

**ECOLOGY OF REGENERATION AND PHENOLOGY OF
SEVEN INDIGENOUS TREE SPECIES IN A DRY TROPICAL
AFROMONTANE FOREST, SOUTHERN ETHIOPIA**

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ABSTRACT

The Munessa-Shashemene Forest, a typical dry afro-montane forest located on the eastern escarpment of the Rift Valley at about 250 km from Addis Ababa, is under severe pressure due to logging, cattle grazing and conversion of the forest to arable land. Ecology of regeneration and phenology of seven indigenous tree species known to have considerable socio-economic and ecological importance were investigated. Seedling growth experiment within the forest was carried out in three light environments for 136 days and their survival followed for 12 months in the permanent plots. About 1200 understorey seedlings located systematically at different sites within the forest were marked and monitored for their mortality and herbivory rates for a period of 2 years. Seedling densities and their spatial distribution along gradients of altitude, disturbance and canopy light were investigated in the forest using quadrats having sizes of 10 m x 5 m along line transects. Tree and sapling densities, their spatial distribution along altitudes, and size-class distribution were investigated using quadrats of 20 m X 20 m along line transects. About 210 focal mature trees have been monitored for their leaf, flower and fruit every month for a period of two years. Various statistical tools and ecological software were employed for the data analyses.

Seedling morphological and physiological traits showed significant variation among species and light levels. Seedling growths such as total plant biomass, height, total leaf area and root length were highly responsive to light levels while, specific leaf area, leaf area ratio, leaf, root and stem mass ratios were more of species-specific. Relative growth and net assimilation rates were highly influenced by the plant biomass. Understorey seedling mortality and herbivory rates year⁻¹, respectively, ranged 11% (*Podocarpus*) – 67 % (*Syzygium*), and 0 (both *Croton* and *Podocarpus*) - 56 % (*Celtis*). They were significantly different between dry and wet seasons of the year. Mean densities of seedlings varied among species from 0 (*Polyscias*) to 5,334 (*Prunus*) individuals ha⁻¹, while trees and saplings varied from 3 (*Polyscias*) to 102 (*Podocarpus*) plants ha⁻¹. Size-class distributions of the species have shown three major groups:- (1) species with inverse J-shape curve, and thus having healthy regeneration status, (2) species with higher proportion of individuals in the lowest size-class, but missing individuals in the subsequent middle size-classes and thus hampered regeneration and; (3) species with no individuals in the lowest and middle height classes, but represented by large

sized individuals only and thus at risk of local extermination. Better reproductive performance evidenced by high seedling densities (e.g. *Celtis* and *Prunus*) or adaptive defenses to herbivory (e.g. *Croton* and *Podocarpus*) were common attributes of healthy regenerating species.

In deciduous species, the period of leaflessness/shedding lasted from January to March. Leaf flushing peaked in April coinciding with start of small rains. In most species, flowering pattern was strongly seasonal and annual. Unlike flowering, fruiting was non-seasonal and extended over several months of a year. The peak fruiting period was occurred around mid to late of the long dry season. Rainfall and temperature triggered the phenological cycles in the tree species. In general, understorey light environment, drought (soil moisture stress), seedling herbivory damage, reproduction, and human disturbances were among the major factors affecting regeneration of tree species in the forest. Species of high conservation priority in the immediate future are *Polyscias* and *Pouteria*; while *Celtis*, *Croton* and *Prunus* are encouraged for sustainable utilization options. The implications of the results of seedling growth, survival, herbivory damage, plant population structure and phenology of the species are discussed in detail.

1. INTRODUCTION

Tropical dry forest ecosystems are the main repositories of biodiversity, sources of timber, medicinal and wild edible plants, fuel, fodder, and play a critical role in watershed protection. They also contribute substantially to the global carbon pool and net primary productivity of terrestrial ecosystems. Tropical dry forest zones have often been preferred for human settlement to wetter forest zones because of biological and ecological reasons. Due to their attractive environment, tropical dry forests have been under exploitation for thousands of years. The growing human populations during the last century have put increasing pressure on tropical dry forests, threatening to cause irreversible damage to these ecosystems.

Regeneration is a central component of tropical dry forest ecosystem dynamics and restoration. Sustainable forest utilization is only possible if adequate information on the regeneration dynamics and factors influencing the regeneration of important canopy tree species are available. The main reasons for studying regeneration in tropical dry forests are:- (1) the tropical dry forests, which originally represented 42 % of the tropical vegetation worldwide (Murphy and Lugo, 1986), are the most threatened tropical terrestrial ecosystem, due to the conversion of these areas into agricultural land (Janzen, 1988); (2) there have been insufficient studies of dry tropical forests and to date only 3 % of the literature on tropical forest focuses on dry forests (Sanchez-Azofeifa *et al.*, 2005); (3) tree species in tropical dry forests have particular natural regeneration attributes that makes them distinct from other forest species (Daniel *et al.*, 2006) and; (4) problems of natural regeneration have already been reported for some of the tree species in tropical dry forests (Poorter *et al.*, 1996; Demel Teketay, 1997).

Thus, scientific knowledge of the regeneration ecology of tropical dry forests is important for conservation and restoration of degraded forests.

The Ethiopian highlands contribute to more than 50 % of the land area in Africa with afro-montane vegetation (Yalden, 1983), of which dry afro-montane forests form the largest part. The dry Afro-montane forests are either mixed *Juniperus-Podocarpus* forests or predominantly *Podocarpus* forests, both with an element of broad-leaved species. They occur in both northwestern and southeastern highlands, especially on the plateau of Oromia, Tigray, Amhara and Southern Nations, Nationalities and Peoples (SNNP) Regional States at altitudes from 1500- 2700 m (Friis, 1992).

As in most tropical countries where human populations are increasing rapidly, forest conservation is a critical issue in Ethiopia. Historical evidences indicate that forests used to cover large areas of the Ethiopian highlands than the present (von Breitenbach, 1963; Friis, 1992). By the late 1980s and 1990s only 2- 3 % of Ethiopia remained covered by natural forest (Anonymous, 1988; EFAP, 1994). At present, the natural forest cover of the country is about 4,798,000 hectares (4 % of the total landmasses) of which the dense forest covers 2,981,000 ha, while the remaining 1,817,000 ha are highly degraded forests (Mayaux *et al.*, 2004). The rate of deforestation is estimated between 150,000 and 200,000 ha year⁻¹ (EFAP, 1994). In recent years, the afro-montane forests are attracting the eyes of several investors that aim to convert the highly diverse ecosystem by monoculture or less diverse agriculture. This scenario has produced an ongoing conflict between the attempts to conserve or restore the few remaining natural forests together with the associated unique biodiversity resources and the

land use needs of the country's increasing human population as well as large-scale investments.

Furthermore, the options available to slow or halt the decline in forest ecosystems and restore degraded forests as well as maintenance of diversity of the indigenous tree species are limited. Until recently, exotic species plantation forests have been the focus for restoration of indigenous species on degraded forestlands in the country. One of the factors contributing to the difficulties of maintaining remnant forests and restoring deforested areas is the lack of knowledge on regeneration ecology and propagation of the indigenous tree species (Legesse Negash, 1995; Getachew Tesfaye *et al.*, 2002). Scientific information on the dynamics of natural regeneration including seedling growth, survival, herbivory effect, tree population structure and reproductive ecology of even dominant trees of the dry afro-montane forests in Ethiopia are very limited. Such knowledge would enhance conservation through sustainable management of the remaining forests and restoration through inclusion of the indigenous species in enrichment plantation and other tree planting programs thus, facilitating both in-situ and ex-situ conservation of threatened species. Knowledge of tree phenology patterns in tropical dry forests is basic to the understanding of biological processes and functioning of the ecosystem. The timing and duration of flowering and fruiting for instance, is crucial in understanding forest regeneration dynamics as the pronounced seasonality affects the reproductive output and performances such as seed production, germination, survival, and seedling growth (Augsburger, 1981; Daniel *et al.*, 2006).

In the present study comprehensive examination of critical regeneration processes involved from seedling phase to mature tree including growth, survival, herbivory/grazing effect, population density, distribution and structure of seven indigenous tree species in the dry afro-montane forest of Munessa-Shashemene, southern Ethiopia was undertaken. Reproductive phenology of the species was investigated to understand the links/relationships between regeneration dynamics and reproduction. Moreover, this study was the first to investigate the phenology of indigenous tree species in Ethiopia. The collective information from the multiple methodological approaches and the links among the different processes provided clear picture of the over all species natural regeneration dynamics, species response or adaptations to various ecological factors, and major bottlenecks that hamper their regeneration. The nature of disturbance in the Munessa-Shashemene Forest (e.g. selective tree cutting, grazing, logging) is typical of many natural forests in Ethiopia and therefore such study results can help inform management decisions in similar other afro-montane forests of the country.

This study is part of a multidisciplinary research project ‘Functional Ecology and Sustainable Utilization of the Munessa-Shashemene Forest’ jointly executed by The University of Bayreuth, Martin Luther University Halle (Germany) and, Addis Ababa University and The Ethiopian Institute of Agricultural Research (Ethiopia).

2. STATE-OF-THE ART

2.1. Growth and Biomass Allocation in Tropical Forest Tree Seedlings

The complex natural processes which exist in a forest ecosystem and the environmental heterogeneity are critical in determining the pathways of tree regeneration and replacement

patterns. Seedling growth in the understorey of tropical forests encounters a highly dynamic light environment, which varies both spatially and temporally (Chazdon *et al.*, 1996). Tropical forest understoreys generally receive 1-2 % of the incident light. The ability of plant species to respond to changing understorey light environment determines the successional pathways and canopy replacement patterns (Pompa and Bongers, 1988; Osunkoya *et al.*, 1994; Poorter, 1999). Based on their germination and growth requirements tropical tree species are classified into two functional groups- as pioneers and shade-tolerants (Whitmore, 1996). In the presence of disturbance that changes the light environment, already existing undergrowth seedlings (shade-tolerant species) are released and grow-up to succeed the canopy and successively maintain their population. In contrast, seedlings that are newly recruited from seeds in the soils or recently dispersed fill large gaps formed by clear feelings (Bazzaz, 1991; Whitmore, 1996). Seedlings of shade-tolerant species can survive prolonged periods of shade in forest understorey and show a narrower range of photosynthetic responses when grown under different irradiances than do pioneer species (Riddoch *et al.*, 1991; Poorter, 1999). Their growth, however, is greater in gaps than in understorey shade. On the other hand, pioneer species exhibit higher growth rates than shade tolerant species, with less biomass allocation to root systems and larger to leaf fractions (Pompa and Bongers, 1988).

Growth rates in tropical tree seedlings have been variously measured as biomass accumulation, height increase, leaf production, relative growth, or allocation to leaf, root and stem (Pompa and Bongers, 1988; Kitajima, 1994). Seedling growth analyses mainly emphasize on inter- and intra-specific differences in relative growth rates (RGR) together with their causes (Poorter, 1990; Lambers and Poorter, 1992; Kitajima and Bolker, 2003). The inherent differences in

RGR are ecologically important because RGR is one of the primary variables that determine the outcome of the competitive interaction between plants growing in natural condition (Grime, 1979, 1994). Recent studies also revealed that several species change their rank (crossover) growth rates when grown under different light conditions (Sack and Grubb, 2001). Some studies investigated whether the ranking in RGR reverse between pioneer and shade tolerant species when grown under low and high light environments (Kitajima, 1994; Kitajima and Bolker, 2003). Similarly, differences in leaf life span, leaf mass ratio (LMR), leaf area ratio (LAR) and specific leaf area (SLA) between species of the two functional groups were evaluated (Poorter *et al.*, 1990; Reich *et al.*, 1991). The variations in physiology and morphological traits among tree species have been related to their differences in growth habitat conditions (Pompa and Bongers, 1988; Kitajima, 1994).

In forest understorey, growth and survival of regenerating seedlings are closely linked to their capacity to intercept light efficiently under contrasting light environments. Morphological and physiological responses to light environment vary with position along the light gradient (Poorter, 1990, 1999). At low irradiance, shade grown plants enhance interception of light by large biomass fraction in leaves (LMR). In combination with a large leaf area per unit leaf biomass (SLA), this leads to a large interceptive leaf area per unit plant mass (LAR). Plants at high irradiance, on the other hand, are faced with high radiation loads and, therefore, nutrient and water availability may limit plant growth. Accordingly, sun plants invest relatively more biomass in roots (i.e. they have a large root mass ratio, RMR). Biomass production increased by the formation of thick leaves with a higher light-saturated photosynthetic rates, increasing biomass growth per unit leaf area (net assimilation rate, NAR) and RGR (Poorter and

Oberbauer, 1993). Similarly sun-grown plants display greater morphological plasticity as they produce more leaves and root length per unit time compared with shade- grown plants.

Several studies have provided evidence relating light heterogeneity and plasticity in specific traits that may enhance carbon gain of tropical forest tree seedlings (Pompa and Bongers, 1988; Reich *et al.*, 1998). Recent advances have been made in understanding the relationship between carbon- exchange physiology, morphology and growth (Poorter and Remkes, 1990; Poorter, 1990; Watling *et al.*, 1997; Reich *et al.*, 1998; Poorter, 1999; Souza and Valio, 2003). However, few studies have attempted to address ecophysiology and growth of seedlings of tropical montane forest tree species in Ethiopia (Masresha Fetene and Yonas Feleke, 2001). Information on responses of indigenous tree seedlings to changing light environment in the montane forests of Ethiopia is central to understand the regeneration ecology of species, to enhance the growth of desired species and promote indigenous tree planting programs.

2.2. Mortality and Herbivory in Understorey Seedlings in Tropical Forest

Several tropical forest regeneration studies have investigated mortality of tree seedlings in relation to understorey biotic and abiotic factors. Potential causes of seedling mortality include abiotic stress such as drought or soil moisture stress, disturbance, and biotic influences, such as herbivory, disease pathogen or competition (Augsburger, 1984; Louda *et al.*, 1990). Information on factors that govern seedling dynamics in tropical forest understorey can have significant implications on sustainable management and conservation of forests.

Drought induced mortality especially at the seedling stage affect the successful regeneration of tropical forest species (Condit *et al.*, 1995; Bongers *et al.*, 1999). Various studies indicated that seedling mortality in the dry season is strongly associated to the availability of water in the soil, the ability to tolerate dessication and the vapor pressure deficit in the environment (Poorter and Hayashida-Oliver, 2000). The actual water stress experienced by the plant depends on the physiological and morphological characteristics. Some hypotheses predict that under limiting light availability, soil moisture (water) limitations may have less impact on plant performance (Canham *et al.*, 1996). Accordingly, shade by the tree canopy has indirect effects, such as reducing leaf and air temperatures and vapor pressure deficit that would rather alleviate the impact of drought. A contrary hypothesis predicts that deep shade will aggravate the stress imposed by drought, based on the proposed trade-off mechanism that shaded plants allocate more to shoot, and to leaf area (or a high specific leaf area), than to root, thereby diminishing the ability to capture water from the soil and increasing water loss through transpiration (Smith and Huston, 1989). Such plant traits confer an advantage in the shaded understory (also during wet season) as they enhance light interception in a light-limited environment. In fact, some studies have found a higher impact of water stress on shaded plants (Valladares and Pearcy, 2002). A third group of hypotheses argues that the effects of shade and water-shortage are independent, that is, their impacts are orthogonal (Sack and Grubb, 2002). Inter-specific difference in tolerance to water stress (or drought) is considered to be of paramount importance for explaining regeneration dynamics and species distributions in tropical forests.

