</sup>
Mixed indigenous plantation	19	41	26.7 ± 2.7 <sup>a</sup>	9.0 ± 0.9 <sup>abc</sup>
Old secondary forest	19	54	34.0 ± 3.5 <sup>a</sup>	14.3 ± 2.8 <sup>c</sup>
<i>Pinus</i> plantation	14	38	19.3 ± 2.4 <sup>a</sup>	9.5 ± 1.5 <sup>abc</sup>
Young secondary forest	5	5	5.0 ± 1.0 <sup>c</sup>	2.7 ± 0.0 <sup>a</sup>
Mean tree species per ha: ( $F_{(1,8)} = 12.30$ ; $p < 0.001$ ); <i>l.s.d.</i> = 8.34			( $F_{(1,8)} = 5.46$ ; $p = 0.002$ ); <i>l.s.d.</i> = 5.34	

Forest vegetation types with different superscripts had significantly different number of woody species.

**Table 2.** Woody species representation in different forest canopy strata of nine forest vegetation types in Kakamega Forest in western Kenya.

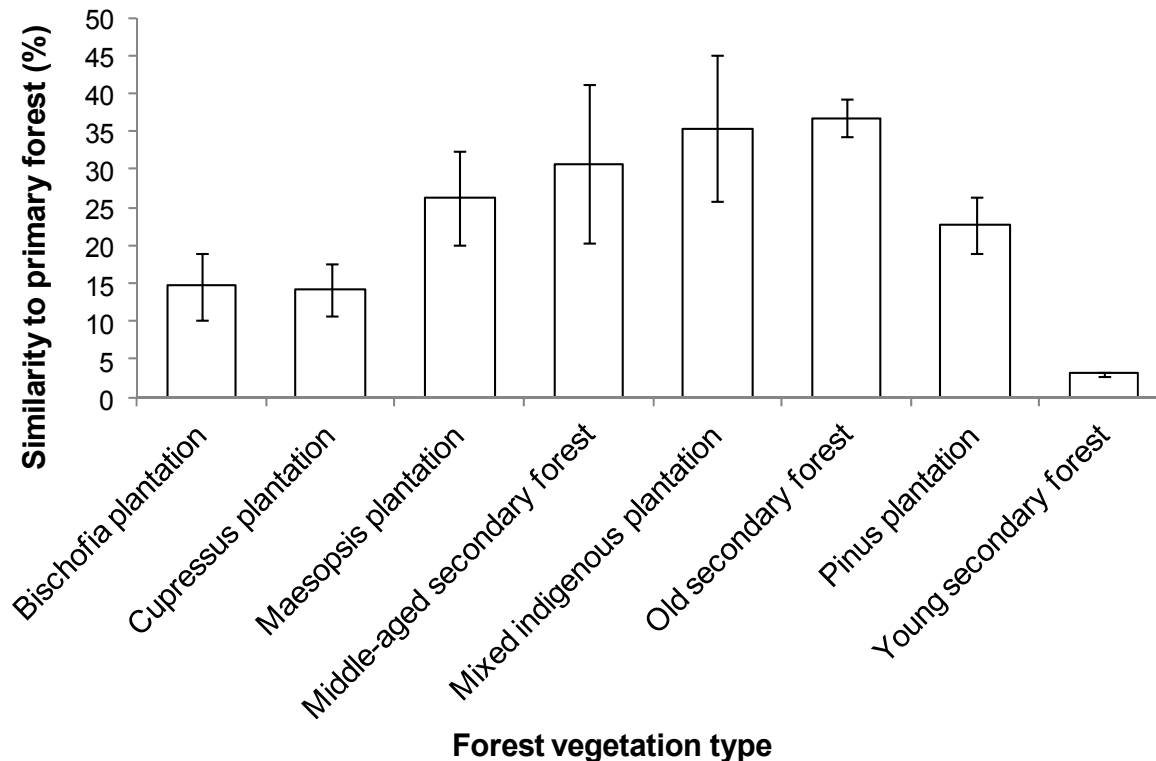
Vegetation	Mean tree species per ha			
	Main	Sub-canopy	Understorey	Shrub
<i>Bischofia</i> plantation	2.3 ± 0.7 <sup>ab</sup>	4.33 ± 0.7 <sup>ab</sup>	4.0 ± 1.0 <sup>ab</sup>	6.33 ± 0.3 <sup>ab</sup>
<i>Cupressus</i> plantation	2.3 ± 0.7 <sup>abc</sup>	1.67 ± 0.3 <sup>a</sup>	4.67 ± 0.3 <sup>abc</sup>	6.0 ± 2.0 <sup>ab</sup>
Disturbed primary forest	17.3 ± 1.3 <sup>e</sup>	14.7 ± 0.3 <sup>d</sup>	11.0 ± 1.5 <sup>d</sup>	14.33 ± 3.3 <sup>ab</sup>
Middle-aged secondary forest	8.0 ± 2.7 <sup>d</sup>	12.3 ± 1.7 <sup>cd</sup>	9.0 ± 1.7 <sup>bcd</sup>	16.7 ± 2.7 <sup>b</sup>
<i>Maesopsis</i> plantation	5.5 ± 1.3 <sup>abcd</sup>	8.0 ± 0.3 <sup>bc</sup>	9.3 ± 1.5 <sup>bcd</sup>	11.0 ± 3.3 <sup>ab</sup>
Mixed indigenous plantation	8.0 ± 2.0 <sup>bd</sup>	12.7 ± 0.3 <sup>cd</sup>	7.0 ± 1.0 <sup>abcd</sup>	13.3 ± 0.9 <sup>ab</sup>
Old secondary forest	15.7 ± 0.9 <sup>e</sup>	16.0 ± 0.6 <sup>d</sup>	10.0 ± 1.5 <sup>cd</sup>	16.0 ± 3.1 <sup>b</sup>
<i>Pinus</i> plantation	3.7 ± 2.2 <sup>abcd</sup>	8.3 ± 1.8 <sup>bc</sup>	6.0 ± 1.5 <sup>abcd</sup>	10.3 ± 2.4 <sup>ab</sup>
Young secondary forest	1 ± 0 <sup>a</sup>	3.0 ± 0.3 <sup>ab</sup>	2.7 ± 0.3 <sup>a</sup>	4.0 ± 0.3 <sup>a</sup>
<b>Mean</b>	7.2 ± 1.2	9.0 ± 1.0	7.1 ± 0.6	10.9 ± 1.0
Mean tree species per ha by canopy strata: ( $F_{(1,3)} = 3.38$ ; $p = 0.021$ ); <i>l.s.d.</i> = 2.79				

Different superscripts in the same column denote significant difference.

