ADDIS ABABA UNIVERSITY

SCHOOL OF GRADUATE STUDIES

TREE SEEDLINGS AND SAPLINGS IN TREEFALL GAPS AND UNDER CANOPY SHADES IN SHASHEMENNE-MUNESSA NATURAL FOREST

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June, 1999

TREE SEEDLINGS AND SAPLINGS IN TREEFALL GAPS AND UNDER CANOPY SHADES IN SHASHEMENNE-MUNESSA NATURAL FOREST

A thesis submitted to the School of Graduate Studies of Addis Ababa University in partial fulfillment of the requirements for the Degree of Master of Science in Botanical Sciences

BY

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June, 1999

ACKNOWLEDGEMENTS

I am greatly indebted to my research advisor Dr. Masresha Fetene for his invaluable advice, guidance, devoted assistance and encouragement. The critical comments and corrections made by Dr. Masresha are highly appreciated.

I am also grateful to Dr. Sileshi Nemomissa for his assistance in species identification and constant moral support.

The encouragement and material support I got from Ato Diriba Aderie is worth mentioning. I express my thanks and appreciation to Ato Diriba. Also I would like to thank Ato Dessisa Kebeta for his financial and moral support and W/t Asegedech Tefera for her wonderful work in the computer preparation of the thesis and for her patience during the writing and rewriting of the thesis.

I also thank the staff members of the library of International Livestock Research Institute (ILRI) for their cooperation.

Finally, I wish to express my thanks to Oromia Education Bureau for sponsoring me, the Department of Biology for all their supports and the Swedish Agency for Research Cooperation with Developing Countries (SAREC) for financial support.

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Abstract

Eleven sites including treefall gaps and surrounding shades (under canopy) were studied in the Shashemenne-Munessa natural forest to investigate the dominance, frequency, density and overall importance of established seedlings and saplings of high forest tree species. Examination of the established seedlings and saplings of tree species in the gaps showed that *Croton macrostachyus, Rapanea melanophloeos, Maesa lanceolata, Podocarpus falcatus* and *Vernonia auriculifera* constitute the most important species in the gaps studied. *Croton macrostachyus* was found to have the highest percentage value as overall and definitive gapfiller, whereas, *Maesa lanceolata, Podocarpus falcatus and Juniperus procera* were found to be the most important gapmakers. These gapmakers constituted 76% of the canopy composition in the Shashemenne-Munessa natural forest. The replacement proportions in gaps were examined to assess their role in the forest community and no evidence was found to support self or reciprocal replacement. The gapmakers-gapfillers comparisons indicated preferential replacement of almost all species by *Croton macrostachyus,* suggesting that the community is undergoing successional change. No significant correlations were found between the gapmakers and gapfillers, canopy composition and gapfillers, gap size and dominance as well as importance values of species. However, statistically significant correlations were found between species composition and gap size and also between relative density of some species and gap size. Tree species were classified as pioneers and climax. The study revealed that *Podocarpus falcatus, Maytenus addat, Rapanea melanophloeos, Dovyalis abyssinica, Bersama abyssinica* and *Teclea nobilis* could be categorized as climax species, whereas, *Juniperus procera, Maesa lanceolata, Vernonia auriculifera* and *Croton*

macrostachyus could be classified as forest pioneer species. Furthermore, the diversity of tree species was found to be greater in the gaps than under the closed canopy.

1. INTRODUCTION

Forest gap is defined as an opening formed in a forest canopy as a result of fallen single tree, part of a tree (branches) or few trees in a group or under standing dead trees, where regenerating trees have not reached more than two-third of the average canopy tree height (Lawton and Putz, 1988; Spies and Franklin, 1989; Whitmore, 1989; Liu and Hytteborn, 1991; Gray and Spies, 1996; Yamamoto, 1996). Disturbances that create or open up gaps in forests include high winds, lightning, earth quakes, wildfire, the death of a tree through disease or old age, etc. (Lawton and Putz, 1988; Begon *et al.*, 1996).

Treefall gaps are the most prevalent (Lawton and Putz, 1988) and also frequent source of stand turnover (Denslow *et al.*, 1998) in tropical forests. These gaps are the major modifying forces in forest ecosystems (Young and Perkocha, 1994) and they are found to be necessary for the establishment and/or growth to maturity of many forest trees (Runkle, 1989). Establishment refers to the occurrence of new individuals greater than or equal to 5 cm tall in a treefall gap and under closed canopy (Uhl *et al.,* 1988). Treefall gaps are important for regeneration and gap dynamics (Platt and Strong, 1989; Liu and Hytteborn, 1991). Regeneration can be defined as the growing again of seedlings and saplings in the forest gap. Ashworth (1991) has defined regeneration as the young trees and seedlings that have become established on a plot of land. Regeneration includes reforestation and the development of a new generation of young trees under an existing canopy. According to Brokaw (1985) gap phase regeneration of trees occurs when canopy gaps are filled with the growth of previously suppressed or newly colonizing saplings. Many authors (Schemske and Brokaw, 1981; Brokaw, 1985; Connel, 1989; Whitmore, 1989, 1993; Begon *et al.*, 1996) have discussed that regeneration (regrowth) in the gap occurs from three sources: seeds, suppressed seedlings and saplings and lateral growth. The fourth important source of regeneration is coppicing (Demel Teketay, 1996).

Treefall gap is important for both the dormant seeds in soil and the suppressed seedling in shade because the former will germinate and establish and the latter will grow to maturity by making use of the increased light energy.

In general, in tropical forests, gaps are very important for establishment and growth of different tree species (Runkle, 1989). Treefall gaps induce spatial and temporal heterogeneity in regeneration opportunities and since the responses of species to the heterogeneous environment vary, the possibility of multi-species coexistence (diversity) in the gap increases (Runkle and Yetter, 1987; Uhl, *et al.*, 1988; Rebertus and Veblen, 1993; Lertzman, 1995; Yavitt *et al.*, 1995).

Species diversity can be defined as a measure of the variety of taxa in a community that takes into account the relative abundance of each one (Ricklefs, 1997). It is the combination of richness (the number of species in some area within a community) and evenness (the distribution of individuals among the species). That is, species diversity is species richness weighted by species evenness (Barbour *et al.*, 1987; Begon *et al.*, 1996; Huston, 1995, Ricklefs, 1997).

The establishment of seedlings and saplings is greater in the gap phase than under the closed canopy because of the fact that there are more space and resources such as light and nutrients in gap-phase than under the closed canopy (Runkle and Yetter, 1987; Denslow and Spies, 1990; Reader *et al.,* 1995; Gray and Spies, 1996; Denslow *et al.*, 1998). Based on their light requirements for germination and establishment, tropical tree species can be categorized into two ecological groups called pioneer (light-demanders or shade intolerant) and climax (shade tolerant) species (Augspurger, 1984; Whitmore, 1989, 1993). The light demanding pioneer tree species can germinate, establish, and grow to maturity only in gaps whereas the climax tree species germinate and establish primarily in shade, but often attain maturity when juveniles are released from suppression (Brokaw, 1985; Schupp *et al.*, 1989; Whitmore, 1989, 1993; Leemans, 1991; Houle, 1994; Yamamoto, 1996; Crawley, 1997; Denslow *et al.,* 1998). The treefall gaps promote the coexistence of tree species by maintaining shade intolerant species in the forest community (Lertzman, 1995). Denslow and Spies (1990) pointed out that the gap microclimates may enhance seed germination and increase sapling growth rates in comparison to rates in the forest understorey. Not only light and nutrients but also soil moisture content has been found to be greater in gaps than under shade (Denslow *et al.*, 1998).

Gap dynamics is defined as the process of tree-by-tree replacement in a forest (Yamamoto, 1996). The forest dynamics is driven by disruption, with heterogeneity in disturbances producing forests that are inherently heterogeneous and ever-changing (Platt and Strong, 1989). Lertzman (1995) discussed that gaps are the site of tree-by-tree successional replacement and the sum of the individual transitions of space from the trees whose mortality creates gaps (gapmakers) to those who replace them (gapfillers) is an estimate of whether the species composition of the forest is changing or not.

According to the review of Martinez-Ramos *et al.* (1989) treefall disturbances play a crucial role in the structure and dynamic processes of forest communities. They further discussed that treefalls generate gap dynamics (tree-by-tree replacement processes) in forest populations, these gap dynamics promote the expression of a floristic-structural mosaic of vegetation which may be subject, by virtue of repeated disturbance events, to recurrent successional phases.

Tropical dry forests can be defined as forests (tree communities) growing in climates with a pronounced seasonality in rainfall, with a drought period of about half of the year in one or two periods and an annual precipitation between 400 and 1700 mm (Gerhardt and Hytteborn, 1992; Olivares and Medina, 1992). These forests occupy a larger area in the tropics than do rain forests (Olivares and Medina, 1992), and also support a large human population than the humid forests (Gerhardt and Hytteborn, 1992).

Dry tropical forests are the most threatened of all forest types as a result of their being exposed to severe large-scale changes through cutting of valuable trees, creation of pastures, and accidental and intentional fires (Gerhardt and Hytteborn, 1992; Olivares and Medina, 1992; Sabogal, 1992; Swaine, 1992).The main effects of the degradation of dry tropical forests have been summarized by Sabogal (1992) as follows:-

1. Deterioration of the ecological functions of forests, causing problems of soil and wind erosion, alteration of the water regime and the soil fertility, etc.
2. Reduction of biodiversity, and negative effects on species reproduction,
3. Loss of the economic value of the impoverished vegetation and fauna; and
4. Shortage of forest products, having effects not only on the local economies but also at the regional level of firewood.

The principal management objectives for any tropical dry forest should be maintenance as forest, which is more productive and biologically diverse than any system (e.g. savannas) which might replace them (Swaine, 1992). Management options for rehabilitation of tropical dry forests could include conservation, natural forest management and reforestation. The natural forest management has been found to facilitate sustainable production of forest products according to the multiple-use objectives, combining biodiversity conservation, environmental functions and social services in the area (Sabogal, 1992). It is a management option that heavily relies on the regeneration potential of the existing vegetation and on information on the gap dynamics of a particular forest. Gap dynamics is one of the natural forest management approaches because the main management objectives such as biodiversity conservation (Denslow and Spies, 1990), environmental protection (Struhsaker, 1997) and forest product supply (Lorimer, 1989; Denslow and Spies, 1990; Jenkins and Parker, 1998) are met by applying the concepts of gap dynamics.

Little is known about the dynamics of dry forests in the tropics and the ecophysiological properties of their woody components compared to the information accumulated from rain forests or savannas (Olivares and Medina, 1992; Swaine, 1992). In Ethiopia, in particular, the information on the gap dynamics of the forests in general, and dry Afromontane remnant forests in particular, is scanty. A study worth mentioning in this respect is the investigation of Demel Teketay (1996), who worked on the regeneration of seedlings of high forest species in Menagesha and Gara Ades (dry Afromontane forests of

Ethiopia). The following study originates from this understanding.

In the study, treefall gap characteristics, established seedlings and saplings in gaps, species relationships to gap size, proportions of gap phase replacements, regeneration guilds of tree species and comparison of the gap and shade environments are examined in Shashemenne-Munessa natural forest, Ethiopia.

The main objectives of the study are:-

- To identify the dominant seedlings and saplings of tree species in the treefall gaps of the forest
- To make comparisons among the tree seedlings and saplings in the treefall gaps using the importance value
- To examine relationships between established tree species in gaps and gap size, canopy composition and gapmakers
- To identify and categorize pioneer and climax tree species in the forest
- To generate information that may be useful in the management of Ethiopian forests and regeneration trials.