Because of their size and limitation of nutrient availability, seedlings are more sensitive to herbivores damage than older plants (Swaine, 1996). Herbivores can affect plant fitness and population dynamics in several ways (Crawley, 1989; Louda *et al.*, 1990), (1) directly, through biomass removal; (2) indirectly, by altering morphological traits that determine competitive ability and; (3) indirectly, by altering the environment that the plant experiences. The effect of herbivory is highly variable among species, in some cases and seasons the whole cohorts of seedlings can be lost to herbivory, and at others it may seem to be unimportant. The accumulated evidence from numerous studies has shown that herbivory affects reproductive success of the individual plant, survival, structure, composition and regeneration of forest (Silvertown, 1982; Hendrix, 1988). Because of the pronounced long dry season occurring in dry afro-montane forests in Ethiopia and high pressure from livestock grazing through them (Getachew Tesfaye *et al.*, 2002) information on the effect of drought and herbivory on seedlings would provide better insight on regeneration dynamics of the afro-montane forests.

2.3. Plant Population Density, Size- class Distribution and Regeneration Pattern

Tropical forests revealed variation in pattern of regeneration both through differences in their constituent species and the environmental variables in which they grow (Denslow, 1987; Bazzaz, 1991; Whitmore, 1996; Demel Teketay, 1997; Kyereth *et al.*, 1999). They regenerate from one or more pathways: seed rain (recently dispersed seeds), the soil seed bank (dormant seeds in the soil), the seedling bank (established, suppressed seedlings in the understorey), and coppice (root/shoot sprouts of damaged individuals) (Garwood, 1983; Whitmore, 1996; Demel Teketay, 1997; Getachew Tesfaye *et al.*, 2002).

Studies on seedling density, distribution and pattern of population structure of the major tree species enrich our knowledge that can help understand the status of species, and thereof, history and ecology of the forest (Harper, 1977; Hubbel and Foster, 1986). Seedling pools in forest understorey are dynamic and rates may vary both among species and within species in gaps and shade (Bazzaz, 1991; Demel Teketay, 1997). The frequency and magnitude of disturbance would affect the species composition, demography and the regenerative process. Studies of factors preventing or promoting seedling establishment of woody species may help in future restoration of degraded tropical forestlands through the application of the appropriate management scheme. Such works have shown that studies on seedling ecology can provide options to forest development through improvement in recruitment, establishment and growth of the desired seedlings. Information on tree seedling ecology has significant implications on the management and conservation of natural forests (Whitmore, 1993; Swaine, 1996). However, little attention has been paid so far to investigate seedling demographic traits and population structure of indigenous trees together with their relationship to disturbances in afro-montane forests of Ethiopia (Demel Teketay, 1997).

Regeneration of tree species is commonly assessed by the distributions of size-classes measured as diameter at breast height (DBH) or height. The size class structure of the species show whether regeneration is taking place or not. If regeneration were taking place continuously then the species would have a stable population distribution with inverse- J shape, which is an indicator of good regeneration (Harper, 1977; Silvertown, 1982). Such population structures (inverse- J shape) are common in natural forests where external disturbances are limited. On the other hand, bell-shaped or variable size-class distribution has

been attributed to disturbed forest where regeneration is hampered (Poorter *et al.*, 1996). Population structure (size-class distribution) gives good indication of the impact of disturbance and the forest successional trends. Such information is critical in increasing our understanding of the conservation needs of tropical forest ecosystems (Hubbell and Foster, 1986; Condit, 1995).

Several forests and forest tree species in Ethiopia have shown variation in their population structure and regeneration pattern (Demel Teketay, 1997; Getachew Tesfaye *et al.*, 2002; Feyera Senbeta, 2006). Most species accumulated persistent seedlings (seedling bank strategy) in the forest understorey and still many others follow seed bank regenerative pathway (Demel Teketay, 1997; Getachew Tesfaye *et al.*, 2002, 2004). Tree population density also varied among sites and species. Moreover, species showed variation in their population structure forming strong peaks at certain size classes and with little or no individuals in other size classes (Tamrat Bekele, 1994; Demel Teketay, 1997). The variations in relative abundance and population structure of tree species were the result of past and present disturbances as well as management history of the forest. Human caused disturbance such as intensive removal of trees for timber, construction, and forest grazing have placed significant impact on the structure and regeneration of the species. Understanding of the mechanisms which determine the regeneration of tree species in the forest are useful also in predicting changes in species composition and successional patterns of the forest over time (Condit *et al.*, 1989; Henriques and Sousa, 1989; Geldenhuys, 1993; Poorter *et al.*, 1996).

2.4. Phenology of Tropical Forest Tree Species

Phenology is the study of the periodicity or timing of recurring biological events. In the case of plants, phenological events involve germination, flowering, fruiting and leaf flushing. The schedule of these events has important effects on plant survival, reproductive success and thus regeneration.

Plant phenologies are the results of interactions of biotic and abiotic factors. Over evolutionary time and through natural selection, these biotic and abiotic factors have entrained rhythmicity in plant life that resulted in an appropriate timing of flowering, fruiting and leaf flushing and efficient growth and reproduction (van Schaik *et al.*, 1993). Knowledge of phenological patterns is basic to the understanding of biological processes of tropical trees, of the interactions with other organisms and of the functioning of the ecosystems. For example, leaf fall in dry forests results in a modification of forest microclimates and the timing of new leaves, flowers, and fruits and also controls the activities of many herbivores, pollinators and frugivores (Frankie *et al.*, 1974; van Schaik *et al.*, 1993).

Tropical dry forest trees exhibit substantial seasonality in flowering, fruiting, and leaf-flushing events (Chapman *et al.*, 1991; van Schaik *et al.*, 1993; Sun *et al.*, 1996). They often show temporal variations in phenological patterns that are associated with seasonality in climate or abundance or pressure of biotic factors (Frankie *et al.*, 1974; Sakai, 2001). According to Lobo *et al.* (2003), phenological events in plants are affected by proximate or ultimate causes. Accordingly, proximate causes principally include short-term environmental events that may trigger phenological patterns, while ultimate causes include evolutionary forces that are

responsible for these patterns. Climatic variables such as seasonal variations in rainfall (Opler *et al.*, 1976), temperature (Ashton *et al.*, 1988), and irradiance (van Schaik, 1986; van Schaik *et al.*, 1993) have been identified as proximate causes triggering phenological events in tropical plants.

On the other hand, biotic factors, for example, differential preference of pollinators (Augspurger, 1981; Robertson, 1985; Appanah, 1985; Sakai *et al.*, 1999; Lobo *et al.*, 2003), animal seed dispersal agents (Snow, 1965), or avoidance of seed predation and seedling herbivory (Marquis, 1988; Aide 1993; van Schaik *et al.*, 1993) have been recognized as ultimate causes that could trigger phenological patterns in tropical plants.

In forests with a marked dry season, flowering and leaf flushing may be more sensitive to seasonal rainfall, changes in water availability and soil moisture (Borchert, 1984; Lieberman and Lieberman, 1984; Van Schaik *et al.*, 1993). High water availability may also enhance fleshy fruit production and seed germination (van Schaik *et al.*, 1993; Justiniano and Fredericksen, 2000). In strongly seasonal dry forests leaf flushing peaks during late dry season and ends in the rainy season (Justiniano and Fredericksen, 2000; McLaren and McDonald, 2005; Anderson *et al.*, 2005). Apparently, the majority of tropical plants flower regularly during peaks in temperature and their fruits ripen towards the end of the dry season or yet in the rainy season, and this result in a better survival of the seedlings (Frankie *et al.*, 1974; van Schaik *et al.*, 1993).

In the study of tree phenology in tropical dry forests, which are subjected to a more or less regular oscillation of rainfall and temperature, must also consider these factors during periods of the preceding year (Chapman *et al.*, 1991). In addition, it is known that different species can respond to the same conditions in different ways (Anderson *et al.*, 2005). Since climatic variables are highly correlated, influence of these variables on plant phenology requires not only finding the appropriate relationships but also the careful examination of the interplay between phenology and the climatic variables (Tyler, 2001; Anderson *et al.*, 2005).

The dry forests in the Ethiopian mountains represent one of the largest remaining tracts of afro-montane forests (Friis, 1992) and understanding the reproductive phenology of the species is critical in conservation of biodiversity and maintenance of these ecosystems. As pronounced seasonality affects dynamic processes in forests, and thus affects plant reproductive success and regeneration, the climatic variables are very crucial. Although scientific knowledge on the phenology of tropical forest tree species has been accumulating globally during the last decade, there is no information on phenology of woody species of the afro-montane forests in Ethiopia. In addition, ecological factors that influence the phenology of perennial species in the afro-montane forests in Ethiopia, or elsewhere in eastern Africa, have not been investigated. Such information is crucial in the understanding of the biological processes of tropical trees, sustainable management and conservation of the last remaining forests in Ethiopia, or in neighboring eastern African countries having similar forest ecosystems.

3. OBJECTIVES OF THE STUDY

3.1. General Objective

The general objective of the study was to investigate the regeneration dynamics and phenology of seven indigenous tree species in the Munessa-Shashemene Forest and major ecological factors affecting them.

3.2. Specific Objectives

The specific objectives were to:-

- 1). Investigate intra- and inter-specific variation in terms of survival, growth, biomass allocation and morphology of seedlings with change in light environments in the Munessa-Shashemene Forest;
- 2). Examine the relationships between seedling growth variables and predictors of relative growth rate (RGR) with change in light environment;
- 3). Investigate seedling survival and herbivory rates in the forest understorey and their influence on seedling population dynamics of the species;
- 4). Assess the distribution of seedlings, sapling and tree population densities along altitudinal gradient;
- 5). Examine population structure of the species using size class distributions;
- 6). Examine the phenology of leaf, flower and fruit of trees;
- 7). Investigate environmental factors that may trigger those rhythmical phenomena and;
- 8). Examine the overall regeneration status of each species and major ecological factors affecting their regeneration.

4. MATERIALS AND METHODS

4.1. Study Site

The study was conducted in Munessa-Shashemene Forest, southern Ethiopia, located at 7°13' N and 38°37' E (Fig. 1). It is a dry afro-montane forest and extends over an altitudinal range from 2100 to 2700 m asl. The total area of the forest is 21,000 hectares comprising plantations of exotic tree species of about 6,000 ha which is 28 % of the total area. The Munessa-Shashemene Forest is one of the major timber supplier forests of the country and this ironically puts the natural forest under severe pressure from illegal logging. In addition, transportation facilities between the forest and the timber market in the capital Addis Ababa are good because of high quality roads, which favour smuggling of forest products and contribute to the degradation of the natural forest to a secondary forest. Moreover, grazing in the forest by livestock and encroachments due to agriculture has become increasingly important in recent years. The mean annual temperature is 15 °C with daily fluctuations between 8 °C to 24 °C (EMA). The mean annual rainfall varies between 900 and 1500 mm in a bimodal pattern where the small unreliable rainy season is from March to May and the long rainy season from July to September. The long dry season is from October to February and small dry season from May to June. Relative humidity of the air ranges from 35- 70 % in the dry season to well above 90 % during the rainy season. Climate information (temperature and rainfall) recorded for five years period at Kuke site, i.e. at 2300 m altitude in the studied forest is presented in Figure 2. The soils of the study area are classified Mollic Nitisols/ Typic Palehumult according to FAO (1998) and Soil Survey Staff (1999), respectively. The soils developed from volcanic parent materials, principally, volcanic lavas, ashes and pumices from quaternary volcanic activities in the Rift Valley. According to Fritzsche *et al.*, (2006) kaolinite is the dominant in the Munessa-

Shashemene Forest with well-drained profiles, which exhibited a systematic transition of soil characteristics with climate and relief. The soils are fine textured with clay mineral and loams, and the color is brownish (Munsell Hue YR) and become reddish with decreasing elevation. The soil structures are relatively less well-developed at the upper portion of the forest. The organic carbon stock increases with elevation and similar pattern for nitrogen contents, and the C/N ratios are 11.0 to 13.6 within the Munessa-Shashemene forest.

Mixed broad-leaved deciduous and evergreen trees characterize the forest vegetation at the Munessa-Shashemene. The dominant tree species are *Podocarpus falcatus*, *Prunus africana*, *Croton macrostachyus*, *Maytenus addat* and *Nuxia congesta*. At the lower elevation of the forest, the most characteristic species of the tree layer includes *Cassipourea malasona*, *Olea capense*, *Maytenus addat*, *Millettia ferruginea* and *Allophylus abyssinicus*; the shrub layer includes *Rytigynia neglecta*, *Bersama abyssinica*, *Calpurnea aurea* and *Canthium oligocarpum*. At the middle elevation, characteristic species of the tree layer includes *Cassipourea malasona*, *Allophylus abyssinicus* and *Maytenus addat*; the shrub layer consists of *Bersama abyssinica*, *Teclea nobilis*, *Galiniera saxifraga* and *Rytigynia neglecta*. At the upper elevation of the forest, characteristic species of the tree layer includes *Maesa lanceolata*, *Hagenia abyssinica*, *Ilex mitis*, *Olinia rochetiana* and *Dombeya torrida*; the shrub layer composed of *Rapanea simensis*, *Galiniera saxifrage*, *Brucea antidysenterica* and *Hypericum revolutem* species.