There was a significant variation in the representation of the 85 tree species among the nine forest vegetation types ( $F_{(1,8)} = 12.30$ ;  $p < 0.001$ ) (Table 1). A comparison of means indicated that the variation in species representation was caused by a significantly low number of tree species in *Bischofia javanica* and *Cupressus lusitanica* monoculture plantations, and the young secondary forest. Apart from the young secondary forest and *Bischofia javanica* and *Cupressus lusitanica* plantations, the number of tree species did not vary significantly between natural forest stands (disturbed primary forest, old-growth secondary forest and middle-aged secondary forest) and other plantation forests (mixed indigenous plantation, and *Maesopsis eminii* indigenous monoculture plantation and *Pinus patula* exotic monoculture plantation) ( $F_{(1,5)} = 0.96$ ;  $p = 0.463$ ). Apart from the young secondary forest, natural forest stands had higher Shannon diversity indices than

plantation forests, which suggested that they were relatively more species-rich than the latter ( $F_{(1,8)} = 5.46$ ;  $p = 0.002$ ) (Table 1). Among plantation forests, mixed indigenous, *Maesopsis eminii* and *Pinus patula* plantations had higher Shannon indices than *Cupressus* and *Bischofia* plantations.

Although the number of tree species did not vary significantly between natural forest stands and plantation forests except for *Bischofia javanica* and *Cupressus lusitanica* plantations and young secondary forest, a comparison of the distribution of tree species in the main canopy, sub-canopy, understorey and shrub canopy strata of the nine forest vegetation types indicated significant differences in species representation ( $F_{(1,3)} = 3.38$ ;  $p = 0.021$ ). The number of tree species in the four forest canopy layers was significantly higher for old-growth secondary forest than all the plantation forests (Table 2). Middle-aged secondary forest had more tree



**Figure 1.** The similarity of different forest vegetation types to the disturbed primary forest in tree species composition in Kakamega Forest in western Kenya.

species in the main canopy and shrub layer than all plantation forests, but it had comparable species representation with mixed indigenous, *Maesopsis eminii* and *Pinus patula* plantations in the sub-canopy and understorey layers. The disturbed primary forest had the largest number of tree species representation in the understorey and main canopy layers. The distribution of woody species in the young secondary forest, *Bischofia javanica* and *Cupressus lusitanica* forest plantations was significantly lower in all the canopy strata. Mixed indigenous plantation had significantly more tree species representation in the main and sub-canopy layers than other plantation forests.

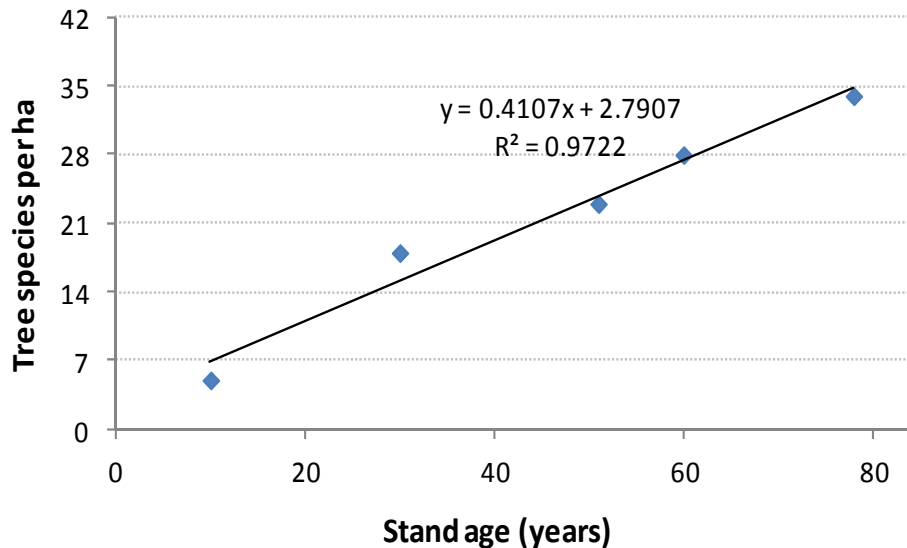
#### **Similarity of species composition to the primary forest**

There was a significant variation among forest vegetation types in tree species similarity to the disturbed primary forest ( $F_{(1,7)} = 8.08$ ;  $p < 0.001$ ). Tree species similarity to the disturbed primary forest ranged between 3.1% and 36.8%. The similarity of secondary forest stands to the disturbed primary forest increased with stand age. Old-growth secondary forest was more similar in species composition to the disturbed primary forest (36.8%) than middle-aged secondary forest (30.7%) and young

secondary forest (3.1%) (Figure 1). Among plantation forests, mixed indigenous plantation had higher similarity to the disturbed primary forest (35.4 %) than *Maesopsis* indigenous monoculture plantation (26.3%), and *Pinus* (22.7%), *Bischofia* (14.7%) and *Cupressus* (14.2%) exotic monoculture plantations.