2. MATERIALS AND METHODS

2.1. STUDY SITES

The study was conducted in Shashemenne-Munessa natural forest, a dry Afromontane natural forest of Ethiopia located 200 km south of Addis Ababa at 7°13'N, 38°37'E. The main forest blocks of Shashemenne-Munessa forest are found on the escarpment and associated plateau lying between the Rift Valley lakes and the eastern edge of the Rift Valley. The altitude of the forest extends from about 2100 to 2700 m (Demel Teketay and Granstrom, 1995). The forest has a mean annual rainfall of about 1250 mm and mean annual temperature that ranges between 15 and 20° c. The soil type in the forest is humic ferrisols with a basalt parent rock (Lundgren, 1971). The vegetation can be categorized as belonging to the dry Afromontane evergreen forest region. The most common species in the forest include *Podocarpus falcatus* (most frequent), *Juniperus procera, Prunus africana, Apodytes dimidiata, Allophylus abyssinicus, Bersama abyssinica, Croton macrostachyus, Maesa lanceolata* (most frequent), *Dombeya torrida, Teclea nobilis, Buddleja polystachya, Rapanea melanophloeos, Hagenia abyssinica, Dovyalis abyssinica* and *Vernonia auriculifera,* in agreement with the report of Chaffey (1979).

Site Selection

A reconnaissance survey was done in two rounds in October and November 1998. It was very difficult to find natural treefall gaps which can show change in vegetation composition as one moves from the centre of a gap to the shade where the amount of sun light coming to the forest floor is a small percentage of that received by the centre of the gap. Nevertheless, sites were selected where a more or less clear transition in light intensity existed from the centre of gap to partial shade and deep shade (about 20% and < 5% of light intensity of gap, respectively). A total of eleven natural treefall gaps were selected for the study in two blocks of the forest known as Kacha Dhangango and Ittisa Fincha, both of which are located north east of the Shashemenne Forest Industry Head Office. Five of the sites were in Kacha Dhangango (sites 1, 2, 6, 7 and 8) and six in Ittisa Fincha (sites 3, 4, 5, 9, 10 and 11). The selection of sites was primarily based on the presence of established seedlings and saplings in gaps and also the existence of enough canopy shade surrounding the gaps.

The selected sites are located deep into the forest and can be described as little affected by human activity due to problems of accessibility. In the selection of sites only those gaps were selected which still had part of the fallen tree trunk at the site or the stumps of trees with splinters (indicating non-human cause). It is possible that some seedlings and saplings might have been established before the gaps were created. However, since the emphasis in the present study was to identify seedlings and saplings currently growing in gaps, vis-a-vis those that are found in shade, no attempt was made to determine age of gaps.

Species Identification

Most of the species were identified at the sites. In cases where species could not be identified without doubt samples were brought to the National Herbarium for expert identification. Voucher specimens of the identified species are deposited in the National Herbarium. Species nomenclature follows the published volumes of Flora of Ethiopia and Eritrea.

2.2. METHODS

2.2.1. DATA COLLECTION

1. Point-Centered Quarter Method

The density, dominance, frequency and importance value of seedlings (between 5 cm and 100 cm)(Reader *et al.*, 1995) and saplings (between 1-4 meters in height)(Brokaw, 1985; Brokaw and Scheiner, 1989) were sampled from each gap using the point-centered quarter method.

The point-centered quarter method has been described as the most efficient of the available distance methods (Yamamoto, 1996). The method is known to have greater information value per sampling point (Mueller-Dombois and Ellenberg, 1974). In this study, the point-centered quarter method was applied as described in Mueller-Dombois and Ellenberg (1974). In each gap site, species name, diameter at base (stem circumference) and distance of seedlings and saplings from each sampling points were recorded along line transects which were started from randomly picked starting points. A total of 20 sampling points were considered in all gap sites. The sampling points on the line transects were located at 5 meters interval and the line transects were 3 meters apart from each other.

2. Belt Transects

Belt transects were used to record changes in the species composition and diversity of seedlings and saplings between the gap and shade phases following Williams (1991). The belt transects were established in each site at four directions starting from the centre of the gap extending to the shade. The width of the belt transect was 2 m and the length depends on the area of the gaps with the area of the quadrat used being 2 m x 5 m = 10 m^2. However, care was taken in using equal area of the gap and shade parts for the sampling purpose. All established seedlings and saplings of tree species encountered on the belt transect at 5 m interval were recorded. Note that establishment was not studied in time but only the occurrence of young seedlings and saplings of tree species greater or equal to 5 cm in gaps and under closed canopy was used for the study. To identify pioneer and climax tree species in the present study, the frequency of occurrence in the transect only in shade, both in shade and gap and only in gap was analyzed.

3. Other Measurements

I. Soil Moisture Determination

Soil moisture or wetness is generally defined as the water content of the soil that can be driven off by heating a sample at 105°c (Moore and Chapman, 1986). Two methods of soil moisture determination were employed in this study:-

1. Soil moisture analyzer
2. Gravimetric analysis

The soil moisture content at several points within gaps and shade was recorded by the soil moisture analyzer (TRASE). The result of per cent soil moisture obtained by soil moisture analyzer was checked by gravimetric analysis using soil samples which were brought to the laboratory from gaps and shades of the forest. The soil samples of both shade and gap phase were oven dried until a constant weight was reached as recommended in Moore and Chapman (1986) and then the difference was recorded.

II. Amount of light

The amount of light in shade, partial shade and gap phase was measured by a **Li-cor light meter** from constant places within 5 minutes intervals. A total of 60 such measurements were used to calculate difference in percent light levels in partial and deep shades taking the gap phase as 100%.

III. In each gap site (including the gap and shade places), the name of all **canopy trees** surrounding the gaps and their diameter at breast height (at 1.4 m height) were recorded. The canopy height range was determined using **clinometer**.

IV. The **area** of gaps was calculated by using the formula $A=\Pi d^2/4$ where d is diameter. The diameter is the average value of the longest distance between gap edges (length) and the longest distance perpendicular to length (width) as discussed in Yamamoto (1996).

V. Leaves of seedlings and saplings from shade and gap phase were sampled for the determination of **chlorophyll content.** Chlorophyll was determined following Arnon (1949).

2.2.2. DATA ANALYSIS

1. The absolute dominance and frequency, relative density, relative dominance, relative frequency and importance value of seedlings and saplings in the gaps were analyzed following Mueller-Dombois and Ellenberg (1974).

Absolute dominance = mean basal area (ba) per tree x number of trees in species.

$$\text{Absolute frequency} = \frac{\text{number of points with species}}{\text{total points}} \times 100$$

$$\text{Relative density} = \frac{\text{number of individuals of species}}{\text{total number of individuals}} \times 100$$

$$\text{Relative dominance} = \frac{\text{dominance of a species}}{\text{dominance of all species}} \times 100$$

$$\text{Relative frequency} = \frac{\text{frequency of a species}}{\text{sum frequency of all species}} \times 100$$

Importance Value = relative density + relative dominance + relative frequency.

2. The Spearman rank correlation coefficient (r_s), product moment correlation coefficient (r) and coefficient of determination (r^2) were used to examine species relationships to gap size, the relationships between canopy composition, gapmakers and gapfillers. The following formula was used to

calculate the Spearman rank correlation coefficient (r_s) (Fowler and Cohen, 1997):

$$r_s = 1- [6\Sigma d^2/(n^3-n)]$$

where n is the number of units in a sample, d is the difference between ranks, Σd^2 is the sum of d^2 and 6 is a constant peculiar to this formula.

3. Matrix of transition frequencies between gapmakers and gapfillers were constructed as described in Lertzman (1992) to determine the proportion of gap phase replacement. Also the chi-square test was done to know the distribution of gapfiller species. For the sake of this study, overall gapfillers are considered as established tree species in gaps greater or equal to 10 cm but less than 4 m in height (Dalling *et al.*, 1998) whereas definitive gapfillers are established tree species in gaps with a height $\geq$ 1.3 m but $\leq$ 4 m.

4. The Shannon Diversity Index was employed for the comparison of species diversity in shade and gap following Begon *et al.* (1996) and Huston (1995).

Shannon index of species diversity was calculated by the formula:

$$H = -\sum_{i=1}^{S} p_i \ln p_i$$

Where H = the Shannon diversity index

S = the total number of species

Pi = proportion of total individuals in the i^{th} species

5. T-test for comparing the means of two small samples was employed to detect the significance of differences.

3. RESULTS

3.1. TREEFALL GAP ENVIRONMENT

3.1.1. Gap Characteristics

The eleven gap sites selected for investigation in the natural forest of Shashemenne-Munessa have been characterized as follows.

The altitude of the selected sites ranged between 2340 and 2500 m. The area of the gaps ranged between 188.8 m^2 and 352.8 m^2 with the mean 273.58 (± 53.71) m^2 and median 273.0 m^2. Out of the eleven, seven sites (63.6%) had gaps of sizes between 200 and 300 m^2, three sites (27.3%) between 300 and 400 m^2 and one site (9.1%) was below 200 m^2.

All the gaps were found to be multiple treefall gaps. *Maesa lanceolata* was the most frequent (44.44%) gapmaker followed by *Podocarpus falcatus* (22.22%). The mean canopy height ranged between 13.4 and 39.9 m. On average, the DBH of all the canopy trees in the investigated sites was between 0.28 and 0.77 m (Table 1).

Table 1. Diameter at breast height (DBH) of dominant canopy trees

Site	Canopy Trees	Minimum DBH (m)	Maximum DBH(m)	Mean DBH (m)
1	*Podocarpus falcatus*	0.35	2.46	1.31
	Maesa lanceolata	0.33	0.44	0.39
2	*Podocarpus falcatus*	0.24	2.20	1.52
	Maytenus addat	0.29	0.41	0.36
3	*Juniperus procera*	0.48	0.56	0.53
	Maesa lanceolata	0.16	0.56	0.31
4	*Maesa lanceolata*	0.23	0.80	0.42
5	*Maesa lanceolata*	0.22	0.47	0.33
6	*Maesa lanceolata*	0.26	0.39	0.32
7	*Podocarpus falcatus*	0.44	1.05	0.85
8	*Podocarpus falcatus*	0.30	0.60	0.39
	Maesa lanceolata	0.13	0.25	0.21
9	*Juniperus procera*	0.25	0.29	0.26
10	*Maytenus addat*	0.26	0.58	0.42
11	*Juniperus procera*	0.24	0.71	0.50

There is a wide variation between the minimum and maximum DBH of *Podocarpus falcatus*. This may be because of the fact that *Podocarpus falcatus* is a climax tree species and as a result had both the adult (old) and juvenile (young) age groups together.

3.1.2. Tree Seedlings and Saplings in Gaps

In general, 15 established seedlings and saplings of tree species were encountered during the field work and the presence of each species in the eleven gaps is presented in (Table 2a and 2b).