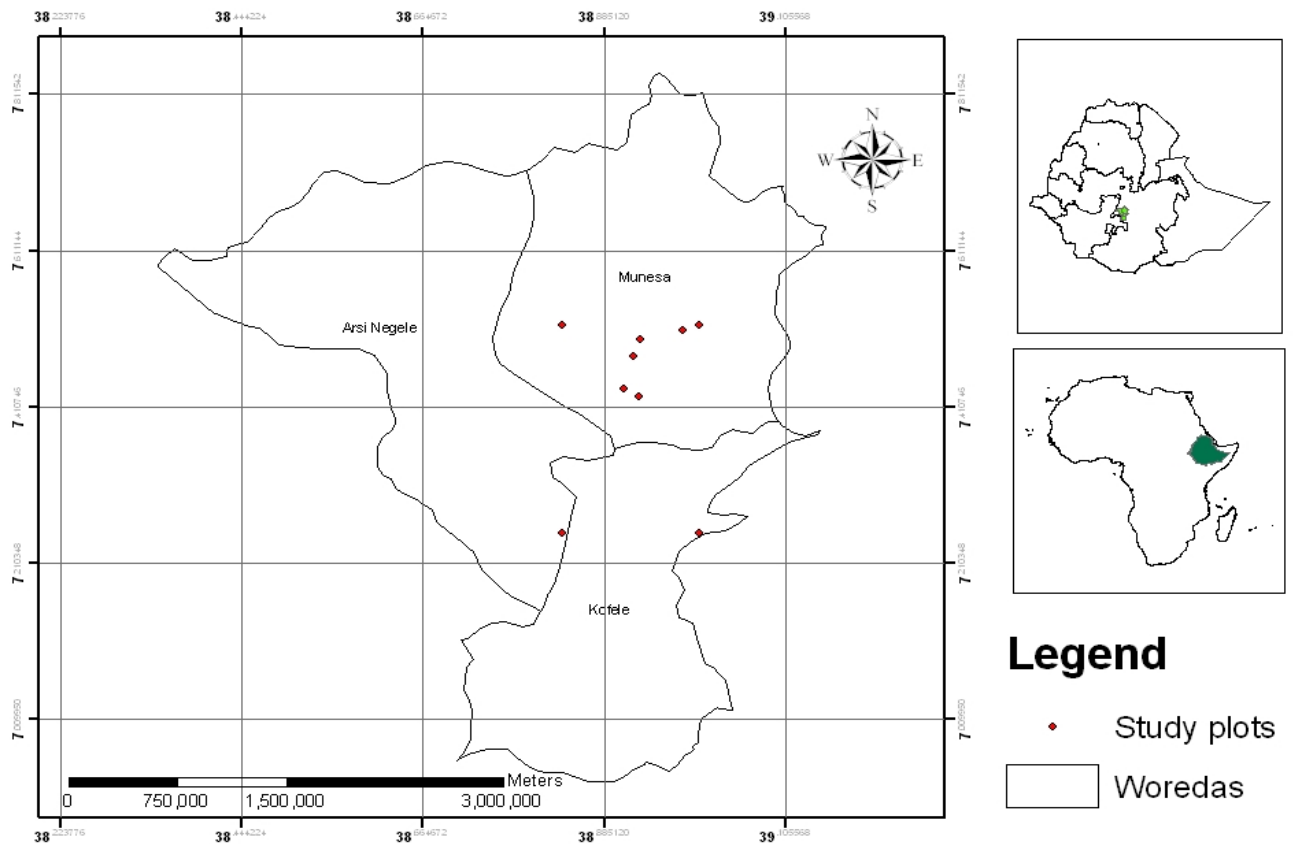


Figure 1: Map of Ethiopia showing the study site, Munessa-Shashemene Forest

4.2. Species Considered for the Study

Seven indigenous tree species, namely, *Celtis africana*, *Croton macrostachyus*, *Podocarpus falcatus*, *Polyscias fulva*, *Pouteria adolfi-friederici* (formerly *Aningeria*), *Prunus africana* and *Syzygium guineense* (see also Table 1; hereafter referred by their generic names) were selected for the study, because they are of significant ecological and economic importance in the Munessa-Shashemene Forest. The seven species are economically important as they made a

significant proportion of the total timber harvest in the country in the past (Chaffey, 1979). Ecologically they all accounted between 85 – 91 % dominance at the study site (Getachew Tesfaye, data not shown). In addition, they constituted 95 % of the total tree basal area and 77% of the Importance Value Index (IVI) of trees of the Munessa-Shashemene Forest (Getachew Tesfaye, data not shown), which underlines the significance of the present study for the entire forest management. The species comprised shade-tolerant and pioneers (light-demanding) and they were grouped based on the requirements for seeds to germinate, establishment and growth of seedlings. For classification, available literature information and observation in the field were used. *Croton*, *Celtis* and *Polyscias* are typical pioneer species, whose seeds germinate and establish soon after disturbance (Demel Teketay, 1997; Getachew Tesfaye *et al.*, 2004). They are encountered in larger tree fall gaps, along roadsides, at the edges of forests and on logged sites. *Prunus*, *Pouteria*, *Podocarpus* and *Syzygium* are shade tolerant species whose seeds germinate and establish in shaded understorey and persist for longer time as seedling bank (Demel Teketay, 1997; Getachew Tesfaye *et al.*, 2002). These four species, but also the pioneer *Croton* constituted major proportions of the canopy layer while *Celtis* and *Polyscias* are typical sub-canopy species.

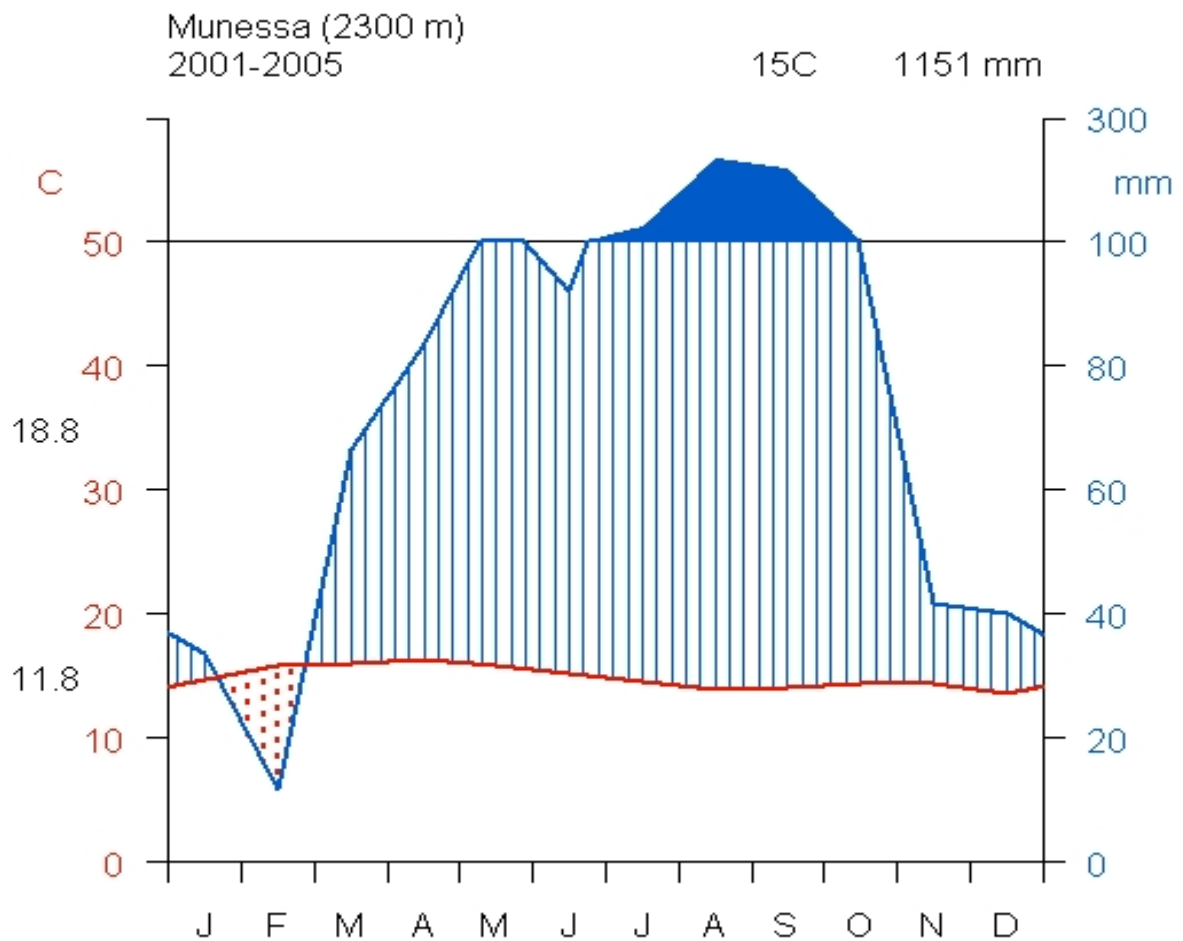


Figure 2: Climate diagram of the study site for the period from May 2001 to May 2006.

There are only limited information on the biology of the seven tree species considered in the present study in particular on their reproduction (seeds or clonally), seed storage behavior, germination and dispersal agents. The available information is summarized below.

1. Most of the species (e.g. *Pouteria*, *Croton*, *Podocarpus* and *Polyscias*) regenerate from seeds and the contributions from clonal growth, if exist, is very rare (Getachew Tesfaye, unpublished data). On the other hand, species of *Prunus* and *Celtis* reproduce

- either clonally or from seeds. In these two species reproduction from their seeds accounts still a significant proportions in the afro-montane forests in Ethiopia: However clonal reproduction may become quite high often on highly disturbed sites and upper altitudes within a forest (Getachew Tesfaye, unpublished data).
2. Seed germination behaviors of the seven tree species also vary considerably. The seeds of *Pouteria* and *Syzygium* germinate shortly after dispersal or within one-year period while *Prunus* may germinate in two years period. These species, therefore, cannot be stored for a longer period of time (Getachew Tesfaye, data not shown). These species generally lacks seed dormancy. Seeds of *Podocarpus* on the other hand can be stored for a relatively longer period. The seeds of *Podocarpus* can germinate after being stored for several years, but with a substantial reduction of seed viability over time (Demel Teketay and Granstorm, 1997). According to Girma Balcha and Blyth (2002), the seed storage behavior of *Podocarpus* fits into an intermediate category (i.e. between those of orthodox and recalcitrant seeds). On the other hand, seeds of *Croton* can be stored over a longer period without much reduction on the viability (Demel Teketay and Granstorm, 1997).
 3. Study on the seed dispersal agents at the study site had shown that at least more than 30 species of dispersal animals were recorded from December to July 2005 & 2006 (Getachew Tesfaye, data not shown). The animals were seen picking and feeding on the fruits/seeds of the seven-tree species considered in the present study. These include both birds and mammalian species. Some of the major dispersal animals recorded at the study site, among others, include:- Abyssinian Black-and- White Colobus, Common Babbon, and Vervet Monkey (Mammals); Olive Thrush, White-checked

Turaco, Red-winged Starling, White thighed Hornbill and Yellow-fronted Parrot (Birds) (Geachew Tesfaye, data not shown).

4.3. Methods

4.3.1. Growth and Survival Experiment of Planted Seedlings Under different Light Climates in Munessa-Shashemene Forest

Three experimental plots each of 10 m X 10 m size were selected at different light climates, in an shaded understorey situation (low-light, LL), in a canopy gap (medium-light, ML), and at the edge of forest (high-light, HL). To warrant undisturbed growth of seedlings the plots were fenced. Photosynthetically Active Radiation (PAR) measured at seedling height at the three plots, namely, LL, ML and HL were on average $52 \mu\text{mol m}^{-2} \text{s}^{-1}$ (3 %), $293 \mu\text{mol m}^{-2} \text{s}^{-1}$ (14 %) and $1724 \mu\text{mol m}^{-2} \text{s}^{-1}$ (75 %), respectively. The three plots were located on similar altitude (i.e. at 2300 m asl), on flat lands and similar soils (organic carbon = 8- 10 %; C/N ratios = 10-14; N = 0.8- 1 g kg⁻¹). Similarly, the vegetation cover and canopy height (ranged from 28 to 35 m) at the three sites were also comparable. Major canopy trees surrounding the three plots were *Podocarpus*, *Celtis*, *Croton*, *Prunus* and *Syzygium*. In each plot, 210 young seedlings (35 seedlings except *Polyscias* of equal sized per species) with at least two fully expanded leaves were collected from the forest, randomly assigned to the different plots and carefully transplanted. At transplanting, seedlings were randomly assigned to the different plots of light conditions. Each experimental plot was divided into 6 blocks, each containing individuals of all species. Distance between the blocks was 1 meter and the seedlings were planted in a row at every 30 cm. Translanting was finished by June 30th 2004 when the growth experiment started. The seedlings were checked for two months and within this period, new one replaced dead seedlings. On October 26th 2004, a first harvest 15- 20 seedlings per species were

harvested in all three plots. After harvesting, the plants were divided into leaves, stem plus petioles, and roots. Plant parts were then oven dried at least for 48 hr at 60 °C and weighed. At the initial harvest, stem length, root length, total leaf area, and leaf, stem and root masses were determined following Kitajima (1994) and Poorter (1999). The final harvest was conducted on 12th March 2005. Seedling survivorship monitored every month, and continued for 12 months period. Leaf area was measured using (Leaf) Area Meter- AM 100. From the primary data, the following variables were derived: total plant biomass, root mass ratio, stem mass ratio, leaf mass ratio, specific leaf area, leaf area ratio and root/shoot ratio.

4.3.2. Survival (or Mortality) of and Herbivore Damage on Naturally Regenerated Understorey Seedlings in Munessa-Shashemene Forest

Eight permanent plots of 20 m X 20 m (400 m²) were laid down at ecologically different places within in the forest in June 2004 to monitor mortality rates of undertorey seedlings and investigate its causes. Each plot was divided into grids to facilitate mapping of the seedlings and the location of healthy seedlings found in the quadrat was mapped except *Polyscias*. About 1200 seedlings (200 seedlings per species) were found and tagged, and their height measured. The plots were re-visited after the long rainy season October 2004 and 2005 and long dry dry season June 2004 and 2005 and the status of the seedlings was examined. The seedlings were found in various conditions. Some of them had just died but normally rooted, others were uprooted from their original spot but found within the vicinity of the established plots and several others were removed and could not be found any more. Accordingly, the seedlings were categorized as healthy, defoliated, uprooted, dead and standing, or missing. As far as possible, the casue of seedling's death was noted. Damage of seedlings by herbivores

was investigated in the same quadrats with the tagged seedlings. Massive or partial defoliation of seedlings and removal of meristematic tips was considered as damage caused by herbivore.

4.3.3. Seedling, Tree and Sapling Densities, and Their Distributions Along the Altitudinal Transect

Seedling, tree and sapling were investigated from April to May 2006. For the purpose of this study, the terms “seedling”, “sapling” and “tree” were re-defined by plant height i.e. < 150 cm, 150 - 300 cm, and > 300 cm, respectively, following (Demel Teketay, 1997; Getachew Tesfaye *et al.*, 2002). To examine the altitudinal gradients of tree and sapling densities six line transects were established in north to south direction and with 300 m distance between them. Altitude considered as the main environmental factor here because of the considerable variations in temperature, rainfall and radiation with change in every 100 m of altitude (Daniel, 1988) which in turn affects plant species distribution as well. At every 100 m drop in altitude, quadrats of 20 m x 20 m (400 m²) were selected in each transect. About 42 quadrats (equivalent to a total area of 1.68 ha) were investigated for the tree and sapling density and distribution. To determine the density and altitudinal distribution of seedlings the size of quadrats was reduced to 10 m x 5 m (50 m²). In each quadrat the number and height of all seedlings, trees and saplings of the seven species were recorded. For seedlings additional information on light condition and disturbance were noted. The light condition in each quadrat was determined visually as gap or shade. Estimating the percentage of the quadrat occupied. When more than 75% of the quadrat was covered by the tree crowns, the light condition was termed as “shade”. The degree of human disturbance in the plots was recorded by using a 1- 4 scale as: 1 = no cut stems; 2 = one cut stem; 3 = 2-3 cut stems; 4 = more than 3 cut stems.