#### **Effect of stand age on woody species richness**

There was a strong relationship between stand age and woody species richness among secondary forest stands ( $y = 0.4107x + 2.7907$ ;  $R^2 = 0.9722$ ) (Figure 2). For instance, ten year-old young secondary forest stands had between four and five early successional woody pioneers, such as *Psidium guajava* L., *Bridelia micrantha* (Hochst.) Baill. and *Harungana madagascariensis* Poir. The species composition of 30 year-old middle-aged secondary forest stands comprised an average of 18 tree species per ha which consisted of both early successional pioneers and long-lived pioneers, such as *Polyscias fulva* (Hiern) Harms and *Sapium ellipticum* (Hochst.) Pax. together with one or two shade-tolerant species, such as *Funtumia africana*. In middle-aged secondary forest stands of about 50 years in age, most early successional pioneers had disappeared, the number of long-lived pioneers increased, while more



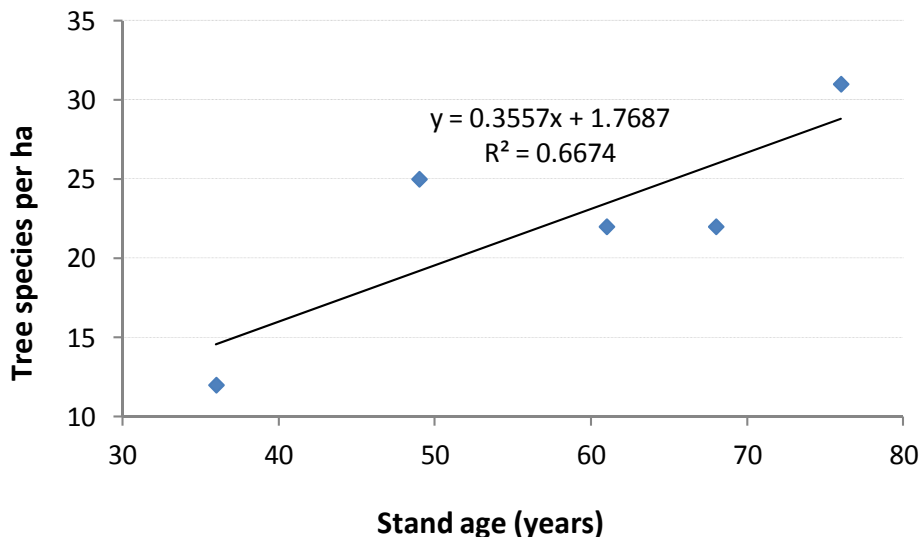
**Figure 2.** A linear regression relationship between stand age and species richness in secondary forest stands in Kakamega Forest in western Kenya.

shade-tolerant species, such as *Ficus sur* Forssk., *Antiaris toxicaria* and *Albizia gummifera* (J.F. Gmel.) C.A. Sm. were represented. For instance, *Bridelia micrantha* and *Psidium guajava* that were represented in ten and 30 year-old secondary forest stands had completely disappeared. The only early secondary pioneer species that was left was *Harungana madagascariensis*, which was present in the two earlier stands, but its abundance had decreased from 36 % in the ten year-old stand to 23 % in the 30 year-old stand to 14 % in the 50 year-old stand. The 50 year-old secondary forest stand had an average of 23 tree species per ha. In old-growth secondary forest stands of about 60 years in age, there were no early secondary pioneer species. The number of long-lived species had reduced, while the number of shade-tolerant species increased. For instance, *Funtumia africana*, *Antiaris toxicaria*, *Trilepsium madagascariense*, *Croton megalocarpus*, *Ficus exasperata* and *Aningeria altissima* (A. Chev.) Baehni., which were among the most abundant species in the disturbed primary forest, were represented among the ten most abundant species in 60 year-old secondary forest stands. The stand had approximately 28 tree species per ha. In 78 year-old secondary forest stands, the number of long-lived species had reduced further, while the number of shade-tolerant species increased. Comparing these stands with the 60 year-old secondary forest stands, the number of ten most abundant species in the disturbed primary forest increased from six to seven. The 78 year-old secondary forest stands had approximately 34 tree species per ha.

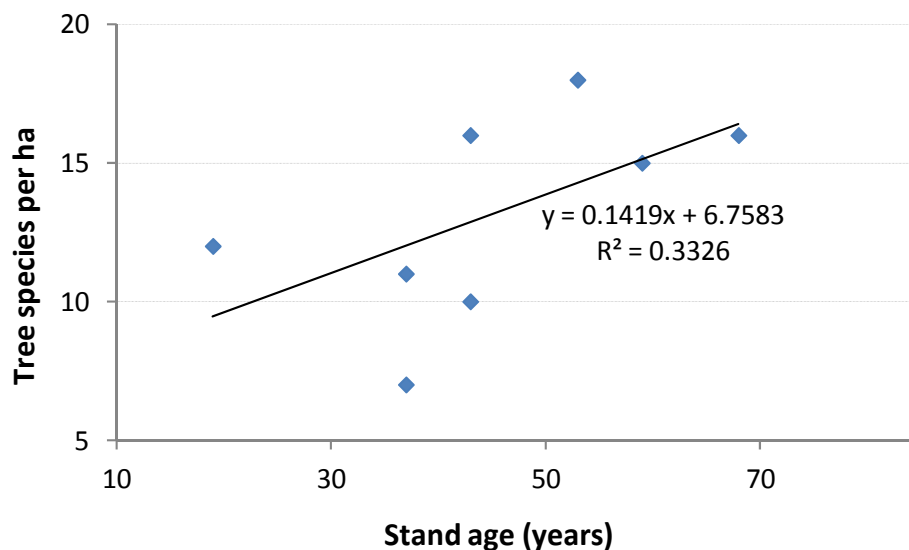
In indigenous plantation forests, the relationship between stand age and woody species richness was strong, but relatively weaker than that of secondary forest stands ( $y = 0.3557x + 1.7687$ ;  $R^2 = 0.6674$ ) (Figure 3).

For instance, a 61 year-old mixed indigenous plantation lacked early secondary pioneers, but had more long-lived pioneers and fewer shade-tolerant species than a 76 year-old stand, while the latter had more shade-tolerant species and fewer long-lived pioneers. Apart from *Prunus africana*, *Olea capensis*, *Trilepsium madagascariense* and *Zanthoxylum gillettii* which were planted, the 61 year-old stand had another 21 woody species, which recruited through forest succession. The species composition of a 61 year-old mixed indigenous plantation forest resembled that of a 50 year-old middle-aged secondary forest stand. A 76 year-old mixed indigenous forest plantation had about 30 other woody species apart from planted species and resembled a 60 year-old secondary forest stand. In *Maesopsis* indigenous monoculture plantations, a 36 year-old plantation had 12 woody species; a 49 year-old plantation had 25 woody species, while a 68 year-old plantation had 22 woody species apart from *Maesopsis eminii*, which was planted.