Table 2a. Species presence in gaps

Species	**Sites**										
	1	2	3	4	5	6	7	8	9	10	11
Podocarpus falcatus	+	+	+	+	+	+	+	+	+	+	-
Juniperus procera	-	-	+	+	+	-	-	+	+	-	+
Croton macrostachyus	-	+	+	+	+	+	+	+	+	+	-
Vernonia auriculifera	+	+	+	+	+	+	+	+	-	-	-
Dovyalis abyssinica	-	+	-	-	-	-	+	+	+	-	-
Maytenus addat	-	+	-	+	-	+	+	+	+	+	-
Maesa lanceolata	+	-	+	+	-	-	+	+	+	+	+
Sp.x	-	+	+	-	-	-	-	-	-	-	+
Teclea nobilis	+	+	-	-	-	+	+	-	+	-	-
Prunus africana	+	-	-	-	-	-	-	-	-	-	-
Allophylus abyssinicus	+	-	-	-	-	-	-	-	-	-	-
Bersama abyssinica	-	-	+	+	-	+	+	+	+	+	+
Rapanea melanophloeos	-	-	+	+	-	-	-	+	+	+	+
Dombeya torrida	-	-	-	-	-	+	-	-	-	-	-
Olea europaea subsp. *cuspidata*	-	-	+	-	-	-	-	-	-	-	-

\+ = Presence

\- = Absence

NB. Sp.x is unidentified species at the time of writing the thesis.

Table 2b. Overall absolute and relative frequency of the species :-

Species	Absolute frequency	Relative frequency
Podocarpus falcatus	90.91%	12.66%
Juniperus procera	54.54%	7.59%
Croton macrostachyus	81.82%	11.39%
Vernonia auriculifera	72.73%	10.13%
Dovyalis abyssinica	45.45%	6.33%
Maytenus addat	63.64%	8.86%
Maesa lanceolata	72.73%	10.13%
Sp.x	27.27%	3.80%
Teclea nobilis	45.45%	6.33%
Prunus africana	9.09%	1.26%
Allophylus abyssinicus	9.09%	1.26%
Bersama abyssinica	72.73%	10.13%
Rapanea melanophloeos	54.54%	7.59%
Dombeya torrida	9.09%	1.26%
Olea europaea subsp. *Cuspidata*	9.09%	1.26%

Seedlings and saplings of *Podocarpus falcatus* were the most frequent in the gaps followed by *Croton macrostachyus*. Besides, the data on the overall gap dominance rank indicated that *Croton macrostachyus, Maesa lanceolata* and *Rapanea melanophloeos* were the three most dominant species in the gaps whereas *Vernonia auriculifera, Maytenus addat* and *Podocarpus falcatus* were the second most dominant species (see Appendix I for the detailed description of the dominance, frequency and importance value of each species).

With overall importance value index analysis *Croton macrostachyus* was found to have the first place in the gaps followed by *Vernonia auriculifera*. The third species with the highest overall importance value index was *Rapanea melanophloeos* (Table 2c).

Table 2c. Overall relative importance value indices of established tree species in the gaps

Species	Importance Value (%)	Importance Value Rank
Podocarpus falcatus	9.6	4
Juniperus procera	7.2	7
Croton macrostachyus	21.7	1
Vernonia auriculifera	17.9	2
Dovyalis abyssinica	2.1	9
Maytenus addat	5.7	8
Maesa lanceolata	9.4	5
Sp.x	1.2	11
Teclea nobilis	1.3	10
Rapanea melanophloeos	15.6	3
Dombeya torrida	0.15	12
Bersama abyssinica	7.9	6

Croton macrostachyus was not only among the most frequent species (Table 2b) but also had the highest importance value index (Table 2c) in the gap phase. Although *Podocarpus falcatus* was the most frequent species (12.66%), its overall importance value index in the gaps was less than that of *Croton macrostachyus, Vernonia auriculifera* and *Rapanea melanophloeos*.

3.1.2.1. Relationships between Species and Gap Size

The relationship between gap size and relative importance value of the species is shown in Table 3.

Table 3. Relationships between relative importance value of species and gap size

Species	Spearman Rank Correlation Coefficient (r_s)
Croton macrostachyus	0.36
Podocarpus falcatus	0.47
Vernonia auriculifera	-1.0
Juniperus procera	0.20
Maesa lanceolata	-0.14
Rapanea melanophloeos	0.10
Maytenus addat	0.40

There was perfect negative correlation between gap size and relative importance value in the case of seedlings and saplings of *Vernonia auriculifera*, a weak correlation (both positive and negative) in the cases of *Croton macrostachyus, Juniperus procera, Maesa lanceolata* and *Rapanea melanophloeos*. On the other hand, there was a modest correlation between gap size and relative importance value in the cases of *Maytenus addat* and *Podocarpus falcatus*.

However, the correlation between gap size and importance value of species was not statistically significant at $p \leq 0.10$. Furthermore, the Spearman Rank Correlation Coefficient was calculated for eight selected tree species to investigate relationships between gap size and relative density (Table 4) and dominance (Table 5).

Table 4. Relationship between gap size and relative density

Species	SRCC* (r_s)	Strength of the Correlation	Statistical significance	Significance level (two-tailed test)
Podocarpus falcatus	0.67	Modest	Significant	p=0.10 (n=8)
Juniperus procera	0.54	Modest	Non-significant	$P \leq 0.1$ (n=6)
Croton macrostachyus	0.75	Strong	Significant	P=0.1 (n=7)
Vernonia auriculifera	-1.0	Very Strong	Significant	P=0.1 (n=5)
Maytenus addat	0.71	Strong	Non-significant	$P \leq 0.1$ (n=6)
Maesa lanceolata	0.29	Weak	Non-significant	$P \leq 0.1$ (n=7)
Bersama abyssinica	0.24	Weak	Non-significant	$P \leq 0.1$ (n=8)
Rapanea melanophloeos	0.43	Modest	Non-significant	$p \leq 0.1$ (n=6)

* SRCC is for the Spearman rank correlation coefficient.

There was a significant correlation ($p \leq 0.10$) between gap size and relative density of *Podocarpus falcatus, Croton macrostachyus* and *Vernonia auriculifera.* The correlation was direct in the case of *Podocarpus falcatus* and *Croton macrostachyus* (the strength being modest and strong, respectively) but negative (inverse) in case of *Vernonia auriculifera.*

Table 5. Relationship between gap size and dominance

Species	SRCC (r_s)	Strength of the Correlation	Statistical significance	Significance level (two-tailed test)
Podocarpus falcatus	0.036	Very weak	Non-significant	$P \leq 0.1$(n=7)
Juniperus procera	-0.60	Modest	Non-significant	$P \leq 0.1$(n=5)
Croton macrostachyus	-0.071	Very weak	Non-significant	$P \leq 0.1$(n=7)
Vernonia auriculifera	-0.60	Modest	Non-significant	$P \leq 0.1$(n=5)
Maytenus addat	0.70	Strong	Non-significant	$P \leq 0.1$(n=5)
Maesa lanceolata	-0.371	Weak	Non-significant	$P \leq 0.1$(n=6)
Bersama abyssinica	-0.714	Strong	Significant	$P = 0.1$(n=7)
Rapanea melanophloeos	0.10	Very weak	Non-significant	$p \leq 0.1$(n=5)

The relationship between gap size and dominance was not statistically significant, except in the case of *Bersama abyssinica*, where there was a strong statistically significant inverse (negative) relationship (Table 5).

The percentage of definitive gapfillers (saplings in the gaps $\geq$ 1.3 m in height) of *Maesa lanceolata*, *Croton macrostachyus, Bersama abyssinica* and *Maytenus addat* increased with gap size (Table 6). On the other hand, the percentage of definitive gapfillers of *Podocarpus falcatus* decreased with increasing gap size.

Table 6. Gap size and definitive gapfillers (%)

Species	Gap size Class (m^2)			Number of Definitive Gapfillers
	100-200	200-300	300-400	
Podocarpus falcatus	0	60.3	39.7	63
Juniperus procera	10.5	79.0	10.5	19
Croton macrostachyus	2.3	39.8	57.9	176
Maytenus addat	0	48.4	51.6	31
Maesa lanceolata	8.8	14.7	76.5	68
Bersama abyssinica	4	32	64	25
Rapanea melanophloeos	0.7	74.5	24.8	149

3.1.2.2. Species Composition and Gap Size

The relationship between gap size and species composition is shown in Table 7.

Table 7. Relationships between gap size and species composition

Gap size (m^2)	Rank of Gap Size	Species composition (Sc)	Rank of Sc	d	d^2
188.60	1	4	2.5	-1.5	2.25
228.20	2	5	5.5	-3.5	12.25
230.89	3	4	2.5	0.5	0.25
234.94	4	3	1	3.0	9
244.50	5	7	9.5	-4.5	20.25
273.00	6	5	5.5	0.5	0.25
281.90	7	5	5.5	1.5	2.25
298.50	8	6	8	0	0
329.90	9	10	11	-2.0	4
346.18	10	7	9.5	0.5	0.25
352.80	11	5	5.5	6.5	42.25
					$\Sigma d^2=93.0$
					$r_s = 1- [6\Sigma d^2/n^3-n)] = 0.58$

A value of $r_s = 0.58$ suggests a modest positive correlation between gap size and species composition. The statistical test confirmed that the relationship is significant at $p \leq 0.10$.

3.1.2.3. Gap Diameter: Canopy Height Ratio versus Dominance, Relative Density and Importance Value of Species

The ratio of gap diameter (D) to average canopy height (H) (D/H), gives an indication of the increase of light level in a gap (Midgley *et al.* 1995). Based on this, the correlations between D/H and dominance, relative density and importance values of species were determined (Table 8).

Table 8. Relationships between gap diameter: canopy height ratio (D/H) and dominance, relative density and importance value of species

Species	Spearman Rank Correlation Coefficient (r_s)		
	Dominance	Relative Density	Importance Value
Croton macrostachyus	0.24	0.72	0.56
Podocarpus falcatus	-0.65	-0.65	-0.62
Juniperus procera	0.57	0.07	0.07
Maesa lanceolata	-0.94	-0.60	-0.60
Rapanea melanophloeos	-0.10	-0.10	-0.10
Maytenus addat	-0.60	-0.66	-0.60

The correlation between the D/H as a measure of light levels in gaps and dominance, relative density and importance value of *Croton macrostachyus* was positive. There was a strong positive correlation between the relative density of *Croton macrostachyus* and D/H ratio which was statistically significant (r_s = 0.72; n=7) at $p \leq 0.10$. There was a statistically non-significant modest correlation between dominance of *Juniperus procera* and D/H ratio (r_s = 0.57; n = 5). The correlations between D/H ratio and dominance, relative density and importance value for *Podocarpus falcatus, Maesa lanceolata*, *Maytenus addat* and *Rapanea melanophloeos* were inverse. There was a strong negative correlation between D/H ratio and dominance of *Maesa lanceolata* which was statistically significant (r_s = -0.94; n = 6 at $p \leq 0.05$). But the modest negative correlations between D/H ratio and the dominance, relative density and importance value of *Maytenus addat* were not statistically significant at $p \leq 0.10$. The product moment correlation analysis showed that there was strong inverse correlation between D/H and relative density of *Podocarpus falcatus* (r = -0.86; n = 7 at p = 0.05 and p = 0.01) was statistically highly significant. The coefficient of determination (r^2 = 0.74) indicated that 74% of the variation in relative density of *Podocarpus falcatus* was accounted for by variation in D/H. In general, at high D/H (as light levels increased), the relative density of *Croton macrostachyus* increased; that of *Podocarpus falcatus* decreased and the dominance of *Maesa lanceolata* decreased.

3.2. COMPARISON OF GAP AND SHADE ENVIRONMENTS

3.2.1. Amount of Sun Light

The mean solar energy recorded for one day in deep shade and partial shade, assuming that gap phase received 100% sun light, was 1.15% and 20.07%, respectively.

3.2.2. Chlorophyll Content

The total chlorophyll content of samples of leaves from shade and gap phase is indicated in Table 9.