Table 1: List of study species with information of their habit, size of propagule, habitat or ecology and geographical distribution inside Africa

Species	Growth Habit and foliage	Size of propagule	Habitat/Ecology	Geographic distribution within Africa
<i>Croton macrostachyus</i> Del. (Euphorbiaceae)	Tree, up to 30 m deciduous	Seeds, 7x4 mm	Montane and evergreen bush land, edges of forest and thickets, savanna, cultivated fields, waste ground, along rivers, 700-3400 m	Ethiopia, west to Guinea, south to Angola, Zambia, Malawi and Mozambique
<i>Podocarpus falcatus</i> (Thunb.) Mirb. (Podocarpaceae)	Tree, up to 45 m evergreen	Fruit, 13-15 mm	Afromontane forest, pure <i>Podocarpus</i> or <i>Juniperus-Podocarpus</i> forest, in relic forest patches farmland; 1550 – 2800 m	Ethiopia, Zaire, Rwanda, Burundi, Uganda, Kenya, Tanzania, Malawi, Mozambique and South Africa
<i>Polyscias fulva</i> (Hiern)Harm (Araliaceae)	Tree, up to 30 m semi-deciduous	Fruit, 4.5x 4 mm	Upland and lowland rainforest, mainly secondary up to 2450 m	Ethiopia, west Africa to Guinea, south to Mozambique and Angola
<i>Pouteria adolfi-friederici</i> (Engl.) Baehni (Sapotaceae) formerly <i>Aningeria</i>	Tree, up to 50 m evergreen	Fruit, 4 x 1.5 mm	Afromontane rainforest upper canopy species; 1350 - 1450 m	Ethiopia through Sudan, Uganda and Kenya, west to D.R. Congo, south to Zambia, Malawi and Zimbabwe
<i>Prunus africana</i> (Hook . f.) Kalkm. (Rosaceae)	Tree, up to 40 m evergreen	Drupe, 1x 0.7 cm	Montane and riverine forest; 1700 - 2500 m	Ethiopia, Cot d' Ivoire, Cameroon, Congo, Uganda, Kenya, Tanzania, Angola, Zambia, Malawi, South Africa, Zimbabwe, Madagascar and Comoros
<i>Syzygium guineense subsp. afromontanum</i> F. White (Myrtaceae)	Tree, up to 35 m evergreen	Fruit, 17x 14 mm	Upland rainforest, forest edge or secondary growth; 1400- 2600 m	Ethiopia, south Sudan, Zaire, Rwanda, south to Angola, Zambia, Malawi and Zimbabwe
<i>Celtis africana</i> Burm. f. (Ulmaceae)	Tree, up to 35 m deciduous	Fruit, 5 x 8 mm	Dry and moist evergreen forest, riverine forest; some times persisting as a relic in disturbed places; 1300- 2300 (-2500 masl in present study)	East to Ethiopia, west to Ghana, south to Angola and South Africa.

4.3.4. Population Structure and Regeneration of the Study Species

‘Population structure’ refers to the size-class distribution of individuals in height classes to determine the regeneration profile of the species by assessing its status of regeneration. Diameter at breast height (DBH) is the most commonly used size measure in the analysis of plant population structure. However, several studies have also used height classes to include seedlings and saplings in such studies (Geldenhuys, 1993; Demel Teketay, 1997; Getachew Tesfaye *et al.*, 2002). The inclusion of seedlings and saplings in the plant population structure can provide additional information on species performances at the early stage of regeneration. Nine line-transects were established as in section 4.3.3 to examine the population structure of each species. At every 100 m altitudinal drop plot of 20 m x 20 m (400 m²) was selected. Accordingly, 72 quadrats (2.88 ha) were surveyed. In each quadrat, the frequency, height and diameter of all individuals of the seven species encountered were recorded. The following height classes were used 1: 0-2 m, 2: 2-4 m, 3: 4-6 m, 4: 6-8 m, 5: 8-10 m, ... 14: 28-30 m and > 30 m; for diameter the classes were 1: 0-10 cm, 2: 10-20 cm, 3: 20-30 cm, ..., 20: 190-200 cm, and > 200 cm).

4.3.5. Phenological Observations

About 210 reproducing mature trees (30 individuals per species) with crowns visible from the ground were selected at three different sites within the forest and marked. Their diameter at breast height (DBH) measured and their position was recorded using GPS (Garmin-etrex). Distances between the three sites ranged from 6-15 km and at least 10 individuals of a species were examined in each site. Phenological events were recorded every month (except during peak flowering when observations were carried out in two weeks) from June 2004 to May

2006. For the inspection binoculars were used. Flowers and fruits dropped from the trees were additionally used as indicators. Flowering (flower buds and open flowers) and fruiting (unripe and ripe fruits) was recorded using four different classes of intensity: 0 (0 %), 1 (1-25 %), 2 (26-50 %), 3 (51-75 %), and 4 (> 75 %), with percentage referring to the proportions of each phenophase in the crown. For leaf phenology, only the two deciduous species (*Celtis* and *Croton*) were investigated and recorded as leaf flush, full foliage/vegetated, senescent (dying) or leafless with similar classes as above. Leafless was defined as when > 75 % of the tree crown had lost its leaves and leaf flush the interval between when leaf buds began opening to when new leaves were covering more than 75 % of the tree crown. Climate parameters, temperature, rainfall, relative humidity and solar (light) radiation were recorded through out the study period with an automatic meteorological station established in an open site close to the research station at Kuke (for details see Fritzsche *et al.*, 2006).

4. Data Analyses

Mean relative growth rate (RGR) and net assimilation rate (NAR) were calculated as: $RGR = (\ln W_2 - \ln W_1) / (t_2 - t_1)$ and, $NAR = [(W_2 - W_1) / (t_2 - t_1)] \times [(\ln A_2 - \ln A_1) / (A_2 - A_1)]$, where W = dry mass, A = leaf area and t = time (time period of the experiment), with index X_1 = initial values, and index X_2 = final values (Hunt, 1982). RGR was calculated for each plant individual using an estimate of initial dry mass. Prior to statistical analysis, data were tested for homogeneity variances (Zar, 1996). Data were log transformed wherever necessary. In all cases where above assumptions of parametric analysis were met or achieved by means of data transformation, comparisons of means were made by the Student's t-test or analysis of variance. Otherwise, data were expressed as medians and were analyzed by non-parametric

techniques, through Kruskal-Wallis test at the 5 % probability level. Correlation analysis was used to investigate relationships between light environment and phenotypic plasticity of the species, and also among the different plant variables across light regimes or climates. Plant responses were evaluated using two-way ANCOVA, with light regime and species as independent variables. The interaction between species and biomass was also included in the analysis as an ontogenetic change. Regression analysis was conducted to determine the predictors of plant relative growth rates.

The percentage data of seedling mortality and herbivore damage were subjected to two-way ANOVA for testing significant differences between species, seasons and years. Seedling density, tree and sapling density and their frequencies were analyzed following Muller-Dombois and Ellenberg (1974). The data from the seedling surveys were subjected to Canonical Correspondence Analysis using the program CANOCO (Ter Braak, 1995) to get an overview of the relationship between seedling abundance along gradients of altitude, light condition and intensity of disturbance. Spearman rank correlation test was employed for significance of the proportion of individuals per size-class distributions for each species.

Phenological event analyses were based on the following four parameters: onset (first date of an event/phenophase recorded), mean date (time of the year with the highest overlap of an event/phenophase among the individuals of each species), peak (the month(s) with the highest percentage of the event), and duration (the period between the first and the last month the event/phenophase was seen). Similarly, analysis of leaf fall and leaf flush was based on peak, mean date and duration of the event.

Occurrence of seasonality was tested through conducting two analyses to evaluate the patterns of flowering and fruiting of the species. Circular statistic was used to calculate the mean dates of flowering, fruiting, leafless state and leaf flush phenophases (Zar, 1996). The proportion of individuals (of a species) in each phenophase across the months of the year was treated as a circular frequency distribution with data grouped at 30° intervals ($30^{\circ} = 1$ month) with January 1st as the starting point and December 1st ($330^{\circ} = 12$ month) as the month closing the circle. The two circular statistics computed were:- (1) the mean angle (a) which is translated into days representing the mean date of the phenophase and (2) r , which is a measure of the intensity of concentration around the mean. The Kolmogorov-Smirnov Z-test, determines the significance of seasonality in the distribution of the phenophases. The hypotheses tested were: H_0 means a phenophase is distributed uniformly across months around the year or circle and consequently no seasonality present; H_A means a phenophase is not distributed uniformly across the months around the year and consequently there is seasonality. If H_A is accepted, r can be considered as a measure of the `degree` of seasonality.

Since phenological data are time-dependent, time series analyses was employed to evaluate autocorrelation within phenophases and cross-correlations of climate factors and phenophases and correlation between different phenophases. Pearson's correlation was used for that analysis. Cross correlation coefficients were calculated between each phenophase and the climate factors: monthly total rainfall and mean monthly temperature allowing time lags up to 12 months. In this way the lag time giving the greatest and significant correlation coefficient indicated the approximate interval (months) between climate effect and plant response.

Regression analysis was also conducted to determine whether there was a strong relationship between the climate variables and leaf phenology (leaflessness and leaf flush).

Friedman test (ANOVA) was employed to determine the differences in the number of individuals flowering, fruiting, leaf flush and leafless between years (Zar, 1996). When the peak and duration of flowering and fruiting differed between the years, the averages and ranges were used, respectively. Shannon-Wiener diversity index was used to estimate synchrony in flowering among individuals of a species (Magurran, 1988). Similarity in flowering and fruiting pattern among the species was estimated using Similarity Ratio Index using SYN-TAX 2000 for Windows. All statistical tests were carried out using MINITAB 14.0 and STATISTICA 6.0. for Windows. Phenological patterns were classified as sub-annual, annual, continuo or supra-annual following Newstrom *et al.*, (1994).

Table 2: Plant variables derived for growth and morphological analysis in this thesis (abbreviations and units are shown).

Variable	Abbreviation	Units
Relative growth rate- biomass production per unit plant biomass and day	RGR	$\text{g g}^{-1} \text{d}^{-1}$
Net assimilation rate- biomass production per unit leaf area and day	NAR	$\text{g m}^{-2} \text{d}^{-1}$
Leaf area ratio -leaf area/total plant biomass	LAR	$\text{m}^2 \text{kg}^{-1}$
Specific leaf area- leaf area/leaf biomass	SLA	$\text{m}^2 \text{kg}^{-1}$
Leaf mass ratio- leaf biomass/total plant biomass	LMR	g g^{-1}
Stem mass ratio- stem + petiole biomass/total plant biomass	SMR	g g^{-1}
Root mass ratio- root biomass/total plant biomass	RMR	g g^{-1}
Total leaf area	TLA	mm^2

5. RESULTS

5.1. Survival and Growth of Planted Seedlings Along a Light Gradient in Munessa-Shashemene Forest

5.1.1. Seedling Survival (or Mortality)

The survival of transplanted seedlings of all species under different light regime showed significant variation (29 - 96 %) during the period of the experiment (Fig. 3, Table 3). Most of the species had highest survival rates in low light regime except *Croton*, which had highest survival rate in high light regime (Fig. 3). For most species, seedling survival decreased with increasing irradiance (Fig. 3). *Syzygium* had the highest survival rate (93%) which *Croton* had the lowest survival rate (70 %) under low light regime. Under medium light regime, *Podocarpus* had the highest survival rate (89 %) which *Pouteria* had the lowest rate (30 %). Under high light regime, *Croton* had the highest survival rate (96 %) which *Syzygium* had the lowest (33 %). The change in the rank order between *Syzygium* and *Croton* in low- and high-light can be related to their natural growth habitats.

Over all, 31 % of the total transplanted seedlings did not survive. Considerable losses occurred in the high light condition and some of the species suffered up to 67 % mortality by the end of the study period (Fig. 3). The cause of mortality in high light regime was not generally apparent; but in several cases desiccated dead standing seedlings were observed. Few had their leaves defoliated by insects and some had their stem cut at the base.

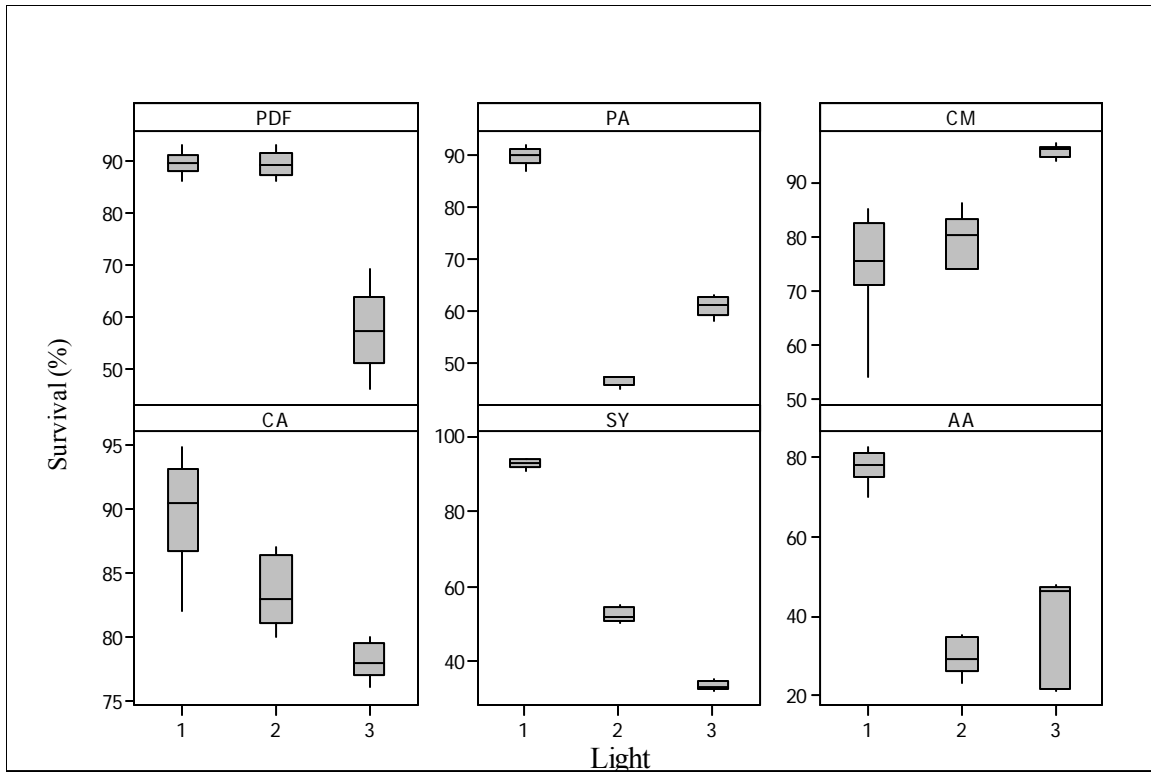


Figure 3: Planted seedlings survival under different light environments (light levels: 1 = LL; 2 = ML; 3 = HL; growth period 12 months) of the six tree species at Munessa-Shashemene Forest (species, PDF= *Podocarpus falcatus*, PA= *Prunus africana*, CM= *Croton macrostachyus*, CA= *Celtis africana*, SY= *Syzygium guineense*, and AA= *Pouteria adolfi-friederici*).