In exotic plantation forests, the relationship between stand age and woody species richness was much weaker than that of secondary forest stands and indigenous plantation forests ( $y = 0.1419x + 6.7583$ ;  $R^2 = 0.3326$ ) (Figure 4). Increase in stand age did not appear to have a significant influence on the number of wood species. For instance, in *Pinus patula* plantations, a 43 year-old stand had 16 tree species, while 53, 59 and 68 year-old stands had 18, 15 and 16 woody species, respectively. The situation was similar in *Bischofia* and *Cupressus* plantations. In *Bischofia* plantations, 37 year-old stands had approximately 11 woody species, while 43 year-old stands had 10 species. In *Cupressus* plantations, 37 year-old stands had about 7 tree species, while 19 year-old stands had 12 species.



**Figure 3.** A linear regression relationship between stand age and species richness in indigenous forest plantations in Kakamega Forest in western Kenya.



**Figure 4.** Relationship between stand age and species richness in exotic forest plantations in Kakamega Forest in western Kenya.

**Stand structure**

**Stem density**

Among families, Phyllanthaceae had the highest number of stems with 16.7% of all the tree stems. Moraceae was second with 11.4% of the stems, while Rhamnaceae was third with 8.2%. Apocynaceae and Euphorbiaceae were fourth and fifth with 8.1 and 7.5%, respectively. Families with the least representation were *Papilionaceae*, *Rhizophoraceae*, *Meliaceae*, *Guttiferae*, *Alangiaceae*,

*Violaceae*, *Ebenaceae*, *Verbenaceae*, *Annonaceae*, *Loganiaceae*, *Boraginaceae*, *Pittosporaceae*, *Myrsinaceae* and *Melanthaceae* with less than one percent of tree stems. Among tree species, *Bischofia javanica* had the largest number of stems at 16.7% of all the stems; *Maesopsis eminii* was second with 8.2%, while *Funtumia africana* was third with 8.1%. *Rothmania longiflora*, *Synsepalum cerasiferum* and *Vitex keniensis* were the least represented tree species with 0.29% of tree stems each. Considering that some of the most abundant species were planted and this certainly

**Table 3.** Relationship between basal area, stem density and mean stem DBH among different forest vegetation types in Kakamega Forest in western Kenya.

Vegetation type	Stand attributes of stems $\geq 10$ cm DBH			
	Stem density (stems $\text{ha}^{-1}$ )	Mean tree height (m)	Mean DBH (cm)	Basal area ( $\text{m}^2\text{ha}^{-1}$ )
<i>Bischofia</i> plantation	542.1 $\pm$ 101.6 <sup>c</sup>	20.2 $\pm$ 0.9 <sup>bc</sup>	29.3 $\pm$ 2.3 <sup>ab</sup>	30.2 $\pm$ 1.1 <sup>b</sup>
<i>Cupressus</i> plantation	354.6 $\pm$ 17.3 <sup>ab</sup>	21.6 $\pm$ 1.3 <sup>bcd</sup>	35.3 $\pm$ 0.4 <sup>b</sup>	26.8 $\pm$ 1.1 <sup>b</sup>
Disturbed primary forest	346.1 $\pm$ 16.8 <sup>ab</sup>	26.7 $\pm$ 1.8 <sup>d</sup>	55.9 $\pm$ 4.2 <sup>d</sup>	48.2 $\pm$ 7.1 <sup>c</sup>
Middle-aged secondary forest	332.9 $\pm$ 21.1 <sup>ab</sup>	18.1 $\pm$ 0.4 <sup>b</sup>	33.9 $\pm$ 2.9 <sup>b</sup>	21.0 $\pm$ 2.0 <sup>ab</sup>
<i>Maesopsis</i> plantation	447 $\pm$ 24.0 <sup>bc</sup>	23.9 $\pm$ 0.3 <sup>cd</sup>	38.2 $\pm$ 5.1 <sup>b</sup>	31.4 $\pm$ 2.3 <sup>b</sup>
Mixed indigenous plantation	303.6 $\pm$ 13.5 <sup>ab</sup>	25.3 $\pm$ 1.3 <sup>d</sup>	51.0 $\pm$ 0.4 <sup>cd</sup>	34.1 $\pm$ 2.5 <sup>b</sup>
Old secondary forest	252.9 $\pm$ 36.5 <sup>a</sup>	24.7 $\pm$ 0.5 <sup>cd</sup>	50.9 $\pm$ 3.1 <sup>cd</sup>	28.8 $\pm$ 4.8 <sup>b</sup>
<i>Pinus</i> plantation	308.3 $\pm$ 31.3 <sup>ab</sup>	25.6 $\pm$ 1.5 <sup>d</sup>	40.5 $\pm$ 1.7 <sup>bc</sup>	27.5 $\pm$ 1.9 <sup>b</sup>
Young secondary forest	404.8 $\pm$ 24.1 <sup>abc</sup>	11.4 $\pm$ 0.2 <sup>a</sup>	20.8 $\pm$ 0.5 <sup>a</sup>	11.0 $\pm$ 0.9 <sup>a</sup>
	( $F_{(1,8)} = 5.63$ ; $p = 0.002$ ); $l.s.d. = 110.1$	( $F_{(1,8)} = 21.46$ ; $p < 0.001$ ); $l.s.d. = 3.2$	( $F_{(1,8)} = 18.20$ ; $p < 0.001$ ); $l.s.d. = 7.99$	( $F_{(1,8)} = 10.51$ ; $p < 0.001$ ); $l.s.d. = 9.21$

Different superscripts denote significant difference.

increased their abundance, we considered also non-planted species separately and *Funtumia africana* emerged the most represented with 14.2% of the tree stems. *Antiaris toxicaria* was second with 6.9%, *Psidium guajava* was third with 5.3%, *Trilepisium madagascariense* was fourth with 5.2%, while *Bridelia micrantha* was fifth with 4.2% of all the stems. However, the list of least represented tree species did not change.