Table 9. Total chlorophyll content of species studied

Species	Total chlorophyll content (microgram per ml) Mean ± sd	
	Gap phase	Shade
Podocarpus falcatus	1.24 ± 0.04	1.87 ± 0.06
Teclea nobilis	2.88 ± 0.05	0.73 ± 0.12
Bersama abyssinica	1.51 ± 0.09	0.87 ± 0.08
Croton macrostachyus	6.37 ± 0.17	-
Maesa lanceolata	1.59 ± 0.10	-

Seedlings and saplings of *Podocarpus falcatus* in the shade had more total chlorophyll than those in the gap phase. The difference was statistically significant. Also the difference between the means of samples of *Teclea nobilis* from shade and gaps was found to be statistically significant and unlike the case in *Podocarpus falcatus*, there was more total chlorophyll in gap phase samples than in those under shade. The difference in the total chlorophyll content of gap phase and shade samples of *Bersama abyssinica* was not statistically significant. As there were no seedlings and saplings of *Croton macrostachyus* and *Maesa lanceolata* in shade, comparison of their chlorophyll content was not done.

3.2.3. Soil Moisture

Results from the soil moisture analysis are presented in Table 10.

Table 10. Per cent soil moisture in treefall gaps and canopy shade

	Mean ± sd	
	Gap	Shade
TRASE	21.31 ± 3.19	14.52 ± 4.36
Gravimetric method	39.23 ± 2.18	32.63 ± 5.44

The soil moisture analyzer (TRASE) indicated that water content of soils in gaps was significantly higher than that in soils under shade ($t = 11.7$; $df = 16$; $p =$

0.01). Further analysis with the gravimetric method also showed the difference between the soil moisture in gaps and under shade was statistically significant ($t = 4.78$; $d_f = 6$; $p = 0.01$). The gravimetric analysis confirmed the result obtained with the moisture analyzer (Table 10) and hence it may be concluded that water content of soils in gaps was greater than that in soils under shade.

3.2.4. Species Diversity

Table 11. Comparison of species composition in the gaps and shade

Site	Altitude (m)	Gap Area (m^2)	Species in	
			Gap	Shade
1	2400	298.45	*Teclea nobilis* *Maesa lanceolata* *Prunus africana* *Vernonia auriculifera* *Podocarpus falcatus* *Allophylus abyssinicus*	*Teclea nobilis*
2	2380	346.18	*Podocarpus falcatus* *Teclea nobilis* *Dovyalis abyssinica* *Sp.x* *Maytenus addat* *Croton macrostachyus* *Vernonia auriculifera*	*Podocarpus falcatus* *Teclea nobilis* *Dovyalis abyssinica* *Sp.x* *Maytenus addat*

3	2430	329.9	*Juniperus procera* *Croton macrostachyus* *Maesa lanceolata* *Vernonia auriculifera* *Dovyalis abyssinica* *Podocarpus falcatus* *Rapanea melanophloeos* *Bersama abyssinica* *Olea europaea subsp. cuspidata* *Sp.x*	*Podocarpus falcatus* *Dovyalis abyssinica* *Rapanea melanophloeos* *Bersama abyssinica* *Maytenus addat* *Sp.x*
4	2420	273.0	*Podocarpus falcatus* *Bersama abyssinica* *Croton macrostachyus* *Juniperus procera* *Maytenus addat*	*Bersama abyssinica* *Podocarpus falcatus*
5	2440	281.9	*Podocarpus falcatus* *Maytenus addat* *Rapanea melanophloeos* *Juniperus procera* *Croton macrostachyus*	*Podocarpus falcatus*
6	2400	234.94	*Vernonia auriculifera* *Croton macrostachyus* *Dombeya torrida* *Bersama abyssinica*	*Podocarpus falcatus* *Teclea nobilis*
7	2340	352.8	*Teclea nobilis* *Podocarpus falcatus* *Dovyalis abyssinica* *Sp.x* *Croton macrostachyus*	*Teclea nobilis*

Site	Altitude (m)	Gap Area (m²)	Species in	
			Gap	Shade
8	2420	188.6	*Vernonia auriculifera* *Maesa lanceolata* *Croton macrostachyus* *Dovyalis abyssinica*	*Podocarpus falcatus*
9	2480	244.5	*Teclea nobilis* *Maytenus addat* *Podocarpus falcatus* *Maesa lanceolata* *Rapanea melanophloeos* *Juniperus procera* *Croton macrostachyus*	*Teclea nobilis* *Maytenus addat* *Podocarpus falcatus* *Dovyalis abyssinica*
10	2500	230.89	*Rapanea melanophloeos* *Croton macrostachyus* *Maesa lanceolata* *Bersama abyssinica*	*Podocarpus falcatus* *Maytenus addat* *Rapanea melanophloeos*
11	2490	228.2	*Rapanea melanophloeos* *Maytenus addat* *Maesa lanceolata* *Juniperus procera* *Vernonia auriculifera*	*Podocarpus falcatus* *Rapanea melanophloeos* *Maytenus addat*

As has been illustrated in Table 11, the composition (diversity) of species increased in the gap phase. There were more seedlings and saplings well established in the gap phase than in shade.

The Shannon diversity index of species in gaps was found to be 2.14 whereas the diversity index for species under canopy shade was 1.64. This implies that gap phase species were more diverse than the species under canopy shade.

3.3. IMPORTANCE OF GAPS

3.3.1. Gap Dynamics

Based on the dominance and importance values, 75% of the gapmakers were replaced by gapfillers of different species. Furthermore, in 87.5% of the cases considered, dominant species established in the gaps were different from the dominant canopy trees (Table 12). It is to be noted that this report is based on the observation made on the gapmakers and established species in gaps and that it was not a long time study.

Table 12. Gapmakers, canopy trees and established seedlings and saplings in gaps

Site	Gapmakers	Dominant canopy trees	The first three species established (respectively) according to	
			Dominance value	Importance value
4	*Maesa lanceolata*	*Maesa lanceolata*	*1. Croton* *2. Rapanea* *3. Podocarpus*	*1. Croton* *2. Vernonia* *3. Podocarpus*
	Juniperus procera *Maesa lanceolata*	*Maesa lanceolata*	*1. Podocarpus* *2. Croton* *3. Vernonia*	*1. Croton* *2. Podocarpus* *3. Vernonia*
6	*Maesa lanceolata*	*Maesa lanceolata*	*1. Croton* *2. Vernonia* *3. Bersama*	*1. Croton* *2. Vernonia* *3. Bersama*
7	*Podocarpus falcatus* *Maytenus addat* *Nuxia congesta* *Allophylus abyssinicus*	*Podocarpus falcatus*	*1. Maytenus* *2. Croton* *3. Dovyalis*	*1. Maytenus* *2. Croton* *3. Vernonia*
8	*Podocarpus falcatus* *Maesa lanceolata*	*Podocarpus falcatus* *Maesa lanceolata*	*1. Vernonia* *2. Bersama* *3. Croton*	*1. Vernonia* *2. Bersama* *3. Croton*
9	*Juniperus procera*	*Juniperus procera*	*1. Maesa* *2. Maytenus* *3. Podocarpus*	*1. Maesa* *2. Rapanea* *3. Podocarpus*
10	*Maesa lanceolata* *Hagenia abyssinica (branches)*	*Maytenus addat*	*1. Rapanea* *2. Bersama* *3. Maytenus*	*1. Rapanea* *2. Bersama* *3. Croton*
11	*Juniperus procera* *Maesa lanceolata*	*Juniperus procera*	*1. Juniperus* *2. Rapanea* *3. Maesa*	*1. Rapanea* *2. Juniperus* *3. Maesa*

3.3.1.1. Relationships between Canopy Composition, Gapmakers and Gapfillers.

Canopy trees, gapmakers and gapfillers are considered to be the replacement categories (Yamamoto, 1996). Out of the 18 tree species encountered in the field study of the gap sites, only 5 species (27.8%) occurred in all the replacement categories. These tree species include *Maesa lanceolata, Juniperus procera, Podocarpus falcatus, Maytenus addat* and *Allophylus abyssinicus*. *Maesa lanceolata* occurred as canopy tree and gapmaker with the highest relative density compared with others. On the other hand, the most important gapfillers (*Croton macrostachyus* and *Rapanea melanophloeos*) did not occur as gapmakers and also their relative density in the canopy composition was among the least values (Table 13).

Croton macrostachyus dominated the overall population of overall gapfillers (25%), definitive gapfillers (29.3%) and also had the highest overall importance value (21.7%) in the gaps. The percentage value of *Croton macrostachyus* in the overall gapfillers represented 8.17 times its presence in the canopy composition. In general, the percentage of overall gapfillers, definitive gapfillers and importance value of *Croton macrostachyus, Bersama abyssinica, Rapanea melanophloeos, Vernonia auriculifera* and *Teclea nobilis* increased relative to their presence in the canopy composition but those of *Maesa lanceolata, Juniperus procera*, *Maytenus addat* and *Allophylus abyssinicus* decreased relative to their presence in the canopy composition (Table 13).

Table 13. Relative percentage (%) of canopy composition, gapmakers, gapfillers and importance value of the tree species

Species	Canopy Composition	Gapmaker	Overall Gapfillers	Definitive Gapfillers	Overall Importance value in Gap
Maesa lanceolata	38.78	44.44	7.04	11.31	9.4
Juniperus procera	19.39	18.52	5.14	3.16	7.2
Podocarpus falcatus	17.35	22.22	8.94	10.48	9.6
Maytenus addat	10.20	10.0	6.80	5.16	5.7
Croton macrostachyus	3.06	0	25.0	29.30	21.7
Bersama abyssinica	3.06	0	7.12	4.50	7.9
Hagenia abyssinica	2.04	3.70	0	0	0
Rapanea melanophloeos	1.02	0	23.02	24.79	15.6
Teclea nobilis	1.02	0	2.22	3.0	1.3
Pittosporum viridiflorum	1.02	0	0	0	0
Allophylus abyssinicus	1.02	3.7	0.08	0.17	0
Apodytes dimidiata	1.02	0	0	0	0
Buddleja polystachya	1.02	0	0	0	0
Nuxia congesta	0	3.7	0	0	0
Sp.x	0	0	5.62	3.33	1.2
Dovyalis abyssinica	0	0	3.32	3.33	2.1
Vernonia auriculifera	0	0	5.70	1.50	17.9
Dombeya torrida	0	0	0	0	0.15

The results of both the Spearman rank correlation coefficient (r_s) and product moment correlation coefficient (r) were uesd to investigate the relationship between gapmakers and definitive gapfillers. The correlation between the gapmakers and definitive gapfillers was very weak in both cases ($r_s = 0.14$; $n = 14$ at $p \leq 0.10$ and $r = 0.08$; $n = 14$ at $p \leq 0.05$) and statistically non-significant. Similarly, the correlation between gapmakers and importance value of species was very weak ($r_s = 0.007$; $n = 15$ at $p < 0.10$ and $r = 0.12$; $n = 15$ at $p < 0.05$) and statistically non-significant. The coefficient of determination (r^2), which is the measure of the proportion of the variability in one variable that is accounted for by variability in another (Fowler and Cohen, 1997), was also calculated for further investigation of the relationships between gapmakers and gapfillers. Accordingly, only 0.64% ($r = 0.08$) of the total variation of the definitive gapfillers was due to their relationship with the gapmakers (Freund and Simon, 1997). That is 99.36% of the variation in definitive gapfillers was not accounted for by their relationship with the gapmakers. Also the coefficient of determination ($r^2 = 0.014$) indicated that 98.56% of the variation in the importance value of species in the gaps was not due to their relationships with gapmakers. Therefore, the present data showed that there was no (or extremely weak) relationship between gapmakers and gapfillers. Similarly, the correlation between canopy composition and definitive gapfillers was found to be very weak ($r = 0.17$, $n = 16$ $p \leq 0.05$) and statistically non-significant. The value of coefficient of determination ($r^2 = 0.029$) indicated that it is only 2.89% of the total variation of definitive gapfillers which was due to their relationship with the canopy composition and 97.11% of the variation in the definitive gapfillers was not accounted for by the composition in canopy. Besides, the correlation between canopy composition and importance value of species was non-significant (r_s = 0.34; n = 17 at $p \leq 0.10$).