5.1.2. Seedling Growth

5.1.2.1. Relative importance of light, species and biomass

There were large variations in plant morphological and physiological traits among species and light levels (Table 3; Figures 4a-h). The explained variation was very high (mean 0.62, range 0.32- 0.94) and most factors were highly significant (Table 3). The F-ratio allows one to compare the relative importance of light, species and biomass for the plant morphological and physiological traits examined. With the exception of RMR, all seedling attributes measured responded significantly to variation in light conditions (Table 3). The most responsive

variables to light were total biomass (absolute growth), height, total leaf area (TLA), survival, and root length (RL) indicating the strong variations or plastic response in these plant morphological variables. Species also varied significantly for all plant morphological and physiological variables measured (Table 3). RGR and NAR were more influenced by plant biomass (ontogenetic drift) as indicated by the significant biomass effect (Table 3). Over all, light was the most important determinant of variation in total biomass, seedling height, total leaf area and root length, whereas LAR, SLA, LMR, RMR and SMR were found to be more of species-specific, i.e. inherent differences among species accounted for more variation than did light responses (Table 3).

Table 3: Results of Two-Way ANCOVA with light (n = 3) and species (n = 6) as fixed effects and biomass as a co-variable. F-values, significance (P) and the explained variation (R²) are shown (NS: P > 0.05; * P < 0.05; ** P < 0.01; *** P < 0.001); (degree of freedom: light (df = 2), species (df = 5), light X species (df = 10), biomass (df = 3)).

Variables	Light		Species		Light X species		Biomass		Biomass X species		R ²
	F	P	F	P	F	P	F	P	F	P	
Total biomass	14.19	***	7.82	***	7.36	***	-	-	-	-	0.54
Height	29.91	***	9.52	***	7.38	***	1.04	NS	2.33	*	0.61
TLA	31.04	***	11.85	***	11.89	***	0.29	NS	0.41	NS	0.67
Survival	186.63	***	98.23	***	40.58	***	0.00	NS	14.25	***	0.94
RGR	25.51	***	9.26	***	3.53	***	49.41	***	16.20	***	0.55
NAR	10.60	***	3.42	**	1.74	NS	22.74	***	4.98	***	0.32
LAR	3.62	*	20.52	***	4.76	***	0.35	NS	3.29	**	0.65
SLA	18.91	***	35.68	***	1.70	NS	1.26	NS	3.66	**	0.73
LMR	7.56	**	41.11	***	4.22	***	1.05	NS	1.64	NS	0.72
RMR	2.62	NS	16.32	***	4.65	***	8.41	**	0.11	NS	0.57
SMR	4.5	**	10.2	***	2.49	**	3.44	NS	1.56	NS	0.51
RL	69.89	***	14.21	***	12.63	***	2.30	NS	4.57	***	0.74

5.1.2.2. Light effects and intra-specific variation in growth

The effects of light on the different plant variables were examined for each species and the results are shown in Table 4. For all species, light had significant effect on total biomass growth (Table 4). Total plant biomass increased with increasing light levels and species attained highest biomass in high light regime (Fig. 4). For most species, seedlings grown in high light regime were several folds greater than plants grown in medium light regime and low light regime. *Croton*, for example, had a total plant biomass nearly 200 and 800 fold greater in high light than in medium and low light regimes (Fig. 4). Similarly, *Celtis* had a total plant biomass 16 and 33 fold greater in high light than plants in medium and low light conditions. *Podocarpus* had a total plant biomass 2 and 5 fold greater in high light than plants in medium and low light. Total plant biomass was low in low light conditions for all species (Fig. 4).

For most species, light had significant positive effect on height and total leaf area (Table 4). Height increased with increasing irradiance except in *Pouteria*, while TLA increased with increasing light regime for all species. Most species, therefore, attained the highest seedling height and total leaf area in high light regime (Fig. 4). *Croton* for example showed 9 to 12 fold increase in seedling height under high light regime than in medium and low light regimes. Similarly, the total leaf area in high light was 179 and 206 fold greater than in medium and low light conditions, respectively. Unlike other species, *Pouteria* attained the highest seedling height growth in medium light. Plant height and total leaf area were generally low in low light conditions for all species (Fig. 4).

RGR had shown significant variation between light conditions for five of the six studied species (Table 4). For most species, RGR increased with increased light level/irradiance (Fig. 4). For example, *Celtis*, *Croton*, *Pouteria* and *Prunus*, had their highest RGR in high light (Fig. 4). However, species of *Podocarpus* and *Syzygium* had highest RGR in medium light than in high light (Fig. 4). On the other hand, RGR remained relatively low in low light for all species (Fig. 4).

NAR significantly varied between light conditions for *Prunus*, *Celtis*, and *Syzygium*; and non-significant for *Podocarpus*, *Croton* and *Pouteria* (Table 4). NAR increased with increased light level/irradiance in *Celtis*, *Croton*, *Prunus* and *Pouteria* and therefore the highest NAR were recorded in high light regime (Fig. 4). *Podocarpus* and *Syzygium* had their highest NAR in medium light (Fig. 4). In general, NAR followed similar pattern with RGR between light conditions for each species and also remained relatively low in low light (Fig. 4).

For most species, SLA varied significantly between light conditions (Table 4). SLA decreased with increased light level/irradiance in most species and therefore the lowest values were recorded in high light (Fig. 4). However, in *Podocarpus* SLA was lower in medium light than in high light (Fig. 4).

Seedling root length varied significantly between light conditions for most species (Table 4). Root length increased with increased light level/irradiance and therefore the highest values were recorded in high light except in *Pouteria* (Fig. 4). *Pouteria* had highest root length in medium light. Over all, seedling root length under the different light conditions followed

similar growth pattern with total leaf area for each species, which in turn also showed similar pattern to total plant biomass and height. On the other hand, Root/Shoot (R/S) ratios varied considerably between light conditions and the R/S ratios had highest values in medium light except for *Podocarpus* (Fig. 4). Although the medium light plants had the highest R/S values, the low light plants were sometimes higher than the high light grown plants (Fig. 3). In general, the pattern in R/S ratio was less regular than other variables.

5.1.2.3. Light effects and inter-specific variation in growth

Plant total biomass growths were significantly different between light conditions and among species (Table 3). For all species, total plant biomass growth ranged between 0.5 g and 132.5 g during the study period (Fig. 4). In high light *Croton* had the highest total biomass growth (132.5 g) followed by *Celtis* (33.4 g) and *Pouteria* had the lowest (2 g). Thus, biomass of the fastest growing species was 161 fold higher than that of the slow growing species. In medium light *Podocarpus* had the highest total biomass (3.5 g), followed by *Prunus* (2.5 g) and *Celtis* had the lowest (1.5 g). In low light *Podocarpus* had the highest total plant biomass (1.2 g) and *Syzygium* had the lowest (0.52 g).

For all species, seedling height growth ranged between 10.7 cm and 223.4 cm (Fig. 4). In high light *Croton* had the highest height growth (223.4 cm), followed by *Celtis* (117 cm) and *Syzygium* had the lowest (33.4 cm). Thus, plant height of the fastest growing species was 6.6 fold greater than that of the slow growing species. In medium light *Podocarpus* had highest height growth (31 cm), followed by *Celtis* (28 cm) and *Syzygium* had the lowest (13 cm). In

low light *Celtis* had the highest height growth (24.8 cm) and *Syzygium* had the lowest (10.7 cm).

For all species, total leaf area ranged between 2,024 mm² and 417,983 mm². In high light *Croton* had the highest total leaf area (417,983 mm²), followed by *Celtis* (134,464 mm²) and *Pouteria* had the lowest (5,661 mm²). In medium light *Podocarpus* had the highest total leaf area (36,451 mm²), followed by *Celtis* (13,947 mm²) and *Pouteria* had the lowest (4,077 mm²). In low light *Celtis* had the highest total leaf area (12,394 mm²) and *Croton* had the lowest (2,024 mm²).

RGR among studied species ranged between -0.12 g g⁻¹ d⁻¹ and 3.15 g g⁻¹ d⁻¹ (Fig. 3). In high light *Celtis* had the highest RGR (3.15 g g⁻¹ d⁻¹), followed by *Croton* (2.11 g g⁻¹ d⁻¹) and *Pouteria* had the lowest (0.497 g g⁻¹ d⁻¹). Thus, the RGR of the fastest growing species was six fold greater than that of the slow growing species. In medium light *Syzygium* had the highest RGR (2.16 g g⁻¹ d⁻¹), followed by *Celtis* (1.36 g g⁻¹ d⁻¹) and *Croton* had the lowest (0.326 g g⁻¹ d⁻¹). In medium light, the RGR of the fastest growing species was about six fold greater than that of the slow growing species. In low light *Celtis* had the highest RGR (0.88 g g⁻¹ d⁻¹), followed by *Syzygium* (0.59 g g⁻¹ d⁻¹) and *Croton* had the lowest (-0.12 g g⁻¹ d⁻¹). In low light, RGR of the fastest growing species was seven fold greater than the slowest growing species.

NAR among studied species ranged between 0.044 g m⁻² d⁻¹ and 0.834 g m⁻² d⁻¹ (Fig. 4). In high light *Croton* had the highest NAR (0.834 g m⁻² d⁻¹), followed by *Celtis* (0.439 g m⁻² d⁻¹) and *Podocarpus* had the lowest (0.083 g m⁻² d⁻¹). In medium light *Croton* had the highest NAR

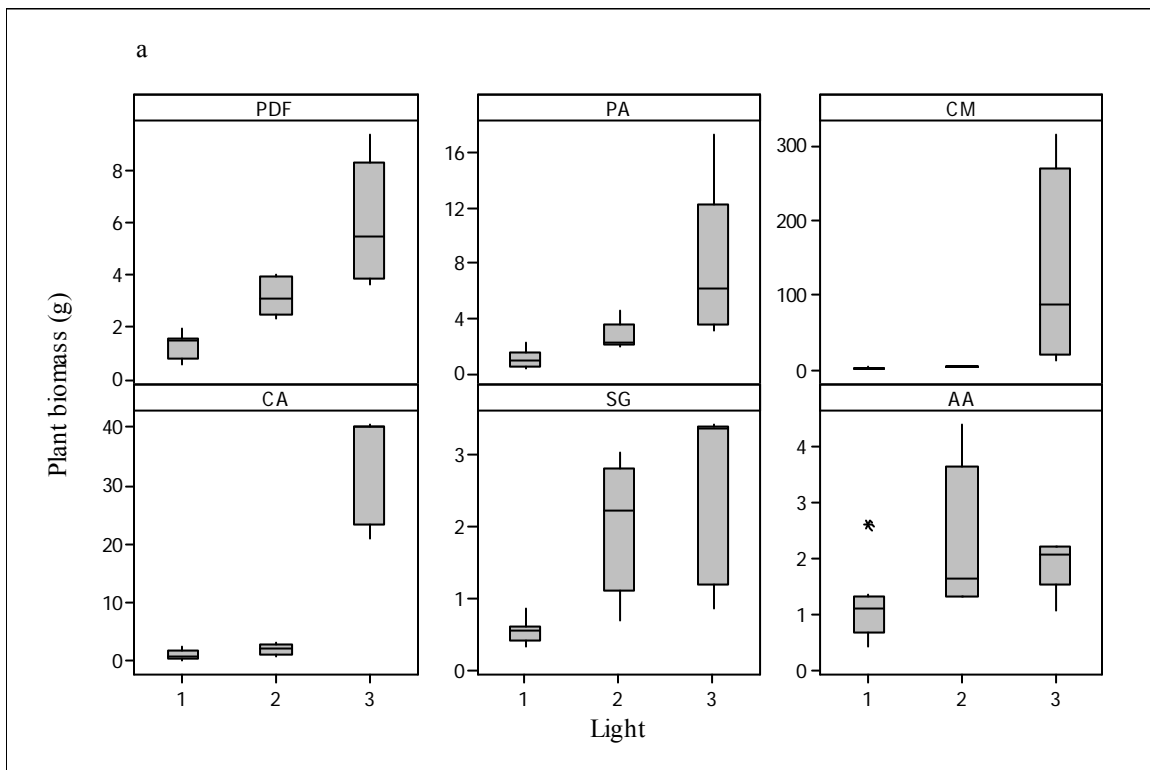
(0.504 g m⁻² d⁻¹), followed by *Syzygium* (0.341 g m⁻² d⁻¹) and *Podocarpus* had the lowest (0.125 g m⁻² d⁻¹). In low light *Celtis* had the highest NAR (0.100 g m⁻² d⁻¹), followed by *Prunus* (0.090 g m⁻² d⁻¹) and *Podocarpus* had the lowest (0.044 g m⁻² d⁻¹). *Podocarpus* had shown the lowest NAR in all light conditions (Fig. 4).