There was no significant variation in stem density for stems  $\geq 0.1$  cm DBH among the nine forest vegetation types ( $F_{(1,8)} = 2.0$ ;  $p = 0.113$ ). Young secondary forest had the highest number of stems  $\geq 0.1$  DBH with 6,266.8  $\pm$  140.4 stems  $\text{ha}^{-1}$ . It was closely followed by *Bischofia* plantations with 6,032.6  $\pm$  304.2 stems  $\text{ha}^{-1}$ . Old-growth secondary forest had the least number of tree stems  $\geq 0.1$  DBH with 3,176.5  $\pm$  563.3 stems  $\text{ha}^{-1}$ . Among tree stems  $\geq 10$  cm DBH, there was a significant variation in stem density among the nine forest vegetation types ( $F_{(1,8)} = 5.63$ ;  $p = 0.002$ ). The variation was attributed to significantly fewer tree stems in old-growth secondary forest stands with 252.9  $\pm$  36.51 stems  $\text{ha}^{-1}$  and significantly more stems in *Bischofia* and *Maesopsis* monoculture plantations with 542.1  $\pm$  101.6 stems  $\text{ha}^{-1}$  and 447.0  $\pm$  23.97 stems  $\text{ha}^{-1}$ , respectively (Table 3).

### Tree height

There was a significant variation in tree height among the nine vegetation types ( $F_{(1,8)} = 21.46$ ;  $p \leq 0.001$ ). The variation was attributed to low tree height in middle-aged secondary forest, young secondary forest and *Bischofia javanica* monoculture plantation (Table 3). Apart from young secondary forest, all vegetation types had shrub, understorey, sub-canopy and main forest canopy layers. The young secondary forest lacked the main canopy and sub-canopy layers.

### Basal area

There was a significant variation in basal area among the nine forest vegetation types ( $F_{(1,8)} = 10.51$ ;  $p < 0.001$ ). The variation was attributed to lower basal area in young secondary and middle-aged secondary forests than the other forest vegetation types (Table 3). Although there was no significant difference in basal area between old-growth secondary forest and plantation forests, the former had a relatively lower basal area than mixed indigenous plantation. This suggests that forest plantations had relatively higher basal area than secondary forests of comparable age. The disturbed primary forest had a significantly higher basal area than all forest vegetation types. Analysis of the relationship between basal area, stem density and mean stem DBH indicated that stem DBH had a stronger influence on stand basal area than stem density (Table 3). For instance, *Bischofia* plantation had the highest stem density (stems  $\geq 10$  cm DBH), but it ranked fourth in basal area because its mean stem DBH was second lowest after young secondary forest. Similarly, young secondary forest was ranked third in stem density, but it had the lowest basal area because it had the lowest mean stem DBH. The disturbed primary forest had a significantly larger mean stem DBH than all forest vegetation types and this is likely to have contributed to its high basal area given that its stem density was not significantly different from other forest vegetation types.

## DISCUSSION

### Species composition

The results of this study confirm earlier indications that plantation forests were undergoing secondary forest



succession in tropical forests (Parrotta et al., 1997; Fawig et al., 2009). The situation is exemplified by the fact that there was no significant difference in the number of tree species between secondary forest stands and most plantation forests. Even the few monoculture plantation forests, such as *Bischofia javanica* and *Cupressus lusitanica* plantations, which had significantly fewer tree species than most secondary forests, had between 10 and 15 naturally recruited indigenous species. Thus, it is reasonable to argue that plantation forests in this rainforest do not differ from secondary forests in tree species composition.

Despite a pattern of tree species convergence between secondary forests and plantation forests, there were four key areas where the two forest types were dissimilar, namely: (i) secondary forest successional pathway, (ii) representation of successional species in canopy strata, (iii) persistence of planted trees in mature plantation forests, and (iv) effect of stand age on species composition. Whereas forest succession often began with early successional pioneers in secondary forest stands, the results of this study suggest that forest succession in plantation forests tended to bypass this light demanding early pioneers' stage. The process appeared to commence with the recruitment of long-lived pioneers and shade-tolerant species in plantation forests. As illustrated by Finegan (1996), Chazdon (2003), Pena-Claros (2003) and Bonner et al. (2013) on changes in species assembly in forest stands, it is likely that the formation of a canopy by planted trees in plantation forests facilitated the recruitment of long-lived pioneer and shade-tolerant species instead of early successional pioneers. This line of reasoning is supported by the fact that natural recruits were represented mostly in the shrub and understorey layers of plantation forests, which suggests that they often recruited when plantation trees had closed the forest canopy. Thus, whereas it took a fairly long period of time for long-lived pioneers and shade-tolerant species to recruit in secondary forests, it took a relatively shorter duration for the same tree species to recruit in plantation forests. The net effect is that secondary forests ended up having fairly similar species composition with plantation forests of comparable or younger age.

The other issue that this study considered was whether similarity in tree species composition would lead to the conversion of plantation forests to secondary forests as reported by Fawig et al. (2009). We looked at this observation from three perspectives, that is the representation of successional species in canopy strata, persistence of planted trees in mature plantation forests, and the effect of stand age on species composition. Our results indicated that successional species were represented in all the forest canopy layers in secondary forests, while in plantation forests, they were located in the shrub and understorey layers of monoculture plantations, and the shrub, understorey and sub-canopy

layers of mixed indigenous plantations. The results indicated also that some mixed indigenous plantations were nearly indistinguishable from secondary forest while monoculture plantations had maintained a plantation physiognomy. Unlike secondary forests where late successional species had replaced early successional pioneers, planted trees persisted in plantation forests, which suggests that chances of shrub and understorey species reaching the main canopy remain slim at this stage. Moreover, the results illustrated that species composition changed with stand age in secondary forests and mixed indigenous plantation, but not in monoculture plantations. Thus, in the absence of logging operations or some major disturbance events that would remove trees in the main canopies of monoculture plantations as suggested by Parrotta et al. (1997) and Hardiman et al. (2013), it is unlikely that natural recruits would dislodge planted trees from the main canopies of monoculture plantations and convert the plantations to secondary forests any time soon. Consequently, the suggestion by Fawig et al. (2009) that plantation forests in Kakamega Forest are likely to develop into old-growth secondary forests in the near future may only apply to mixed indigenous plantations. The phenomenon is akin to findings by Pena-Claros (2003) and Van Breugel et al. (2007) that species changes during forest succession may occur slowly and it may take several decades for understorey and sub-canopy species to replace existing canopy species. In Kakamega Forest, the spacing of planted trees at about three meters may delay the process much longer because this spacing presents natural recruits with a great challenge in reaching the main canopy of mature forest stands. We suspect that it was easier for successional species to reach the sub-canopy in mixed indigenous plantation forests because planted indigenous tree species grew at different rates, which provided recruits with a relatively better chance of competing with slow growers.