3.1.2. Replacement Proportions

The proportion of gap phase replacement was analyzed based on gapmaker-gapfiller comparisons following Lertzman (1992) as indicated earlier. Two matrices of transition frequencies were constructed for the detailed analysis of the replacement proportions in the forest. The first one indicates the replacement proportions for all the established seedlings and saplings in the gaps (Table 14 a) and the second one deals with the replacement proportions of gapmakers by definitive gapfillers (Table 14 b).

The replacement proportions of overall gapfillers with respect to gapmakers indicated that about 70% of the gapmakers were replaced by *Croton macrostachyus* and 28.57% by *Rapanea melanophloeos*. In all cases considered the gapmaker species were replaced by gapfillers of different species. No species showed strong trends towards self replacement, and almost all species were preferentially replaced by *Croton macrostachyus* (Table 14 a).

The chi-square analysis revealed that the gapfiller species were not distributed randomly with respect to gapmaker species and as a result the replacement proportion was not random.

It is to be noted that this study of replacement proportion was based only on the data collected during the period of investigation and hence no further conclusions can be made except indicating the importance of studying replacement patterns for the better understanding of the key changes taking place in the forest vegetation composition.

Table 14 a. Matrix of transition frequencies between species of gapmakers and overall gapfillers. Matrix entries are the proportion of gapfillers that replaced the gapmakers.

Gapmakers	**Gapfillers**												
	Maesa	Maytenus	Croton	Bersama	Podocarpus	Sp.x	Dovyalis	Rapanea	Vernonia	Juniperus	Teclea	Allophylus	N
Podocarpus falcatus	0.071	0.137	0.139	0.201*	0.132	0.016	0.094	0.003	0.130	0.011	0.018	0.002	140.5
Maesa lanceolata	0.071	0.047	0.299	0.053	0.073	0.059	0.026	0.217	0.073	0.065	0.015	0	588.5
Maytenus addat	0.068	0.148	0.545	0.034	0	0.011	0.011	0	0.057	0	0.114	0.011	22.0
Allophylus abyssinicus	0.068	0.148	0.545	0.034	0	0.011	0.011	0	0.057	0	0.114	0.011	22.0
Nuxia congesta	0.068	0.148	0.545	0.034	0	0.011	0.011	0	0.057	0	0.114	0.011	22.0
Juniperus procera	0.057	0.071	0.203	0.061	0.128	0.061	0.031	0.286*	0.017	0.062	0.020	0	400.5
Hagenia abyssinica	0.044	0.015	0.044	0.051	0	0.124	0	0.708*	0	0	0.015	0	68.5
N	89	86	316	90	113	71	42	291	72	65	28	1	1264

Table 14 b. Matrix of transition frequencies between species of gapmakers and definitive gapfillers. Matrix entries are the proportion of definitive gapfillers that replaced the gapmakers.

Gapmakers	**Definitive Gapfillers**												
	Maesa	Maytenus	Croton	Bersama	Podocarpus	Dovyalis	Sp.x	Rapanea	Vernonia	Juniperus	Teclea	Allophylus	N
Podocarpus falcatus	0.180	0.180	0.130	0.178	0.175	0.075	0.022	0.006	0.015	0.012	0.025	0.003	80.5
Maesa lanceolata	0.110	0.036	0.352	0.029	0.094	0.025	0.034	0.240	0.018	0.041	0.020	0	277
Maytenus addat	0.050	0.050	0.550	0.075	0	0	0.025	0	0.025	0	0.200	0.025	10
Allophylus abyssinicus	0.050	0.050	0.550	0.075	0	0	0.025	0	0.025	0	0.200	0.025	10
Nuxia congesta	0.050	0.050	0.550	0.075	0	0	0.025	0	0.025	0	0.200	0.025	10
Juniperus procera	0.117	0.028	0.290	0.014	0.131	0.040	0.023	0.288	0.011	0.037	0.020	0	175.5
Hagenia abyssinica	0.026	0	0.013	0	0	0	0.105	0.830	0	0	0.026	0	38
N	68	31	176	27	63	20	20	149	9	19	18	1	601

Of the gapmakers, 71.43% preferentially replaced by *Croton macrostachyus* (Table 14b). The x^2 test indicated that the definitive gapfillers were not distributed randomly with respect to gapmaker species. Therefore, it may be concluded that the replacement proportion of the gapmakers by the definitive gapfillers was not random. No species showed strong trend towards self-replacement, and all were replaced by different species. The gapmakers were predominantly replaced by *Croton macrostachyus* which did not occur as gapmaker in the sampled gap sites.

3.3.2. Regeneration

Regeneration in treefall gaps can be defined as the establishment of young seedlings of tree species from seed bank, seedling bank or coppicing after disturbances. It can also occur from the lateral growth of branches. The number of established seedlings and saplings recorded using the belt-transects from the eleven sites is presented in Table 15.

Table 15. Regeneration in gaps and shades

Species	Percentage (%) Regeneration in	
	Shade	Gap
Podocarpus falcatus	66.2	33.8
Teclea nobilis	45.2	54.8
Maesa lanceolata	0	100
Vernonia auriculifera	0	100
Dovyalis abyssinica	45	55
Sp.x	66.7	33.3
Maytenus addat	37.5	62.5
Croton macrostachyus	0	100
Juniperus procera	0	100
Rapanea melanophloeos	51.0	49.0
Bersama abyssinica	30.0	70.0
Mean percentage	31.1	68.9

Table 15 clearly indicates that the percentage of established seedlings and saplings was greater in gaps than in shade. In 73% of the cases considered, the percentage regeneration increased in gaps. The seedlings and saplings of *Maesa lanceolata*, *Vernonia auriculifera*, *Croton macrostachyus* and *Juniperus procera* were found only in the gaps and not in shade. The others had established seedlings and saplings both in shade and gap. It should be emphasized that no species that had established seedlings and saplings only under closed canopy (shade) was encountered. Based on the data in Table 15, *Teclea nobilis*, *Dovyalis abyssinica*, *Maytenus addat* and *Bersama abyssinica* had more seedlings and saplings on the gap phase than in shade whereas *Podocarpus falcatus*, Sp.x and *Rapanea melanophloeos* had more seedlings and saplings under shade than on the gap phase.

In general, on average, 69% of the seedlings and saplings were found well established in gaps compared with only 31% under shade. Thus, treefall gaps can be considered to be important for the regeneration and/or growth of seedlings and saplings of the majority of tree species.

3.4. Regeneration Groups of the Tree Species

Table 16. Percentage presence of some species in shades and gaps

Species	**Presence (%)**		
	Only in shade	**Both in shade & Gap**	**Only in gap**
Podocarpus falcatus	44.44	44.44	11.11
Juniperus procera	0	0	100
Teclea nobilis	20	80	0
Maesa lanceolata	0	0	100
Vernonia auriculifera	0	0	100
Dovyalis abyssinica	25	25	50
Maytenus addat	16.67	50	33.33
Croton macrostachyus	0	0	100
Bersama abyssinica	0	33.33	66.67
Rapanea melanophloeos	0	50	50

NB.

Species whose frequency of occurrence in the transect was less than three and on which no other qualitative observations were made have not been included in this comparison.

From the above result, it can be concluded that *Juniperus procera, Vernonia auriculifera, Maesa lanceolata* and *Croton macrostachyus* are gap phase tree species (shade intolerant) and the rest are shade tolerant species.

Other observations made qualitatively and quantitatively include:

1. The seedlings of *Podocarpus falcatus* were observed well established in deep shade near site 2 in an aggregated manner. Similarly, near site 5, seedlings of *Podocarpus falcatus* were found established in the deep shade under a big *Podocarpus falcatus* tree (whose DBH was 2.2 m) where no other seedlings and saplings were established. Also the seedlings of *Podocarpus falcatus* were observed well established under the shade of *Maesa lanceolata* trees and *Podocarpus falcatus* trees in many places in the natural forest of Shashemenne-Munessa.
2. In site 7, 9 seedlings and 3 saplings of *Podocarpus falcatus* were observed established in a deep shade on the south west direction of the gap in a 5.7 m x 5 m = 28.5 m^2 area under shade. Besides, there were two saplings of *Teclea nobilis* in the same area under shade.
3. *Dovyalis abyssinica, Bersama abyssinica, Teclea nobilis* and *Podocarpus falcatus* seedlings were observed well established in the deep shade under *Podocarpus falcatus* (DBH = 2.55 m and canopy height 58 m) and two *Juniperus procera* trees found on the north east direction of site 9.

4. The seedlings of *Podocarpus falcatus* and *Rapanea melanophloeos* were observed established under a deep shade of *Arundinaria alpina* species in a place known as Shuganna in Shashemenne Munessa natural forest.

These and other observations show that seedlings of *Podocarpus falcatus*, *Maytenus addat*, *Rapanea melanophloeos, Dovyalis abyssinica*, *Bersama abyssinica*, and *Teclea nobilis* are shade tolerant tree species and those of *Juniperus procera, Maesa lanceolata*, *Vernonia auriculifera* and *Croton macrostachyus* are shade intolerant.

4. DISCUSSION

4.1. Treefall Gaps and Tree Seedlings and Saplings

4.1.1. The Impact of Gap size on Species Composition

All tree species need a canopy opening for their growth. Treefall gaps have been reported to be necessary for the establishment of seedlings and saplings of forest tree species (Runkle, 1989; Platt and Strong, 1989). The sizes of treefall gaps strongly influence regeneration of seedlings and saplings (Struhsaker, 1997). The examined relationships of species to gap size in the present study indicated differences in species responses to gap sizes. For instance, there was strong positive correlation between gap size and relative density of *Croton macrostachyus*, a modest correlation in the case of *Podocarpus falcatus* and no or negative correlation in others. Differences in gap size has been reported to result in differences in species composition (Whitmore, 1989). The composition of species was also found to increase with gap size. This result is in agreement with the findings of many authors. For example, Runkle and Yetter (1987) reported that species composition varied along gradients of gap size and age. Also Brokaw (1985) and Whitmore (1989) reported that gap size differences resulted in differences in species composition. Similarly, Lertzman (1995) indicated that the number of gapfillers increased with gap size. Gap size determines the species composition of regrowing vegetation in gaps (Yamamoto, 1996). Thus it can be concluded that species composition varies with gap size and since the number of established seedlings and saplings increases as gap size increases, smaller gaps have less species composition than larger gaps.