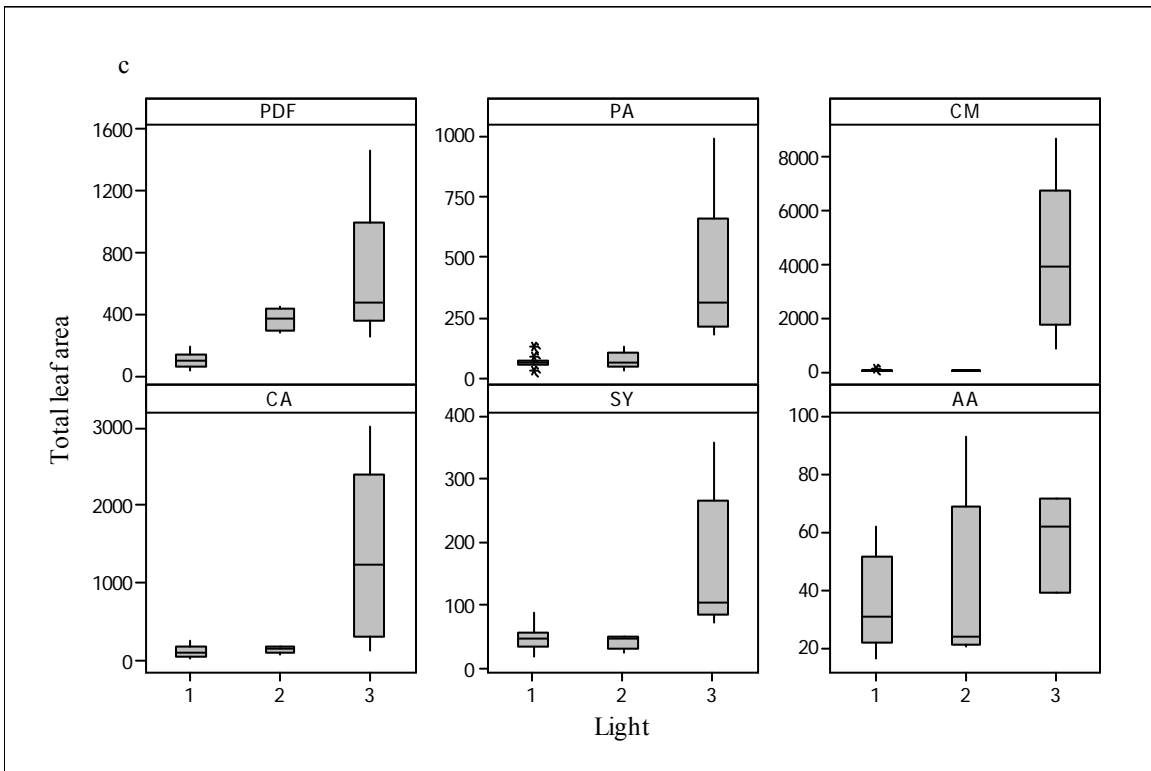
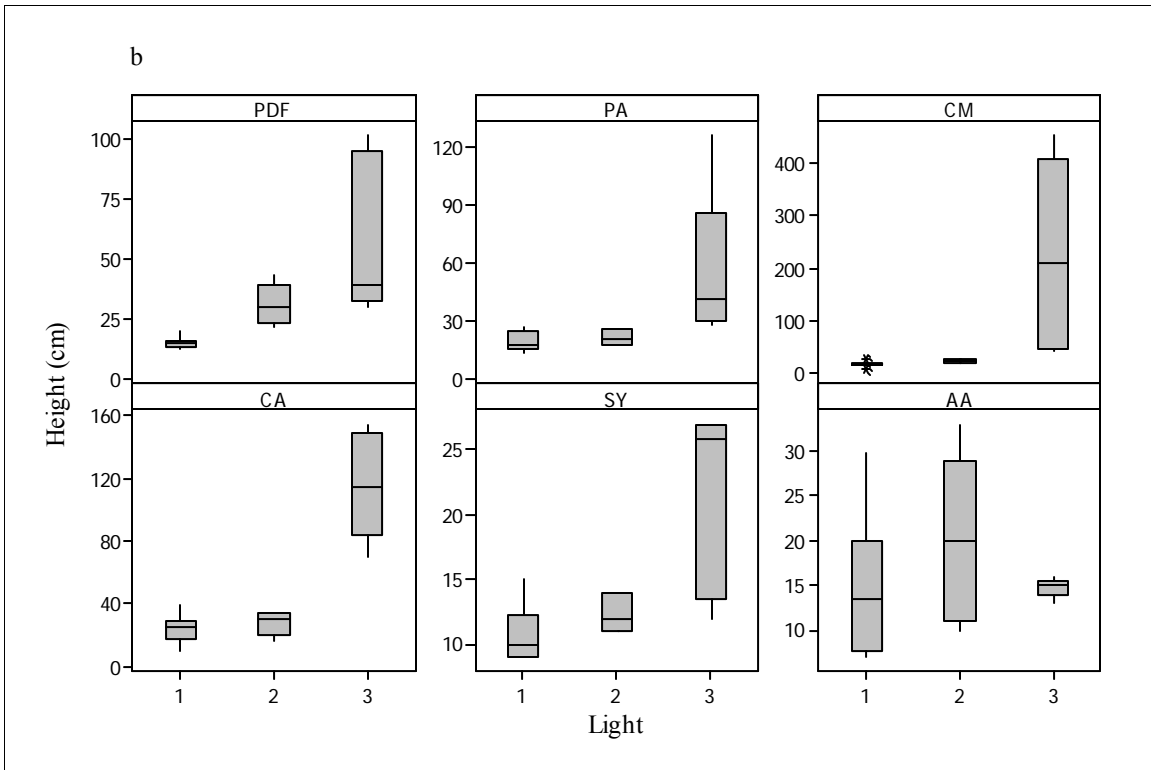
For all species, SLA ranged between 14 m² kg⁻¹ and 59 m² kg⁻¹. *Celtis* had the highest SLA at all light conditions, while *Pouteria* had the lowest. The differences in SLA between the highest and the lowest species were 2.7, 2.7 and 2.5 fold in low-, medium- and high-light conditions, respectively.

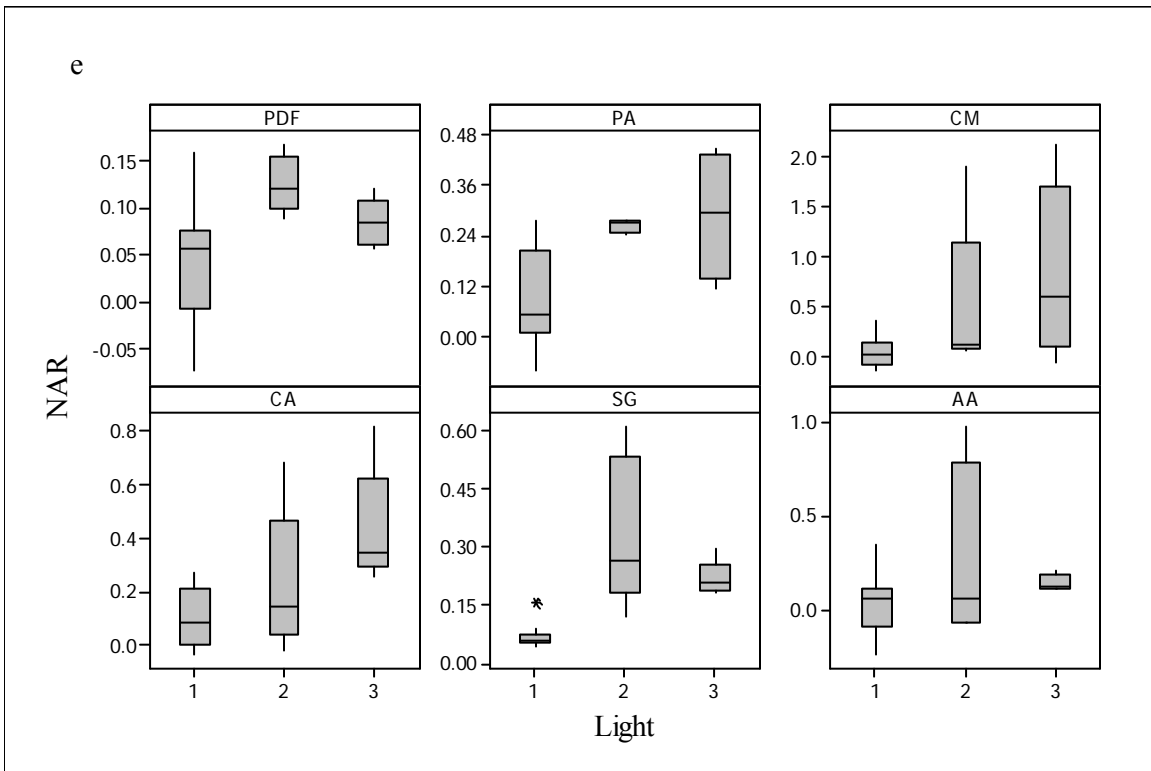
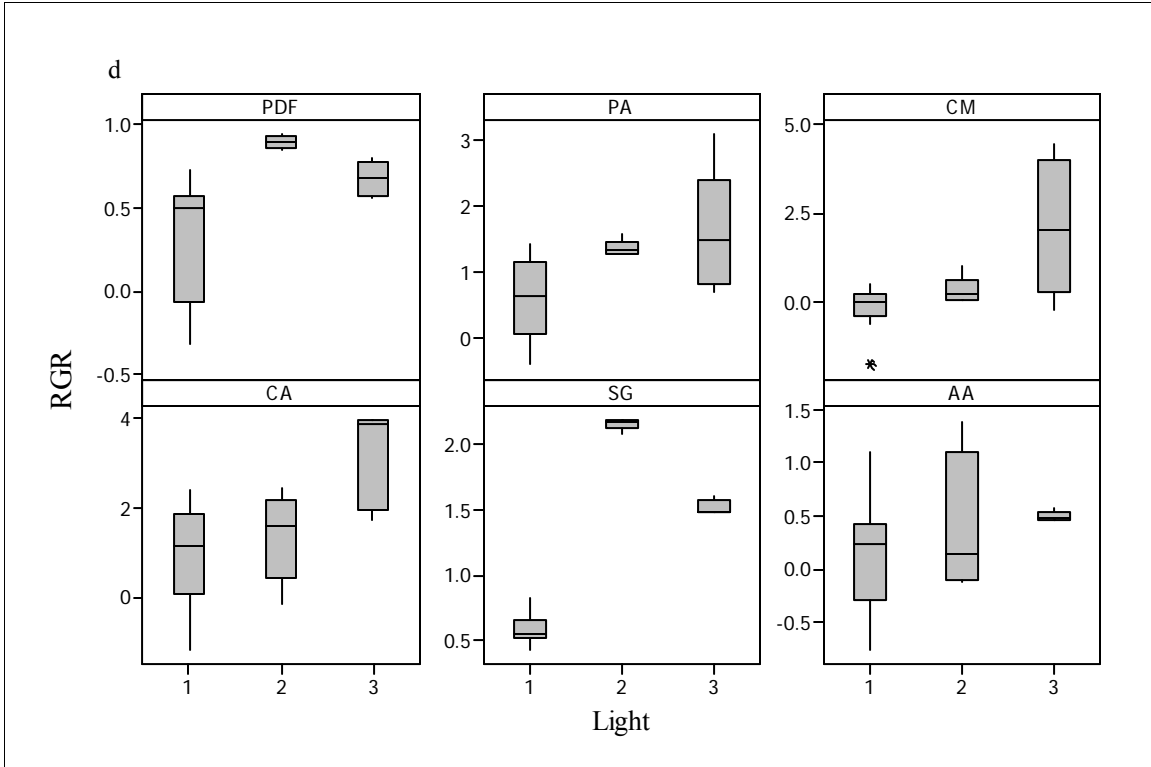
For all species, root length ranged between 15 cm and 234 cm. In high light *Croton* had the highest root length (234 cm), followed by *Celtis* (155 cm) and *Pouteria* had the lowest (19.6 cm). In medium light *Celtis* had the highest root length (28 cm), followed by *Prunus* (22 cm) and *Syzygium* had the lowest (13 cm). In low light *Prunus* had the highest root length (18 cm) and *Syzygium* had the lowest (15 cm). In addition, the relationships between light environment and the different plant variables for each species were examined to know species-specific responses and the results are shown in Table 5. Most plant variables examined showed significant relationships (positive or negative) to light. The sign of the correlation shows how the plant variables change with changing light. Accordingly, light was not correlated with RMR for all species; with LMR for species of *Prunus*, *Croton*, *Celtis* and *Syzygium* and; SMR and LAR for *Prunus*, *Croton*, *Syzygium* and *Pouteria* (Table 5).

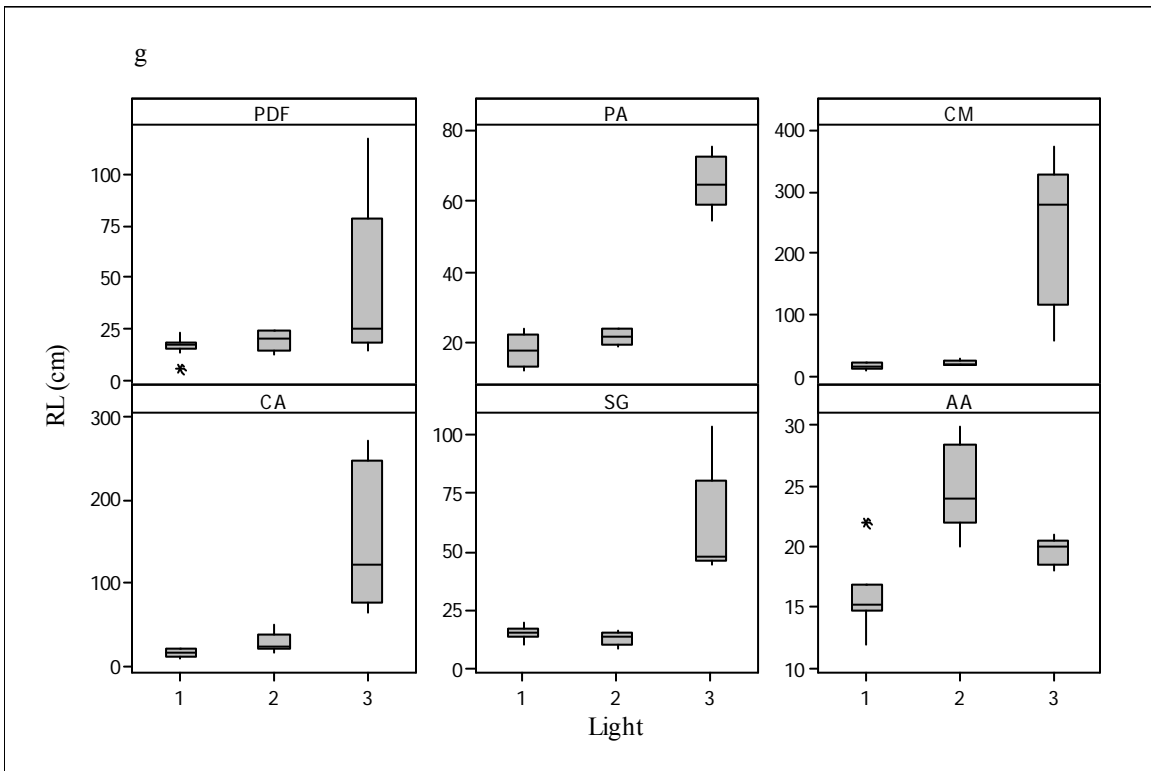
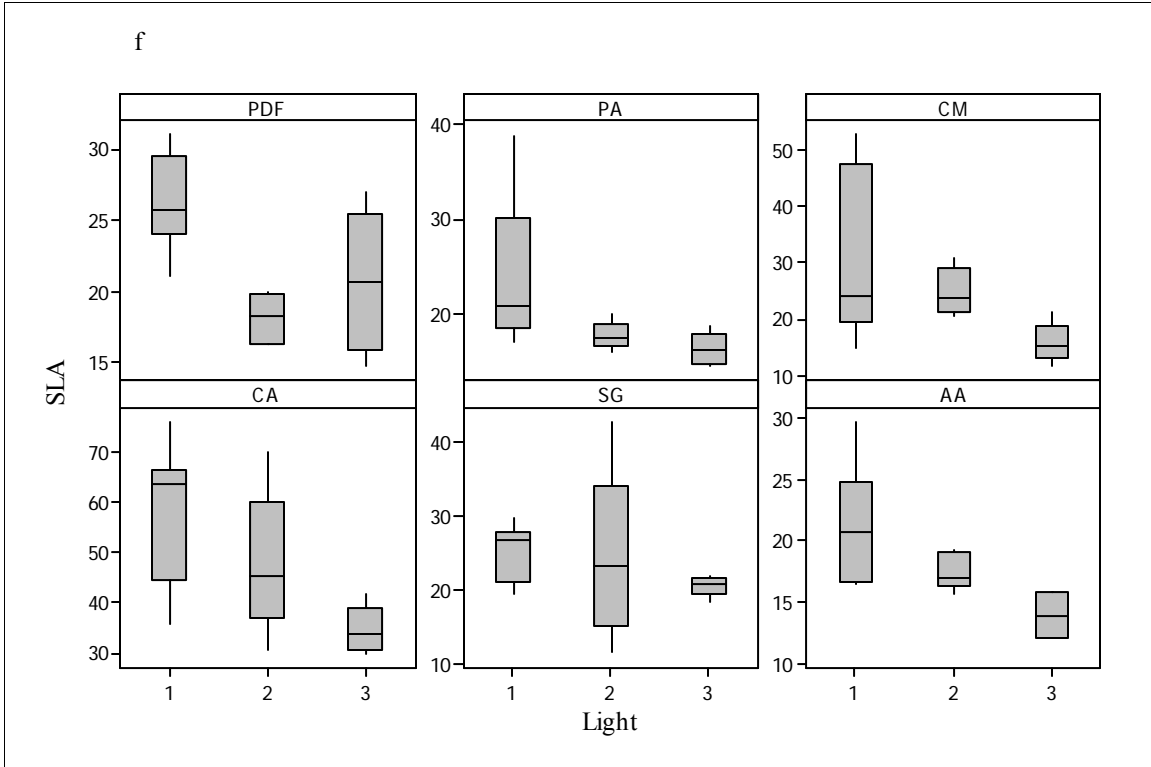
Table 4: Results of One-Way ANOVA with light and seedling growth variables of six tree species. F- values and significance (* P < 0.05; ** P < 0.01; *** P < 0.001) are shown.