### Stand structure

The results of the study indicated that the stem density of young and middle-aged secondary forests was not significantly different from that of plantation forests. However, the stem density of old-growth secondary forest stands was significantly lower than that of plantation forests. Although these results support findings by Fawig et al. (2009) in this forest that stem density can be as high in plantation forests as in secondary forest stands, they create a new phenomenon regarding stand structure in old-growth secondary forest. Since the stem density of disturbed primary forest, young secondary forest and middle-aged secondary forest was not significantly different from all the plantation forests, a significantly lower stem density in all old-growth secondary forest stands can be looked at from two perspectives: (i) old-

growth secondary forest stands were undergoing successional transition after which their stem density would increase or (ii) the stem density of the disturbed primary forest should have been in the same range as old-growth secondary forest, but it was higher as a result of recovery from selective logging operations that it was subjected to between 1960s and early 1980s, which made its stem density to resemble that of young and middle-aged secondary forests. These suggestions notwithstanding, we do not have a conclusive explanation for the low stem density in old-growth secondary forests in this rainforest.

The observation that young and middle-aged secondary forests had significantly lower mean tree height than most plantation forests was consistent with those of Fawig et al. (2009) that there were variations in tree height between plantation forests and secondary forests. Given that the stand age of middle-aged secondary forests was comparable to that of most plantation forests and yet the former were relatively shorter, the results agree with those of Lung (2009) that plantation forests grow faster than secondary forests. However, the fact that the mean tree height of old-growth secondary was not significantly different from most plantation forests of comparable age, supports findings by Pena-Claros (2003) and Ruiz et al. (2005) that tree height and basal area of secondary forests are positively correlated with stand age.

Our results indicated that plantation forests had relatively higher stand basal area than secondary forests of comparable age. The basal area of old-growth secondary forest stands was not significantly different from that of most plantation forests, but middle-aged and young secondary forests had significantly lower basal area than all the plantation forests. As illustrated by Montgomery and Chazdon (2001), McElhinny et al. (2005) and Da Silva et al. (2012) on changes in structural complexity of forest stands, we suspect that the difference in basal area between secondary forest stands and plantation forests can be explained by the results on stem density and mean stem DBH. Generally, it takes natural forest stands a relatively longer duration to attain structural complexity similar to plantation forests. This phenomenon arises from the fact that early successional pioneers, which occupy a secondary forest for the first two to three decades, disappear as long-lived species take over. The emergence of long-lived pioneers and the subsequent disappearance of early successional pioneers (Finegan, 1996; Pena-Claros, 2003; Norden et al., 2009; Bonner et al., 2013) suggest that middle-aged forests, in which they are commonly found, may be aged between 30 and 50 years but are much younger in structural complexity with regard to tree height and mean stem DBH. In old-growth secondary forests, which mostly comprise late successional species, a majority of the trees have persisted long enough to enable them attain tree height and mean stem DBH that is either equal or greater than that of trees in mature plantation forests. In

plantation forests, most planted trees persists to maturity and this gives them a competitive edge in basal area, stem DBH and tree height over secondary forests of comparable age.

## Conclusion

Natural forest regeneration is on-going in both secondary and plantation forests in Kakamega Forest. There is presently no difference in tree species composition between the two forest types. However, natural recruits occupy all the forest canopy strata in secondary forests, but are represented mainly in the shrub and understory layers in monoculture plantation forests, and the shrub, understory and sub-canopy layers of mixed indigenous plantations. This suggests that forest succession in plantation forests commences after canopy closure and hence bypasses the light-demanding early pioneers' stage. Mixed indigenous plantations have become nearly similar to old-growth secondary forests, but monoculture plantations have maintained a plantation physiognomy. Structurally, younger secondary forest stands do not differ from plantation forests in stem density, but old-growth secondary forests have significantly lower stem density. The mean tree height and basal area of old-growth secondary forest stands do not differ from those of plantation forests of comparable age, but young secondary and middle-aged secondary forest stands have significantly lower mean tree height and basal area than plantation forests of comparable age. Overall, forest succession has progressed in plantation forests to an extent that mixed indigenous plantations are likely to perform ecosystem functions, such as carbon sequestration, biodiversity conservation and water catchment protection as effectively as secondary forests. Monoculture forest plantations, on the other hand, may be less effective in performing these functions, but more effective in timber provision.

## Conflict of Interests

The author(s) have not declared any conflict of interests.

## ACKNOWLEDGEMENTS

The study was supported with funds from the Kenya Forestry Research Institute. We thank Simon Mathenge and Joel Mbogani for assisting with the identification of tree species types. We thank two anonymous reviewers for their invaluable critique of an earlier draft.

## REFERENCES

- Althof A (2005). Human impact on flora and vegetation of Kakamega Forest, Kenya: Structure, distribution and disturbance of plant