4.1.2. Comparison of Frequency, Dominance and Importance Value of Species in Gaps

The data on frequency, dominance and importance value of species show that *Croton macrostachyus* was the most important tree species in gaps. It was among the most frequent and dominant species and had the highest percentage relative density and importance value. *Podocarpus falcatus*, although most frequent, was not among the dominant species. Its overall importance value was also much less than that of *Croton macrostachyus* (Table 2 a-c). *Vernonia auriculifera, Maesa lanceolata* and *Bersama abyssinica* were the third most frequent species but they had different importance values. *Vernonia auriculifera* had the highest importance value next to *Croton macrostachyus* but it had less saplings than seedlings and hence it was not important as definitive gapfiller. Although its frequency of occurrence in overall gaps was less, *Rapanea melanophloeos* had higher importance value (next to *Croton macrostachyus* and *Vernonia auriculifera*) (Tables 2 a-c, 6 and 13; Appendix I).

The seedlings and saplings of *Croton macrostachyus* were noted to survive best in larger gaps whereas those of *Podocarpus falcatus* preferred partial shade. When comparison is made between the seedlings and saplings of *Podocarpus falcatus* in deep shade, partial shade and gap, those seedlings in deep shade had deep green color, thin leaves and showed stunted growth. On the other hand, those in partial shade had a very bright green color with attractive appearance whereas the seedlings and saplings in gaps were intermediate (see Fig. 1 and 2). Based on these observations it may be concluded that the preferred site for establishment of *Podocarpus falcatus* seedlings is partial shade. This conclusion agrees with the work of Demel Teketay (1996) in which he discussed that seedlings of *Podocarpus falcatus* survived better under shade. Seedlings and saplings of *Podocarpus falcatus*, which were observed in deep shade seem to be affected by the stress under deep shade.

The establishment of *Croton macrostachyus* was found to increase with an increase in the ratio of gap diameter to canopy height (D/H). However, an inverse correlation was observed in *Maesa lanceolata* and *Podocarpus falcatus* (Table 8). In general, the establishment of tree species in the gaps investigated may be from three sources of regeneration: seed bank, seedling bank and seed rain. Since all the gaps investigated were large in size (> 150 m^2), lateral growth may not be an important source of regeneration. Similar conclusions as in the present study have been reached by many authors (Schemske and Brokaw, 1981;

Brokaw, 1985; Connel, 1989; Whitmore, 1989, 1993; Swaine, 1992; Begon *et al.*, 1996).

Based on the result in the present study (Table 13), the regeneration of *Podocarpus falcatus* appears to be from the suppressed seedlings and saplings under shade whereas that of *Croton macrostachyus* might be from seed bank. According to estimate made during this investigation, *Rapanea melanophloes*, *Maytenus addat, Bersama abyssinica, Dovyalis abyssinica* and *Teclea nobilis* may have regenerated from the seedling banks. Demel Teketay (1996) has pointed out that seedling bank is the major regeneration route of most woody plants (especially climax species) in dry Afromontane forests of Ethiopia.

4.2. Diversity and Resources in Gaps

The diversity of species was found to be greater in gaps than under shade. This finding agrees with the works of many authors (Krebs, 1972 cited in Barbour *et al.,* 1987; Denslow and Spies, 1990; Lertzman, 1992; Denslow *et al.*, 1998). Barbour *et al.* (1987) showed that diversity of species increases as any particular stress level decreases. They further observed that the maintenance of high diversity appears to require episodic, random (stochastic) disturbance. According to Denslow and Spies (1990), the gap microclimates enhance seed germination and increase sapling growth rates in comparison to the rates in the forest understorey. As a result both shade intolerant and shade tolerant tree species can coexist in the gaps (Schupp *et al.*, 1989; Lertzman, 1992) and therefore, species in gaps are more diverse than those under deep shade. The discussion of Valverde and Silvertown (1997) also supports what has been mentioned above. They discussed that the disturbance /regrowth cycle involved in patch dynamics provides a permanent source of environmental heterogeneity, which allows the coexistence of species with different life histories and ecological requirements, thus increasing community diversity

(Fig. 1).

Fig.1. Densely populated and diverse species in the treefall gap (Photo Gemedo D. 1998).

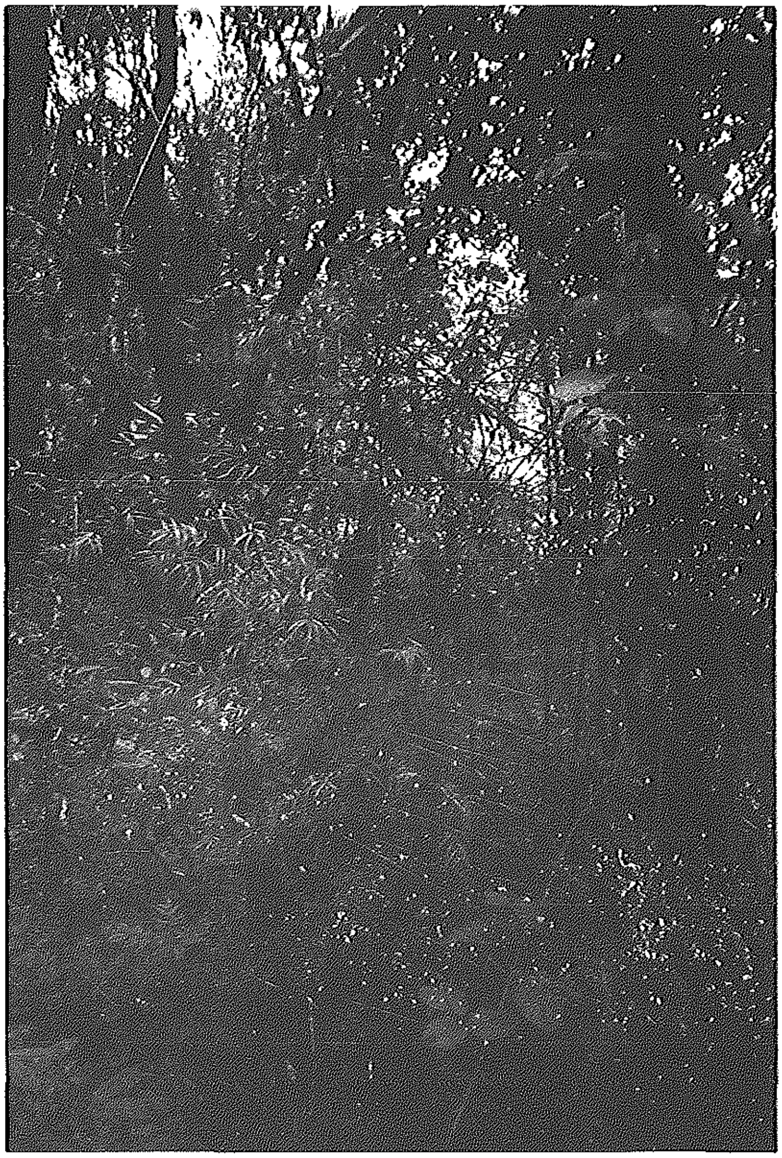

Fig.2. Much less diverse species under closed canopy.

(Photo Gemedo D. 1998).

In the present study, the comparison of gap and shade environments showed that the two were significantly different both in light levels and soil moisture content. The amount of sun light under deep shade and partial shade was 1.15% and 20.07% of the gap respectively. These light levels are similar to those reported by Poulson and Platt (1989). The authors reviewed that light levels beneath intact canopies are about 1% of full sun light. Denslow *et al.* (1998), Augspurger (1984), Whitmore (1989, 1993), Ellison *et al.* (1993) and many other authors have emphasized that the difference (in shade and gap) in the sun light received is one of the most important factors that contributes for differences in the germination, establishment and growth to maturity of tree species. Regeneration in gaps in the present study was much greater than regeneration in shade (Table 15). Ellison *et al.* (1993) and Gray and Spies (1996) reported similar results in which they indicated that there were more abundant established seedlings and saplings in gaps than in closed canopy areas. Rebertus and Veblen (1993) also reported that regeneration in gaps maintained coexistence between species.

Then, what is the major underlying factor for the establishment of tree species to increase much more in gaps than in shade ?

Reader *et al.* (1995) suggested two approaches that may be used to predict differences among tree species in the number of seedlings that become established in a gap. The first approach uses canopy trees to predict seedling establishment.

This approach assumes that seedling establishment reflects seed availability which, in turn, depends on tree density. Hence differences among species in seedling establishment in a gap should be directly related to differences in their density in the tree canopy. However, the data reported here disagrees with the interpretation based on this approach as there was no significant relationship between canopy composition and established tree species in the gap sites studied (Table 13). Therefore, the present study does not support the hypothesis of local seed sources,which states that each species will be most successful in gaps where it is most abundant in the surrounding canopy (Lertzman, 1992). Similar findings that disagree with the above approach have also been reported by Lertzman (1992). Thus, there was no significant relationship between canopy composition and gapfillers. The other approach assumes that seedling establishment is independent of tree density because the number of seeds present is thought to

exceed the num

edling establishment. As a result,

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hed seedlings and saplings in

, 1989; Spies and Franklin,

1993; Ellison *et al.*, 1993) have observed that not only pioneers but also climax tree species are found growing in gaps. According to Ellison *et al.* (1993), the ability of buried seeds and suppressed forest seedlings to respond rapidly to increased light levels following a treefall is a crucial stage in plant life history, and is a fundamental component of stand regeneration in tropical forests. Yamamoto (1996) discussed that climax species regenerate in gaps from seedlings or saplings recruited before gap formation, while pioneers colonize gaps after gap formation. Therefore, the shade tolerance and shade intolerance trait of tree species cannot be a decisive factor for establishment of more seedlings and saplings in gaps. More important, the major factor for the establishment of more tree species in gaps than under shade of the Shashemenne-Munessa natural forest is likely to be the availability of more space and resources (light, moisture, etc.) in gaps compared to the shade. Similar conclusions have been made by many authors (e.g. Runkle and Yetter, 1987; Denslow and Spies, 1990; Reader *et al.*, 1995; Gray and Spies, 1996; Denslow *et al.,* 1998).

4.3. Regeneration Guilds

As has been explained in the introduction, based on their autecology (e.g., microsites preferences for seedling establishment), tree species fall into two regeneration guilds called pioneer and climax (Augspurger, 1984; Whitmore, 1978, 1989, 1993; Ellison *et al.*, 1993). One of the suggested criteria for distinguishing these two groups is simple qualitative observations (Augspurger, 1984; Whitmore, 1989). Seedlings of pioneer tree species can not survive under canopy shade whereas, those of climax species can survive below canopy shade forming a seedling bank (Whitmore, 1989). In the present study, based on their occurrence in shade and gap, *Podocarpus falcatus, Maytenus addat, Rapanea melanophloeos, Dovyalis abyssinica, Bersama abyssinica* and *Teclea nobilis* can be categorized as climax tree species whereas *Juniperus procera, Maesa lanceolata, Vernonia auriculifera* and *Croton macrostachyus* can be classified as pioneer tree species. In agreement with this result, Demel Teketay (1996) reported that *Podocarpus falcatus, Bersama abyssinica* and *Teclea nobilis* are climax tree species. Furthermore, Bussmann (1994) reported that seedlings of *Juniperus procera* establish themselves by invading gaps as pioneers. Also the discussion of Friis (1992) indicated that seedlings and saplings of *Juniperus procera* occur in very open forests with discontinuous canopy. They added that *Juniperus procera* does not regenerate in mature forests where it is replaced by *Podocarpus falcatus.*

4.4. Changes in Vegetation Composition

Disturbances that cause the sequence of changes in structure and composition of species of a community initiate the replacement process of populations called succession (Chapman and Reiss, 1995; Ricklefs, 1997). Forest succession may be thought of as the sum of processes by which one canopy individual is replaced by another (Runkle, 1981; Hofgard, 1993; Battles, 1995). The result of the present study showed that most gapmakers were replaced by gapfillers of different species. Also the canopy trees were different from the dominant tree species established in the gaps. Furthermore, no significant correlations were found either between the gapmakers and definitive gapfillers, or between gapmakers and importance values of the established tree species in gaps. Moreover, there was no significant relationship between canopy composition of trees and established tree species in the gaps. These lack of relationships between gapmakers and gapfillers and also between canopy composition and gapfillers may be taken as evidence that due to treefall disturbances successional changes take place in forest community. In agreement with the present study, Runkle (1981) discussed that in a succession, the individuals tend to be of a different species. Also Whitmore (1989) reported that pioneer species grow more rapidly and so enter the overstorey first, and these are subsequently progressively replaced by more slowly growing climax species. In the present study, observations on *Podocarpus falcatus* appear to fit to this description. Analysis of the replacement proportion indicated that the gapfillers were not distributed randomly with respect to the gapmaker species. In addition, since all species were replaced by *Croton macrostachyus* with a greater frequency than they replace themselves, the hypothesis of self-replacement can be rejected. The gapmakers were preferentially replaced by *Croton macrostachyus* (a pioneer tree) which did not occur as gapmaker and had the least percentage in canopy composition. Similar results have also been reported by Lertzman (1992) and

Dalling *et al.* (1998). Thus, the gap creation and filling processes investigated in the present study may indicate directional change in community composition, i.e. succession (Lertzman, 1992; Rebertus and Veblen, 1993).