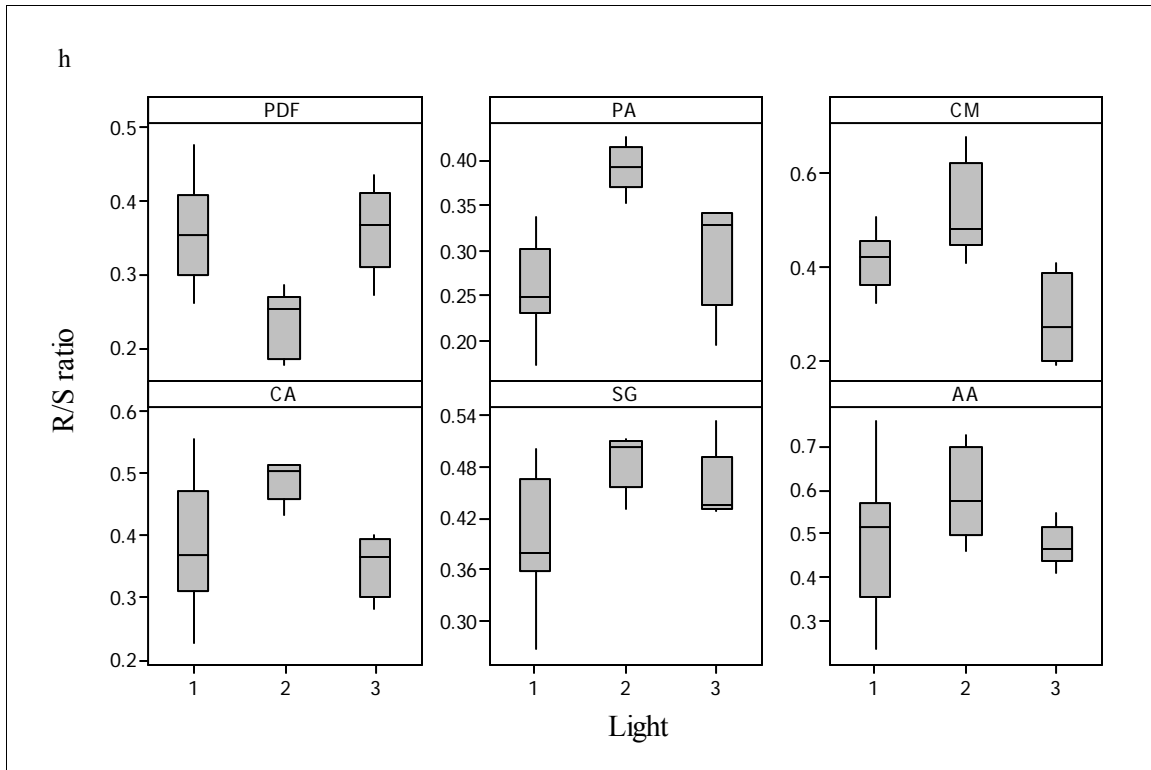
Variables	<i>Podocarpus</i>	<i>Prunus</i>	<i>Croton</i>	<i>Celtis</i>	<i>Syzygium</i>	<i>Pouteria</i>
Total biomass	23.77***	8.77**	7.90**	92.68***	13.80***	4.00*
Height	11.25***	5.52**	9.77**	46.56***	13.07***	0.86
NAR	0.56	5.51**	3.08	7.84**	13.33***	1.61
RGR	3.58*	4.26*	7.45**	8.55**	17.28***	0.66
SLA	10.37***	4.26**	2.76	6.73**	0.97	7.65**
Survival	100.74***	1420.26***	14.57***	21.02***	3152.6***	81.39***
TLA	8.64**	8.36**	15.99***	8.86**	7.44**	1.78
RL	3.06	149.4***	25.3***	17.73***	26.39***	19.54***











Figures 4 a-h: Morphological and physiological responses of seedlings of six tree species to three light conditions in the Munessa-Shashemene Forest (figures refers (a) total plant biomass, (b) plant height, (c) Total Leaf Area (TLA), (d) Relative Growth Rate (RGR), (e) Net Assimilation Rate (NAR), (f) Specific Leaf Area (SLA), (g) Root Length (RL), and (h) Root/Shoot ratio; light levels and species as indicated in Figure 3).

Table 5: Relationships between seedlings light environment of six tree species and their morphological variables. Significance levels are indicated by NS $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Species	Total biomass	Height	TLA	Survival	RGR	NA R	LAR	SLA	LMR	RMR	SMR	RL
<i>Podocarpus</i>	0.85 ***	0.74 ***	0.71 ***	-0.84 ***	NS	NS	0.46 *	-0.56 **	0.64 **	NS	-0.62 **	0.47 *
<i>Prunus</i>	0.68 ***	0.56 **	0.62 **	-0.75 ***	0.55 **	0.50 *	NS	-0.55 **	NS	NS	NS	0.88 ***
<i>Croton</i>	0.61 **	0.64 ***	0.70 ***	0.71 **	0.62 **	0.50 **	NS	-0.45 *	NS	NS	NS	0.76 ***
<i>Celtis</i>	0.84 ***	0.81 ***	0.62 **	-0.84 ***	0.67 **	0.67 **	-0.53 **	-0.66 **	NS	NS	0.56 **	0.74 ***
<i>Syzygium</i>	0.75 ***	0.72 ***	0.58 **	-0.98 ***	0.53 *	0.50 *	NS	NS	NS	NS	NS	0.73 ***
<i>Pouteria</i>	0.42 *	NS	NS	-0.82 ***	NS	NS	NS	-0.70 ***	0.42 *	NS	NS	0.46 *

5.1.2.4. Relationships in plant growth traits and predictors of relative growth rates

The relationships between the plant morphological and physiological traits measured for all species across the different light conditions are shown in Tables 6 & 7. Total plant biomass (absolute growth) in low light was positively significantly related to height, RGR, NAR and RL, but negatively significantly related to LAR and LMR (Table 6); in medium light positively significantly related to RGR and NAR (Table 7); and in high light positively significantly related to total leaf area, survival, RGR, NAR and SMR, but negatively significantly related to RMR and LMR (Table 6). Plant height, which is also another absolute growth feature, positively significantly related to total leaf area and root length across all light conditions, which imply increased height growth was paralleled with increasing light interception and the uptake of water and nutrients. Moreover, NAR showed significant positive correlations with SLA and LMR across all light conditions (Tables 6 & 7). Seedling survival positively strongly related to RGR in low and high light, but the same correlation was not significant in medium light (Tables 6 & 7).

On the other hand, in low light, correlations between RGR and either LAR, SLA or LMR were not significant (Table 6). Again, RMR, SMR, and RL were significantly negatively correlated to LAR. SMR and RMR were significantly negatively correlated with LMR indicating greater allocation to leaves than support structures. In medium light, positive correlation between RGR and either NAR or SLA was not significant (Table 7). LAR and LMR were significantly positively correlated with RGR. RMR and RL were significantly and negatively correlated with LMR, indicating that greater allocation to leaves occurred at the expense of allocation to roots. In high light, positive correlation between RGR and SLA was significant (Table 6).

SMR and RL were significantly positively correlated with RGR; but the same correlation was not significant with LAR. SMR were significantly negatively correlated to LMR. A further correlation analyses for determinants of relative growth rates have shown that RGR in low light ($R^2 = 0.60$, $P < 0.001$) and high light ($R^2 = 0.58$, $P < 0.001$) showed significant positive correlation with net assimilation rates, but no significant correlation with leaf area ratio. In medium light the opposite pattern was found, i.e. relative growth rate significantly correlated with leaf area ratio ($R^2 = 0.24$, $P < 0.05$; $r = 0.5$, $P = 0.01$) but not with net assimilation rate.

Table 6: Correlation matrix for seedling traits of six tree species grown in low or high light conditions. Values in the table are Pearson's correlation coefficients; number above the diagonal refers to plants grown in low light, whereas values below the diagonal refer to plants grown in high light. (Significance levels: * P < 0.05, ** P < 0.01, *** P < 0.001).

	Total biomass	Height	Total leaf area	Survival	RGR	NAR	LAR	SLA	LMR	RMR	SMR	Root length
Total biomass		0.31**	0.19	-0.06	0.72***	0.63***	-0.28*	-0.14	-0.30**	0.11	0.2	0.38**
Height	0.26		0.5***	-0.03	0.30**	0.29*	0.13	0.27*	-0.01	-0.01	0.14	0.34**
Total leaf area	0.39**	0.84***		0.31**	0.24	0.09	0.35**	0.46***	0.29*	-0.03	-0.26	-0.09
Survival	0.56***	0.63***	0.65***		0.11	-0.05	0.51***	0.18	0.64***	-0.35**	-0.32**	-0.06
RGR	0.60***	0.25	0.14	0.51**		0.72***	-0.04	-0.04	-0.08	0.09	-0.06	0.26*
NAR	0.89***	0.25	0.30	0.56***	0.75***		-0.10	-0.25*	-0.22	0.07	0.16	0.22
LAR	-0.30	-0.13	-0.29	-0.21	0.03	-0.36*		0.67***	0.72***	-0.34**	-0.36**	-0.35**
SLA	-0.04	0.12	-0.01	0.25	0.54**	0.05	0.68***		0.27*	-0.08	-0.20	-0.25
LMR	-0.48**	-0.34	-0.37*	-0.44**	-0.37*	-0.51***	0.58***	-0.07		-0.53***	-0.52***	-0.28*
RMR	-0.55**	-0.36*	-0.35*	-0.66***	-0.55**	-0.59***	-0.01	-0.09	-0.02		-0.44***	0.10
SMR	0.73***	0.51**	0.51**	0.79***	0.70***	0.84***	-0.38*	0.12	-0.66***	-0.73***		0.19
Root length	0.29	0.80***	0.83***	0.67***	0.33*	0.31	-0.11	0.28	-0.43**	-0.32	0.54**	

Table 7: Correlation matrix for seedling traits of six tree species grown in medium light condition. Values in the table are Pearson's correlation coefficients (significance levels * P < 0.05, ** P < 0.01, *** P < 0.001).

	Total biomass	Height	Total leaf area	Survival	RGR	NAR	LAR	SLA	LMR	RMR	SMR
Height	0.02										
TLAa	0.32	0.57***									
Survival	0.09	0.49**	0.58***								
RGR	0.37*	-0.34	-0.008	-0.07							
NAR	0.40*	-0.44**	-0.34	-0.23	0.20						
LAR	0.03	0.18	0.68***	0.46**	0.50**	-0.32					
SLA	-0.12	0.09	-0.05	0.40*	0.22	-0.03	0.55***				
LMR	0.25	0.004	0.54**	0.14	0.44**	-0.30	0.69***	-0.14			
RMR	-0.32	-0.03	-0.56***	-0.36*	-0.41*	0.36*	-0.69***	0.11	-0.85***		
SMR	0.12	0.05	0.02	0.39*	-0.22	-0.11	-0.04	0.06	-0.29	-0.24	
Root length	-0.07	0.40*	0.05	0.08	-0.31	-0.12	-0.24	0.24	-0.42**	0.36*	0.12

5.2. Survival and Herbivory Damage on Naturally Regenerated Understorey Seedlings in Munessa-Shashemene Forest

5.2.1. Seedling Survival (or Mortality)

Over 24 months, about 660 of the total 1200 seedlings marked survived. Mean seedling survival rates in the understorey of the forest showed remarkable variations among species and ranged between 33 and 89 percent per year (Table 8). In other words, seedling mortality of the study species ranged between 11 and 67 percent. Mean seedling survival rate was highest for *Podocarpus* and lowest for *Syzygium* (Table 8). Survival was not significantly different among studied species ($F = 3.63$, $P = 0.09$). However, seedling survival differed significantly between the seasons (wet and dry) ($F = 8.87$, $P = 0.03$), and years ($F = 15.15$, $P = 0.01$). For all species, the proportion of seedlings that survived in the wet season (74 %) was significantly greater than in the dry season (26 %) ($t = 4.38$, $P = 0.001$), which implies the strong seasonality effect as a result of rainfall. Similarly, survival was proportionally higher in wet than in dry season for each species. Mean survival was proportionally higher during the second year (65 %) than in the first year (45 %) (Fig. 5a). The mean annual survival of seedlings for all species pooled together was 55% year⁻¹. Generally, four out of the six study species, namely, *Podocarpus*, *Croton*, *Pouteria* and *Celtis* had good survivals (i.e. > 55 % of their seedlings survived), while species of *Prunus* and *Syzygium* exhibited poor survivals (i.e. < 40 % of their seedlings survived) (Table 8). Over all, ranking of the species in the order of decreasing seedling survivals were *Podocarpus* > *Croton* > *Celtis* > *Pouteria* > *Prunus* > *Syzygium*. However, the ranking of species survivals between the years was found non-significant ($r = 0.60$, $P = 0.14$; Table 8), which imply the change in the rank order of the species between the years. On the

other hand, seedling survival rate was not-significantly correlated to the densities of seedlings of the species within the forest ($P > 0.05$, for all species).

Table 8: Percentage seedling survival and herbivory of six indigenous tree species in the Munessa-Shashemene Forest.