- communities in an East African rainforest. Ph.D dissertation University of Koblenz-Landau, Germany. P. 213.
- Bonner MTL, Schmidt S, Shoo LP (2013). A meta-analytical global comparison of aboveground biomass accumulation between tropical secondary forests and monoculture plantations. *Forest Ecol. Manag.* 291: 73–86. <http://dx.doi.org/10.1016/j.foreco.2012.11.024>
- Brockhoff EG, Jactel H, Parrotta JA, Quine CP, Sayer J (2008). Plantation forests and biodiversity: oxymoron or opportunity? *Biodivers Conserv.* 17:925–951. [http://dx.doi.org/10.1007/978-90-481-2807-5\\_1](http://dx.doi.org/10.1007/978-90-481-2807-5_1)
- Brown S, Lugo AE (1990). Tropical secondary forests. *J. Trop. Ecol.* 6: 1–32. <http://dx.doi.org/10.1017/S0266467400003989>
- Buysse W, Stern R, Coe R (2004). GenStat Discovery Edition for everyday use. International Centre for Research in Agroforestry, Nairobi, Kenya. P. 114.
- Capers RS, Chazdon RL, Brenes AR, Alvarado BV (2005). Successional dynamics of woody seedling communities in wet tropical secondary forests. *J. Ecol.* 93:1071–1084. <http://dx.doi.org/10.1111/j.1365-2745.2005.01050.x>
- Chandrasekharan MP, Rajagopalan R (1989). Groupability in an analysis of the properties of binary data matrices for group technology. *Int. J. Prod. Res.* 27:399–416. <http://dx.doi.org/10.1080/00207548908942606>
- Chao A, Chazdon RL, Colwell RK, Shen T (2005). A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecol. Letters.* 8:148–159. <http://dx.doi.org/10.1111/j.1461-0248.2004.00707.x>
- Chua SC, Ramage BS, Ngo KM, Potts MD, Lum SKY (2013). Slow recovery of a secondary tropical forest in Southeast Asia. *Forest Ecol. Manag.* 308:153–160. <http://dx.doi.org/10.1016/j.foreco.2013.07.053>
- Chazdon RL (2003). Tropical forest recovery: legacies of human impact and natural disturbances. *Perspect Plant Ecol.* 6:51–71. <http://dx.doi.org/10.1078/1433-8319-00042>
- Chazdon RL, Finegan B, Capers RS, Salgado-Negret B, Casanoves F, Boukili V, Norden N (2010). Composition and dynamics of functional groups of trees during tropical forest succession in northeastern Costa Rica. *Biotropica.* 42:31–40. <http://dx.doi.org/10.1111/j.1744-7429.2009.00566.x>
- Coe R (2008). Designing ecological and biodiversity sampling strategies. Working paper no. 66. World Agroforestry Centre, Nairobi.
- Da Silva D, Balandier P, Boudon F, Marquier A, Godin C (2012). Modeling of light transmission under heterogeneous forest canopy: an appraisal of the effect of the precision level of crown description. *Ann Forest Sci.* 69:181–193. <http://dx.doi.org/10.1007/s13595-011-0139-2>
- Fashing PJ, Gathua JM (2004). Spatial variability in the vegetation structure and composition of an East African rain forest. *Afr. J. Ecol.* 42:189–197. <http://dx.doi.org/10.1111/j.1365-2028.2004.00512.x>
- FAO (2003). Geovis software. The Africover Initiative. Food and Agricultural Organisation of the United Nations, Rome.
- FAO (2010). Global forest resources assessment 2000–2010. Food and Agriculture Organization of the United Nations, Rome. P. 378.
- Farwig N, Sajita N, Bohning-Gaese K (2009). High seedling recruitment of indigenous tree species in forest plantations in Kakamega Forest, western Kenya. *Forest Ecol. Manag.* 257:143–150. <http://dx.doi.org/10.1016/j.foreco.2008.08.022>
- Finegan B (1996). Pattern and process in neotropical secondary rain forests: the first 100 years of succession. *Trends Ecol. Evol.* 11:119–124. [http://dx.doi.org/10.1016/0169-5347\(96\)81090-1](http://dx.doi.org/10.1016/0169-5347(96)81090-1)
- Forrester DI (2014). A stand-level light interception model for horizontally and vertically heterogeneous canopies. *Ecol. Model.* 276:14–22. <http://dx.doi.org/10.1016/j.ecolmodel.2013.12.021>
- Glenday J (2006). Carbon storage and emissions offset potential in an east African tropical rainforest. *Forest Ecol. Manag.* 235:72–83. <http://dx.doi.org/10.1016/j.foreco.2006.08.014>
- Gregoire TG, Valentine HT (2007). Sampling strategies for natural resources and the environment. Chapman and Hall, London. P. 474.
- Guariguata MR, Ostertag R (2001). Neotropical secondary forest succession: changes in structural and functional characteristics. *Forest Ecol. Manag.* 148:185–206. [http://dx.doi.org/10.1016/S0378-1127\(00\)00535-1](http://dx.doi.org/10.1016/S0378-1127(00)00535-1)
- Hardiman BS, Bohrer G, Gough CM, Curtis P S (2013). Canopy structural changes following widespread mortality of canopy dominant trees. *Forests.* 4:537–552. <http://dx.doi.org/10.3390/f4030537>
- Holt DV, Wolf J, Funke J, Weisbrod M, Kaiser S (2013). Planning impairments in schizophrenia: Specificity, task independence and functional relevance. *Schizophr Res.* 149:174–179. <http://dx.doi.org/10.1016/j.schres.2013.06.018> PMID:23827098
- Kanowski J, Catterall CP (2010). Carbon stocks in aboveground biomass of monoculture plantations, mixed species plantations and environmental restoration plantings in north-east Australia. *Ecol. Manage and Rest.* 11:119–126. <http://dx.doi.org/10.1111/j.1442-8903.2010.00529.x>
- KEFRI (2010). Demonstrating techniques of rehabilitating degraded natural forests in western Kenya. Research Note, Kenya Forestry Research Institute, Muguga, Kenya.
- KFS (2010). Kakamega forest compartment register: Sheet 10. Kenya Forest Service, Nairobi.
- Kokwaro JO (1988). Conservation status of the Kakamega Forest in Kenya - the easternmost relic of the equatorial rainforests of Africa. *Monog Syst Bot.* 25:471 – 489.
- Krull K, Craft C (2009). Ecosystem development of a sandbar emergent tidal marsh, Altamaha river estuary, Georgia, USA. *Wetlands.* 29:314–322. <http://dx.doi.org/10.1672/06-178.1>
- Kuehl RO (2000). Design of experiments: Statistical principles of research design and analysis. Second edn. Duxbury Press, USA.
- Lung M (2009). An analysis of fragmentation effects in Kakamega Forest in relation to reforestation benefits. Working Paper, May 2009, Eco2librium LLC Project, Kakamega, Kenya.
- Lung T, Schaab G (2006). Assessing fragmentation and disturbance of west Kenyan rainforests by means of remotely sensed time series data and landscape metrics. *Afr. J. Ecol.* 44:491–506. <http://dx.doi.org/10.1111/j.1365-2028.2006.00663.x>
- Magurran A (2004). Measuring biological diversity. Blackwell Publishing, Oxford, UK.
- McElhinny C, Gibbons P, Brack C, Bauhus J (2005). Forest and woodland stand structural complexity: Its definition and measurement. *Forest Ecol. Manag.* 218:1–24. <http://dx.doi.org/10.1016/j.foreco.2005.08.034>
- Mitchell N (2004). The exploitation and disturbance history of Kakamega Forest, Western Kenya, BIOTA East Report No. 1, Bielefelder Ökologische Beiträge, Band 20, Bleher B and Dalitz H (eds).
- Montgomery RA, Chazdon RL (2001). Forest structure, canopy architecture and light transmittance in tropical wet forests. *Ecology.* 82: 2707–2718. [http://dx.doi.org/10.1890/0012-9658\(2001\)082\[2707:FSCAAL\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(2001)082[2707:FSCAAL]2.0.CO;2)
- Musila W, Oesker M, Gliniars R, Todt H, Dalitz H (2010). Increasing resilience to climate change of a Kenyan biodiversity hotspot through forest restoration. Paper presented at the 18<sup>th</sup> Commonwealth Forestry Conference, 28th June to 2nd July 2010 Edinburgh, Scotland, United Kingdom.
- Mutangah JG (1996). An investigation of vegetation status and process in relation to human disturbance in Kakamega Forest western Kenya. PhD Thesis, University of Wales, UK.
- NAFORMA (2010). Field manual: Biophysical survey, Document M01-2010. National Forestry Resources Monitoring and Assessment of Tanzania, Forestry and Beekeeping Division, Ministry of Natural Resources and Tourism, Dar es Salaam, Tanzania.
- Nath CD, Pellissier R, Garcia C (2010). Comparative efficiency and accuracy of variable area transects versus square plots for sampling tree diversity and density. *Agroforest Syst.* 79:223–236. <http://dx.doi.org/10.1007/s10457-009-9255-5>
- Newton AC (2007). Forest ecology and conservation: a handbook of techniques. Oxford University Press, Oxford, UK. <http://dx.doi.org/10.1093/acprof:oso/9780198567448.001.0001>
- Norden N, Chazdon RL, Chao A, Yi-Huei J, Vilchez-Alvarado B (2009). Resilience of tropical rain forests: tree community reassembly in secondary forests. *Ecol. Letters.* 12:385–394. <http://dx.doi.org/10.1111/j.1461-0248.2009.01292.x> PMID:19379133
- Omeja PA, Obua J, Rwetsiba A, Chapman CA (2012). Biomass