4.5. Implications for Forest Management

Gaps are heterogeneous (Whitmore, 1989) and the study of gap phase regeneration provides insight into species adaptations and overall patterns of forest species composition, growth and physiognomy (Runkle and Yetter, 1987; Whitmore, 1989). Denslow and Spies (1990) have pointed out that the knowledge of natural gap dynamics is important where forest management objectives include maintaining biological diversity. Gap formation is one of the silvicultural systems or techniques (Matthews, 1996) and the natural gap dynamics may provide the ecological basis of guidelines and models for the sustained management of uneven-aged, mixed-species stands (Denslow and Spies, 1990). Currently, interest has grown in using the uneven-aged management techniques (Jenkins and Parker,1998) and this system of forest management is useful for the conservation of biodiversity, to maintain sustainable yield and to ensure the sustainable forest ecosystem.

Struhsaker (1997) discussed that the principle of applying management plans that attempt to emulate natural ecological processes is appropriate to tropical forests and this approach attempts to incorporate a greater cognizance of forest biology by mimicking natural forest dynamics and minimizing the ecological impact of any resource exploitation. The same author has further discussed that the aim of mimicking natural forest processes and minimizing adverse impacts is to enhance natural regeneration and to give greater emphasis to nontimber values. Tropical forests, including Afromontane forests in Ethiopia are being destroyed at an alarming rate (e.g. Hartshorn, 1989; Sabogal, 1992; Seyoum, 1994; Legesse Negash, 1995; Demel Teketay, 1996). Afforestation with some conifers (such as the *Cupressus lusitanica* in Shashemenne-Munessa plantation forest) and poor forest management are known to be among the factors that cause loss of biological diversity (Crawley, 1997). Large-scale commercial afforestations have negative impacts on biota in addition to far-reaching water-budget, economic and sociological implication (reviewed by Allan *et al.*, 1997). On the other hand, small-scale disturbances that create gaps by killing one to a few canopy trees were reported to play key roles in the development and maintenance of forests structure and also in species coexistence (Lertzman, 1992; Rebertus and Veblen, 1993; Lertzman *et al.*, 1996). According to the discussion of Lertzman *et al.* (1996), the canopy gaps that result from small-scale mortality events have a pervasive influence on various aspects of the ecology of the forests and understorey vegetation dynamics, wildlife habitat, stream ecosystem structure and dynamics and biomass dynamics and carbon budgets.

Natural forest management (that aims at the sustainable production of forest products, based on the regeneration potential of the existing vegetation), together with conservation and reforestation, has been viewed as the main management option for the tropical dry forests (Sabogal, 1992). The gap dynamics discussed in this study is known to promote the natural regeneration of native tree species (Hartshorn, 1989) and also results in uneven-aged forest which has been reported to be useful for the conservation of biodiversity, maintenance of sustainable yield and ensuring the sustainable forest ecosystem (Lorimer, 1989; Matthews, 1996, Lertzman *et al.*, 1996; Jenkins and Parker, 1998). Brockway and Outcalt (1998) reported that periodic degradation of nontimber resource values is a major disadvantage of even-aged silvicultural system. Therefore, efforts have to be made to conserve our forests by applying the concepts of gap dynamics in the natural forest management option.

In summary, tropical forests need to be managed based on the concept of gap dynamics for the following major reasons:-

1. Gap disturbances provide the principal or only means by which most tree species can maintain their representation in closed canopy forests (Yamamoto, 1996). The creation of gaps provides an excellent opportunity for seedlings to become established since more space and resources are available in gaps than under closed canopy (Reader *et al.*, 1995). The gap environments often meet the requirements of species which could not

otherwise establish. Gaps maintain shade intolerant species in the forest community. So forest gaps promote coexistence of species in a mixed stand and hence biological diversity is maintained.

2. It is possible to harvest timber and other forest products from both shade intolerant and shade tolerant tree species (Hartshorn, 1989).
3. Wildlife will have suitable habitat in forests managed by the ecological approach that mimics natural forest dynamics.

Finally we would like to emphasise that the present study is only a preliminary work designed as a prelude to detailed ecophysiological and autoecological work. It is expected and recommended that more work on the role of gap dynamics in the management of our forests will be undertaken. Studies on the successional changes and replacement patterns in the forest gaps are strongly recommended by this study.

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APPENDIX I

Dominance, Frequency and Importance Value of each Species in some selected Gaps.

Site 4

Dominance of		Dominance Rank
Croton macrostachyus	0.421cm^2	1
Vernonia auriculifera	0.104 cm^2	4
Juniperus procera	0.097cm^2	5
Podocarpus falcatus	0.336cm^2	3
Maesa lanceolata	0.08cm^2	7
Bersama abyssinica	0.084cm^2	6
Maytenus addat	0.039cm^2	8
Rapanea melanophloeos	0.340 cm^2	2
Total	1.501 cm^2/100m^2	

Absolute Frequency of

Croton macrostachyus	70%
Vernonia auriculifera	65%
Podocarpus falcatus	20%
Juniperus procera	30%
Maesa lanceolata	25%
Bersama abyssinica	10%
Maytenus addat	10%
Rapanea melanophloeos	10%

Importance Value

1. Relative density of

Croton macrostachyus	35.0%
Vernonia auriculifera	33.7%
Podocarpus falcatus	7.6%
Juniperus procera	8.7%
Maesa lanceolata	7.6%
Bersama abyssinica	2.5%
Maytenus addat	2.5%
Rapanea melanophloeos	2.5%

2. Relative dominance of

Croton macrostachyus	28.0%
Vernonia auriculifera	6.9%
Juniperus procera	6.5%
Podocarpus falcatus	22.4%
Maesa lanceolata	5.3%
Bersama abyssinica	5.6%
Maytenus addat	2.6%
Rapanea melanophloeos	22.6%

3. Relative Frequency of

Croton macrostachyus	29.2%
Vernonia auriculifera	27.1%
Juniperus procera	12.5%
Podocarpus falcatus	8.3%
Maesa lanceolata	10.4%
Bersama abyssinica	4.2%
Maytenus addat	4.2%
Rapanea melanophloeos	4.2%

Therefore, the importance value of each species in the gap site is:-

Species	Relative Density	Relative dominance	Relative Frequency	Importance Value (I.V)	I.V. Rank
Croton macrostachyus	35.0	28.0	29.2	92.2	1
Vernonia auriculifera	33.7	6.9	27.1	67.7	2
Juniperus procera	8.7	6.5	12.5	27.7	5
Podocarpus falcatus	7.6	22.4	8.3	38.3	3
Maesa lanceolata	7.6	5.3	10.4	23.3	6
Bersama abyssinica	2.5	5.6	4.2	12.3	7
Maytenus addat	2.5	2.6	4.2	9.3	8
Rapanea melanophloeos	2.5	22.6	4.2	29.3	4

Site 5

Dominance of		**Dominance Rank**
Croton macrostachyus	1.048cm^2	2
Vernonia auriculifera	0.185cm^2	3
Juniperus procera	0.082cm^2	4
Podocarpus falcatus	1.066cm^2	1
Total	2.381cm ^{2}/100m^2	

Absolute Frequency of

Croton macrostachyus	85%
Vernonia auriculifera	60%
Podocarpus falcatus	55%
Juniperus procera	50%
	250%

Importance Value

1. Relative Density of

Croton macrostachyus	34%
Vernonia auriculifera	27%
Podocarpus falcatus	24%
Juniperus procera	15%

2. Relative Dominance of

Croton macrostachyus	44%
Vernonia auriculifera	7.8%
Juniperus procera	3.4%
Podocarpus falcatus	44.8%

3. Relative Frequency of

Croton macrostachyus	34%
Vernonia auriculifera	24%
Juniperus procera	20%
Podocarpus falcatus	22%

As a result, the importance value of the species is:

Species	Relative Density	Relative Dominance	Relative Frequency	Importance Value	I.V. Rank
Croton macrostachyus	34	44	34	112	1
Vernonia auriculifera	27	7.8	24	58.8	3
Juniperus procera	15	3.4	20	38.4	4
Podocarpus falcatus	24	44.8	22	90.8	2

Site 6

	Dominance of	**Dominance Rank**
Croton macrostachyus	4.00cm^2	1
Teclea nobilis	0.14cm^2	4
Vernonia auriculifera	1.23 cm^2	2
Maytenus addat	0.05cm^2	5
Bersama abyssinica	0.72cm^2	3
Podocarpus falcatus	0.04cm^2	6
Dombeya torrida	0.02cm^2	7

Absolute Frequency of

Croton macrostachyus	85%
Teclea nobilis	5%
Vernonia auriculifera	90%
Maytenus addat	5%
Bersama abyssinica	30
Podocarpus falcatus	5%
Dombeya torrida	5%
	225%

Importance Value

1. Relative density of

Croton macrostachyus	42.5%
Teclea nobilis	1.2%
Vernonia auriculifera	42.5%
Maytenus addat	1.2%
Bersama abyssinica	10.0%
Podocarpus falcatus	1.2%
Dombeya torrida	1.2%

2. Relative Dominance of

Croton macrostachyus	64.5%
Teclea nobilis	2.1%
Vernonia auriculifera	19.8%
Maytenus addat	0.8%
Bersama abyssinica	11.6%
Podocarpus falcatus	0.6%
Dombeya torrida	0.3%

3. Relative Frequency of

Croton macrostachyus	37.8%
Teclea nobilis	2.2%
Vernonia auriculifera	40.%
Maytenus addat	2.2%
Bersama abyssinica	13.3%
Podocarpus falcatus	2.2%
Dombeya torrida	2.2%

Hence, the importance value for each species in this gap site is:-

Species	Relative Density	Relative Dominance	Relative Frequency	Importance Value (I.v)	I.V. Rank
Croton macrostachyus	42.5	64.5	37.8	144.8	1
Teclea nobilis	1.2	2.1	2.2	5.5	4
Vernonia auriculifera	42.5	19.8	40.0	102.3	2
Maytenus addat	1.2	0.8	2.2	4.2	5
Bersama abyssinica	9.9	11.6	13.3	34.8	3
Podocarpus falcatus	1.2	0.6	2.2	4.0	6
Dombeya torrida	1.2	0.3	2.2	3.7	7