- accumulation in tropical lands with different disturbance histories: Contrasts within one landscape and across regions. *Forest Ecol. Manag.* 269:293-300. <http://dx.doi.org/10.1016/j.foreco.2011.12.044>
- Onwuegbuzie AJ, Leech NL (2007). Sampling designs in qualitative research: Making the sampling process more public. *The Qualitative Report.* 12:238-254.
- Otuoma J, Kinyamario J, Ekaya W (2010). Regeneration dynamics of woody species in degraded natural forests in western Kenya. Proceedings of 2nd Regional Universities Forum Biennial Meeting 20-24 September 2010, Entebbe, Uganda.
- Ouma KO, Stadel C, Eslamian S (2011). Perceptions of tourists on trail use and management implications for Kakamega Forest, western Kenya. *Journal of Geography and Regional Planning.* 4:243-250.
- Parrotta JA, Turnbull JW, Jones N (1997). Catalyzing native forest regeneration in degraded lands. *Forest Ecol and Manag.* 99: 1-7. [http://dx.doi.org/10.1016/S0378-1127\(97\)00190-4](http://dx.doi.org/10.1016/S0378-1127(97)00190-4)
- Pena-Claros M (2003). Changes in forest structure and species composition during secondary forest succession in the Bolivian Amazon. *Biotropica.* 35:450 – 461. <http://dx.doi.org/10.1646/01078>
- Pooter L, Bongers F, Sterck FJ, Woll H (2005). Beyond the regeneration phase: Differentiation of height–light trajectories among tropical tree species. *J. Ecol.* 93: 256–267. <http://dx.doi.org/10.1111/j.1365-2745.2004.00956.x>
- Real R, Vargas JM (1996). The probabilistic basis of Jaccard's index of similarity. *Syst Biol.* 45:380-385. <http://dx.doi.org/10.1093/sysbio/45.3.380>
- Ruiz J, Maria CF, Chazdon RL (2005). Vegetation structure, composition, and species richness across a 56-year chronosequence of dry tropical forest on Providencia Island, Colombia. *Biotropica.* 37:520–530. <http://dx.doi.org/10.1111/j.1744-7429.2005.00070.x>
- Schaab G, Khayota B, Eilu G, Wagele W (2010). The BIOTA East Africa Atlas: Rainforest change over time. Karlsruhe University of Applied Sciences, Germany.
- Sokal RR, Rohlf FJ (2012). *Biometry: The principles and practice of statistics in biological research*, Fourth edn. WH Freeman, New York.
- Sykes A (1993). *An introduction to regression analysis*. Law School, University of Chicago.
- Tsingalia MH (1990). Habitat disturbance, severity and patterns of abundance in Kakamega Forest, western Kenya. *Afr. J. Ecol.* 28: 213-226. <http://dx.doi.org/10.1111/j.1365-2028.1990.tb01154.x>
- Tsingalia MH, Kassily FN (2009). The origins Kakamega Forest grasslands: A critical review. *J. Hum. Ecol.* 27(2):129-135.
- UNDP (2000). UNEP, World Bank and World Resources Institute. *A Guide to world resources 2000–2001: People and ecosystems: The fraying web of life*. World Resources Institute, Washington DC, USA. P. 276.
- Van Breugel M, Bongers F, Martinez-Ramos M (2007). Species dynamics during early secondary forest succession: Recruitment, mortality and species turnover. *Biotropica.* 35:610–619.
- VSN International (2013). *Genstat version 16*, Hemel, Hempstead, UK.
- Wass P (1995). *Kenya's indigenous forests: Status, management and conservation*. Gland, IUCN, Switzerland. P. 135. <http://dx.doi.org/10.1111/j.1744-7429.2007.00316.x>
- Wright SJ, Kitajima K, Kraft NJB, Reich PB, Wright IJ, Bunker DE, Condit R, Dalling JW, Davies SJ, Diaz S, Engelbrecht BMJ, Harms K, Hubbell SP, Marks CO, Ruiz-Jaen MC, Salvador CM, Zanne AE (2010). Functional traits and the growth–mortality trade-off in tropical trees. *Ecology.* 91:3664–3674. <http://dx.doi.org/10.1890/09-2335.1> PMID:21302837