Site 7

Dominance of		Dominance Rank
Dovyalis abyssinica	0.59cm^2	3
Teclea nobilis	0.35cm^2	5
Croton macrostachyus	078cm^2	2
Maytenus addat	2.08cm^2	1
Bersama abyssinica	0.09cm^2	7
Podocarpus falcatus	0.03cm^2	8
Vernonia auriculifera	0.57cm^2	4
Maesa lanceolata	0.27cm^2	6
	4.76cm^2/100m^2	

Absolute Frequency of	
Dovyalis abyssinica	45%
Teclea nobilis	20%
Croton macrostachyus	70%
Maytenus addat	45%
Bersama abyssinica	5%
Podocarpus falcatus	25%
Vernonia auriculifera	50%
Maesa lanceolata	5%
	265 percent

Importance Value

1. Relative Density of

Dovyalis abyssinica	14.0%
Teclea nobilis	7.0%
Croton macrostachyus	31.0%
Maytenus addat	19.0%
Bersama abyssinica	1.0%
Podocarpus falcatus	0.9%
Vernonia auriculifera	17.0%
Maesa lanceolata	1.0%

2. Relative Dominance of

Dovyalis abyssinica	12.4%
Teclea nobilis	7.3%
Croton macrostachyus	16.4%
Maytenus addat	43.7%
Bersama abyssinica	1.9%
Podocarpus falcatus	0.6%
Vernonia auriculifera	12.0%
Maesa lanceolata	5.7%

3. Relative Frequency of

Dovyalis abyssinica	17.0%
Teclea nobilis	7.0%
Croton macrostachyus	26.4%
Maytenus addat	17.0%
Bersama abyssinica	1.9%
Podocarpus falcatus	9.4%
Vernonia auriculifera	18.9%
Maesa lanceolata	1.9%

Therefore, the importance value is :

Species	Relative			Importance Value (I.V)	I.V Rank
	Density	Dominance	Frequency		
Dovyalis abyssinica	14.0	12.4	17.0	43.4	4
Teclea nobilis	7.0	7.3	7.5	21.8	5
Croton macrostachyus	31.0	16.4	26.4	73.8	2
Maytenus addat	19.0	43.7	17.0	79.7	1
Bersama abyssinica	1.0	1.9	1.9	4.8	8
Podocarpus falcatus	9.0	0.6	9.4	19.0	6
Vernonia auriculifera	17.0	12.0	18.9	47.9	3
Maesa lanceolata	1.0	5.7	1.9	8.6	7

Site 8

Dominance of		Dominance Rank
Vernonia auriculifera	= 3.51	1
Rapanea melanophloeos	= 0.21	7
Dovyalis abyssinica	= 0.02	9
Croton macrostachyus	= 0.90	3
Maesa lanceolata	= 0.37	6
Bersama abyssinica	= 1.33	2
Podocarpus falcatus	= 0.07	8
Juniperus procera	= 0.76	4
Maytenus addat	= 0.39	5
Total dominance	= 7.56cm^2/100m^2	

Absolute Frequency of

Vernonia auriculifera	95%
Rapanea melanophloeos	5%
Dovyalis abyssinica	5%
Croton macrostachyus	35%
Maesa lanceolata	15%
Bersama abyssinica	35%
Podocarpus falcatus	10%
Juniperus procera	10%
Maytenus addat	5%

Importance Value

1. Relative Density of

Vernonia auriculifera	62.46%
Rapanea melanophloeos	1.22%
Dovyalis abyssinica	1.22%
Croton macrostachyus	8.70%
Maesa lanceolata	3.78%
Bersama abyssinica	12.48%
Podocarpus falcatus	3.78%
Juniperus procera	2.50%
Maytenus addat	3.78%

2. Relative Dominance of

Vernonia auriculifera	46.43%
Rapanea melanophloeos	2.78%
Dovyalis abyssinica	0.26%
Croton macrostachyus	11.90%
Maesa lanceolata	4.89%
Bersama abyssinica	17.59%
Podocarpus falcatus	0.92%
Juniperus procera	10.05%
Maytenus addat	5.16%

3. Relative Frequency of

Vernonia auriculifera	44.19%
Rapanea melanophloeos	2.32%
Dovyalis abyssinica	2.32%
Croton macrostachyus	16.28%
Maesa lanceolata	6.98%
Bersama abyssinica	16.28%
Podocarpus falcatus	4.65%
Juniperus procera	4.65%
Maytenus addat	2.32%
	99.99%

Hence, the importance value is:

Species	Relative			Importance value (I.V)	I.V Rank
	Density	Dominance	Frequency		
Vernonia auriculifera	62.46	46.43	44.19	153.08	1
Rapanea melanophloeos	1.22	2.78	2.32	6.32	8
Dovyalis abyssinica	1.22	0.26	2.32	3.80	9
Croton macrostachyus	8.70	11.90	16.28	36.88	3
Maesa lanceolata	3.78	4.89	6.98	15.65	5
Bersama abyssinica	12.48	17.59	16.28	46.35	2
Podocarpus falcatus	3.78	0.92	4.65	9.35	7
Juniperus procera	2.50	10.05	4.65	17.20	4
Maytenus addat	3.78	5.16	2.32	11.26	6

Site 9

Dominance of		**Dominance Rank**
Maesa lanceolata	7.81	1
Bersama abyssinica	0.79	5
Maytenus addat	2.03	2
Podocarpus falcatus	1.38	3
Croton macrostachyus	0.14	7
Rapanea melanophloeos	1.26	4
Juniperus procera	0.06	9
Teclea nobilis	0.23	6
Dovyalis abyssinica	0.09	8
	13.79cm^2/100m^2	

Absolute Frequency of	
Maesa lanceolata	40%
Bersama abyssinica	30%
Maytenus addat	25%
Podocarpus falcatus	55%
Croton macrostachyus	20%
Rapanea melanophloeos	55%
Juniperus procera	10%
Teclea nobilis	5%
Dovyalis abyssinica	5%
	245%

Importance Value

Relative Density of

Maesa lanceolata	15.0%
Bersama abyssinica	13.97%
Maytenus addat	6.98%
Podocarpus falcatus	21.98%
Croton macrostachyus	5.95%
Rapanea melanophloeos	30.0%
Juniperus procera	1.95%
Teclea nobilis	1.03%
Dovyalis abyssinica	0.03%

Relative Dominance of

Maesa lanceolata	56.63%
Bersama abyssinica	5.73%
Maytenus addat	14.72%
Podocarpus falcatus	10.01%
Croton macrostachyus	1.01%
Rapanea melanophloeos	9.14%
Juniperus procera	0.43%
Teclea nobilis	1.67%
Dovyalis abyssinica	0.65%

Relative Frequency of

Maesa lanceolata	16.33%
Bersama abyssinica	12.24%
Maytenus addat	10.20%
Podocarpus falcatus	22.45%
Croton macrostachyus	8.16%
Rapanea melanophloeos	22.45%
Juniperus procera	4.08%
Teclea nobilis	2.04%
Dovyalis abyssinica	2.04%
	99.99%

As a result, the importance value of each species becomes:-

Species	Relative			(I.V)	I.V
	Density	Dominance	Frequency		Rank
Maesa lanceolata	15	56.63	16.33	87.96	1
Bersama abyssinica	13.97	5.73	12.24	31.94	4
Maytenus addat	6.98	14.72	10.20	31.90	5
Podocarpus falcatus	21.98	10.01	22.45	54.44	3
Croton macrostachyus	5.95	1.01	8.16	15.12	6
Rapanea melanophloeos	30.0	9.14	22.45	61.59	2
Juniperus procera	1.95	0.43	4.08	6.46	7
Teclea nabilis	1.03	1.67	2.04	4.74	8
Dovyalis abyssinica	1.03	0.65	2.04	3.72	9

Site 10

Dominance of		**Dominance Rank**
Maytenus addat	= 0.84	3
Rapanea melanophloeos	= 3.62	1
Croton macrostachyus	= 0.70	4
Bersama abyssinica	= 1.07	2
Podocarpus falcatus	= 0.23	5
Maesa lanceolata	= 0.21	6
	$6.67 cm^2/100 cm^2$	

Absolute Frequency of

Maytenus addat = 15%

Rapanea melanophloeos = 90%

Croton macrostachyus = 45%

Bersama abyssinica = 35%

Podocarpus falcatus = 15%

Maesa lanceolata = 15%

215%

Importance Value

1. Relative Density of

Maytenus addat = 3.75%

Rapanea melanophloeos =57.50%

Croton macrostachyus = 13.75%

Bersama abyssinica = 13.75%

Podocarpus falcatus = 5.0%

Maesa lanceolata = 6.25%

100%

2. Relative dominance of

Maytenus addat = 12.59%
Rapanea melanophloeos = 54.27%
Croton macrostachyus = 10.49%
Bersama abyssinica = 16.04%
Podocarpus falcatus = 3.45%
Maesa lanceolata = 3.15%

3. Relative Frequency of

Maytenus addat = 6.98%
Rapanea melanophloeos = 41.86%
Croton macrostachyus = 20.93%
Bersama abyssinica = 16.28%
Podocarpus falcatus = 6.98%
Maesa lanceolata = 6.98%

Therefore, the importance values of each species is:-

Species	Relative			Importance Value (I.V)	I.V Rank
	Density	Dominance	Frequency		
Maytenus addat	3.75	12.59	6.98	23.32	4
Rapanea melanophloeos	57.50	54.27	41.86	153.63	1
Croton macrostachyus	13.75	10.49	20.93	45.17	3
Bersama abyssinica	13.75	16.04	16.28	46.07	2
Podocarpus falcatus	5.0	3.45	6.98	15.43	6
Maesa lanceolata	6.25	3.15	6.98	16.38	5

Site 11

Dominance of		**Dominance Rank**
Rapanea melanophloeos	= 3.485	2
Juniperus procera	= 5.267	1
Sp.x	= 0.687	4
Bersama abyssinica	= 0.232	5
Maesa lanceolata	= 2.928	3
	$12.599 cm^2/100m^2$	

Absolute Frequency of

Rapanea melanophloeos = 85%

Juniperus procera = 50%

Sp.x = 25%

Bersama abyssinica = 15%

Maesa lanceolata = 30%

205%

Importance Value

1.Relative Density of

Rapanea melanophloeos = 55%

Juniperus procera =17.49%

Sp.x = 11.48%

Bersama abyssinica = 5.00%

Maesa lanceolata = 11.48%

= 100.45%

2. Relative Dominance of

Rapanea melanophloeos = 27.66%

Juniperus procera = 41.80%

Sp.x = 5.45%

Bersama abyssinica = 1.84%

Maesa lanceolata = 23.24%

3. Relative frequency of

Rapanea melanophloeos = 41.46%

Juniperus procera = 24.39%

Sp.x = 12.19%

Bersama abyssinica = 7.32%

Maesa lanceolata = 14.63%

99.99%

Hence, the importance value for each species established on the gap is:-

Species	Relative			Importance	I.V.
	Density	Dominance	Frequency	Value (I.V)	Rank
Rapanea melanophloeos	55.0	27.66	41.46	124.12	1
Juniperus procera	17.49	41.80	24.39	83.68	2
Sp.x	11.48	5.45	12.19	29.12	4
Bersama abyssinica	5.00	1.84	7.32	14.16	5
Maesa lanceolata	11.48	23.24	14.63	49.35	3