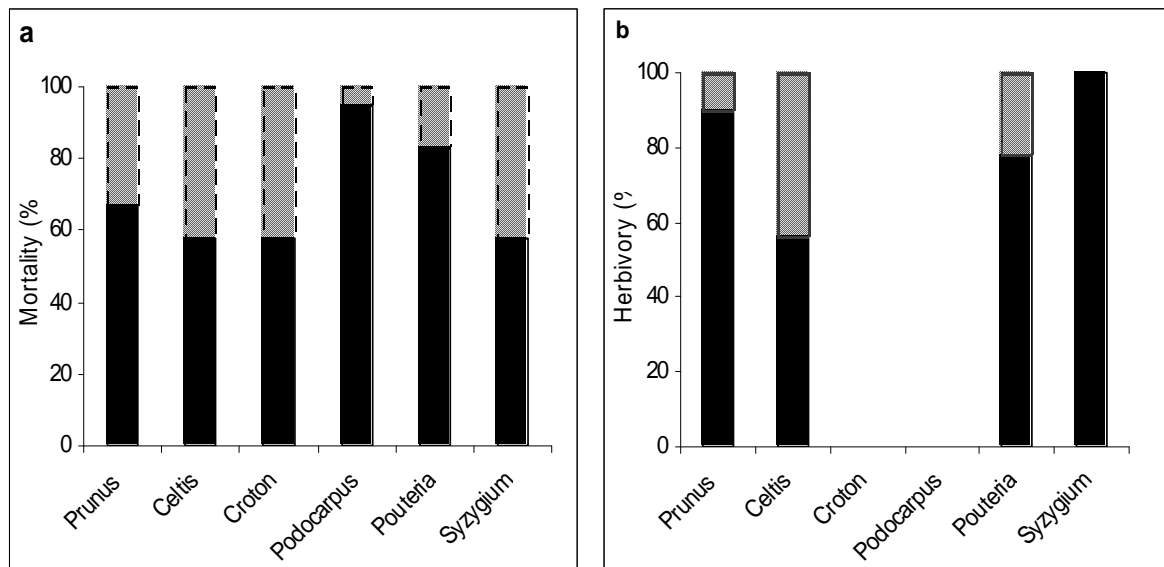
Species	Survival			Herbivory		
	Year 1	Year 2	Mean	Year 1	Year 2	Mean
<i>Croton macrostachyus</i>	40	73	56 a	0	0	0
<i>Pouteria adolfi-friederici</i>	51	61	56 a	16	27	21 a
<i>Podocarpus falcatus</i>	86	91	89 b	0	0	0
<i>Prunus africana</i>	18	61	39 ac	88	9	49 ac
<i>Celtis africana</i>	62	53	58 a	69	42	56 bc
<i>Syzygium guineense</i>	15	50	33 ad	11	73	42 ac

(Similar letters across columns are not significantly different at $P = 0.05$)

5.2.2. Seedling Herbivory

Mean seedling herbivory rate in the understorey of the Munessa-Shashemene Forest showed pronounced variations among species and ranged between 0 and 56 percent (Table 8). The result clearly demonstrated differential susceptibility among species, and two out of the six study species (*Croton* and *Podocarpus*) did not show any signs of herbivory. The development of tough unpalatable leaves appears to be an adaptive defense to herbivory in these two species. Among the four species, mean seedling herbivory was highest for *Celtis*, followed by *Prunus* and lowest for *Pouteria*. Considering the four species only, herbivory was non-significant among species ($F = 2.03$, $P = 0.22$), and years ($F = 14.56$, $P = 0.08$); but significantly different between seasons ($F = 5.64$, $P = 0.04$). Mean seedling herbivory of the four species pooled together was 42 percent per year. Similarly, seedling herbivory for these

species was higher in the dry season (82 %) than in wet season (18 %), which implies the strong seasonality in grazing activities within the study forest (Figs. 5). Herbivory was higher in dry than in wet season for each species (Table 8; Figs. 5). Major factors responsible for leaf browsing/grazing in seedlings include livestock, wild animals and insect herbivores. In *Pouteria* large proportion of leaf defoliation was due to insect herbivores. Of the total seedlings/individuals of *Pouteria*, *Prunus*, *Celtis* and *Syzygium* whose leaves had been browsed/grazed during the first year, about 50, 62, 50 and 56 percent, respectively, survived until the end of the experiment, whereas the rest were unable to recover.



Figures 5 a & b: Seasonality in (a) seedling mortality (b) and herbivory of the six indigenous tree species during dry and wet periods in the Munessa-Shashemene Forest (solid bars indicate dry season and lines indicate wet season).

5.3. Density, Distribution and Population Structure of the Study Species

5.3.1. Seedling Density and Distribution Along the Altitudinal Gradient

The mean density of seedlings of the study species in the Munessa-Shashemene Forest is shown in Table 9. Mean seedling densities show significant variations among species varying between zero (for *Polyscias*) and 5,334 individuals ha⁻¹ (for *Prunus*). High densities were also typical for the two species *Croton* and *Celtis*. On the other hand, frequency distribution of seedlings of the seven species also varied considerably and range between zero (for *Polyscias*) and 78 (for *Podocarpus*). Low seedling frequencies were also observed for species of *Syzygium*, *Pouteria*, *Celtis* and *Croton*.

Figures 6a-g also shows seedling densities and distributions along an altitudinal gradient in the Munessa-Shashemene Forest. The seedling densities of most species (*Celtis*, *Podocarpus*, *Prunus*, and *Croton*) show skewed distribution, i.e. with frequent occurrence of relatively low values and infrequent occurrence of high values along the altitudes. By contrast, seedling density of *Syzygium* was normally distributed whereas *Pouteria* showed log normal distribution along the altitudinal gradient.

Seedling densities of *Celtis* varied between 930 and 13,310 individuals ha⁻¹ across the altitudes. They showed remarkable concentration in the altitude range 2100 - 2400 m. The highest seedling density was recorded at 2200 m asl and the lowest at 2400 m asl. Of the total seedlings of *Celtis* recorded 83 % were less than 50 cm in height.

Seedling densities of *Croton* varied between 52 and 7180 individuals ha^{-1} across the altitudinal gradient. Seedlings of *Croton* showed a distinct elevational peak between 2100 and 2400 m asl. The highest seedling density was recorded at 2200 m asl and the lowest at 2400 m asl. At the part of its range, the density of *Croton* seedlings at the lower elevation was relatively higher than further up. Of the total seedlings of *Croton* recorded, nearly half of them (48 %) were less than 50 cm in height.

Seedlings of *Podocarpus* showed no concentration at any elevation in the Munessa-Shashemene Forest and they occurred along the entire altitudinal range. However, the seedling densities varied considerably with altitude ranging between 43 individuals ha^{-1} at 2300 m and 503 individuals ha^{-1} at 2600 m. Of the total seedlings of *Podocarpus* recorded 67 % were less than 50 cm in height.

Seedlings of *Pouteria* showed distinct elevational concentration occurring between 2100 - 2300 m asl. Seedling density decreased progressively from 1240 individuals ha^{-1} at 2300 m to 2250 individuals ha^{-1} at 2100 m asl. The highest seedling density was recorded at 2100 m asl and the lowest at 2300 m asl. All seedlings of *Pouteria* recorded were less than 50 cm in height.

Seedlings of *Prunus* showed no concentration at any elevation as they occur along the entire altitudinal range. However, seedling densities varied considerably with altitude ranging between 1060 individuals ha^{-1} at 2700 m and 7,900 individuals ha^{-1} at 2500 m. Seedling

densities increased progressively with increasing altitude except at the upper most elevation. Of the total seedlings of *Prunus* recorded 93 % were less than 50 cm in height.

Seedling densities of *Syzygium* varied between 40 and 160 individuals ha⁻¹ across the altitudinal gradient. They showed a distinct elevational concentration occurring between 2100 - 2300 m asl. The highest seedling density was recorded at 2200 m and the lowest at 2300 m. All seedlings of *Syzygium* recorded were less than 50 cm in height.

Not a single seedling of *Polyscias* was recorded along the entire altitudinal range in the Munessa-Shashemene Forest.

In the present study, seedling densities and distributions were strongly correlated to altitudes except for *Prunus*. Seedlings of *Pouteria*, *Croton*, *Celtis* and *Syzygium* all showed significant strongly negative correlation with elevation, whereas those of *Podocarpus* exhibited a strongly positive but non-significant correlation with altitude.

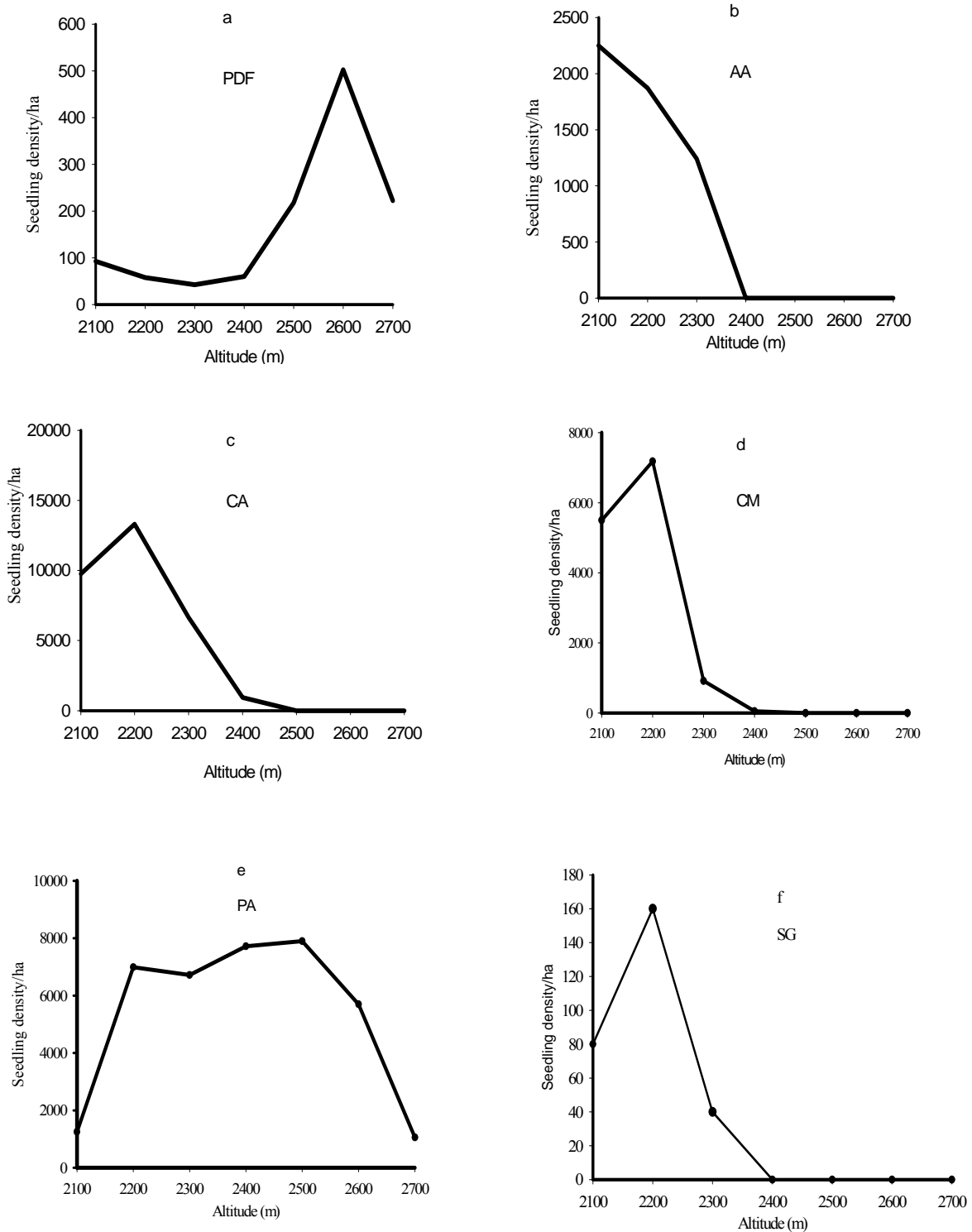
The mean total seedling density of the seven studied species along the altitudinal gradient is shown in Figure 7. The total seedling density of the seven study species peaked at 2200 m (29,567 seedlings), followed by 2100 m (18,922 seedlings) and the lowest at 2700 m (1,282 seedlings) (Fig. 7). *Celtis*, *Croton* and *Prunus* contributed 77 to 93 percent of the seedlings at 2100 m and 2200 m asl peaks implying that majority of the seeding populations in the present study came from the same group.

Table 9: Mean densities (\pm S.E.) and frequency of seedlings, trees and saplings of seven indigenous tree species in the Munessa-Shashemene Forest.

Species	Family	Seedling density*	Seedling Frequency**	Tree and sapling density*	Tree and sapling Frequency**
<i>Celtis africana</i>	Ulmaceae	4377 \pm 2088 ab	33	11 \pm 5 a	22
<i>Croton macrostachyus</i>	Euphorbiaceae	1950 \pm 1155 b	33	94 \pm 65 b	47
<i>Podocarpus falcatus</i>	Podocarpaceae	170 \pm 62 c	78	102 \pm 20 b	89
<i>Pouteria adolfi-friederici</i>	Sapotaceae	766 \pm 377 d	26	4 \pm 1 c	21
<i>Polyscias fulva</i>	Araliaceae	0	0	3 \pm 1 c	14
<i>Prunus africana</i>	Rosaceae	5334 \pm 1112 ae	74	29 \pm 7 d	51
<i>Syzygium guineense</i>	Myrtaceae	40 \pm 23 f	24	19 \pm 10 ad	26

(Similar letters across columns are not significantly different at $P = 0.05$; * mean seedling density ha^{-1} ; ** percentage of quadrats occupied).

Similarly, comparison of mean total seedling densities of the seven studied species were categorized with respect to altitudinal ranges: the highest seedling density (24,245 seedlings ha^{-1}) was recorded in the lower Munessa-Shashemene Forest between 2100 and 2300 m asl. With higher altitudes the seedling densities declined rapidly, amounting to 10,830 seedlings ha^{-1} in the middle range (2400 - 2500 m asl) and only 3,742 seedlings ha^{-1} in the upper forest.



Figures 6a-f: Density and distribution of seedlings of six indigenous tree species recorded along altitudinal gradient in the Munessa-Shashemene Forest (PDF = *Podocarpus falcatus*; AA = *Pouteria adolfi-friederici*; CA = *Celtis africana*; CM = *Croton macrostachyus*; PA = *Prunus africana*; SG = *Syzygium guineense* and; PV = *Polyscias fulva*).

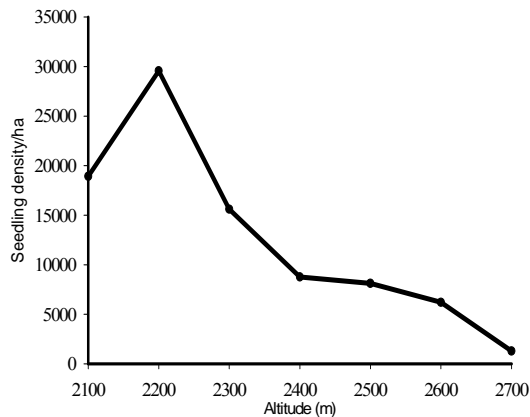


Figure 7: Mean total seedling density of six tree species recorded along altitudinal gradient in the Munessa-Shashemene Forest.

Result from the Canonical Correspondence Analysis (CCA) ordination of seedling distribution along gradients of altitude, light and disturbance is given in Figure 8. The ordination output indicated that the three environmental variables namely, altitude, canopy light and scale of disturbance account for 54 % of the total variation among the six of the seven species considered in this study. Axes 1 and 2 of the CCA (eigen values 0.52 and 0.1, respectively) accounted for 53 % of the total variation, while the third canonical axis explained only an additional 0.8 %. Altitude strongly correlated with the seedling abundance on Axis 1 ($r = 0.91$), while both canopy light ($r = 0.72$) and disturbance ($r = 0.55$) were strongly correlated to Axis 2. Altitude was correlated negatively but non-significantly to canopy light ($r = -0.31$) and disturbance ($r = -0.39$). Expectedly, canopy light and disturbance were strongly correlated ($r = 0.73$). The CCA clearly showed that *Celtis* and *Croton* are favored by disturbance and they were separated from the rest of the species and concentrated in plots with canopy gaps, while the remaining four species were concentrated in plots shaded by a more or less closed canopy. In addition, the CCA revealed that seedlings of *Podocarpus* dominate over the other species in

the upper forest, while *Prunus* seedlings prevail in the middle ranges. *Croton*, *Pouteria* and *Syzygium* dominate in the lower portion of the forest.

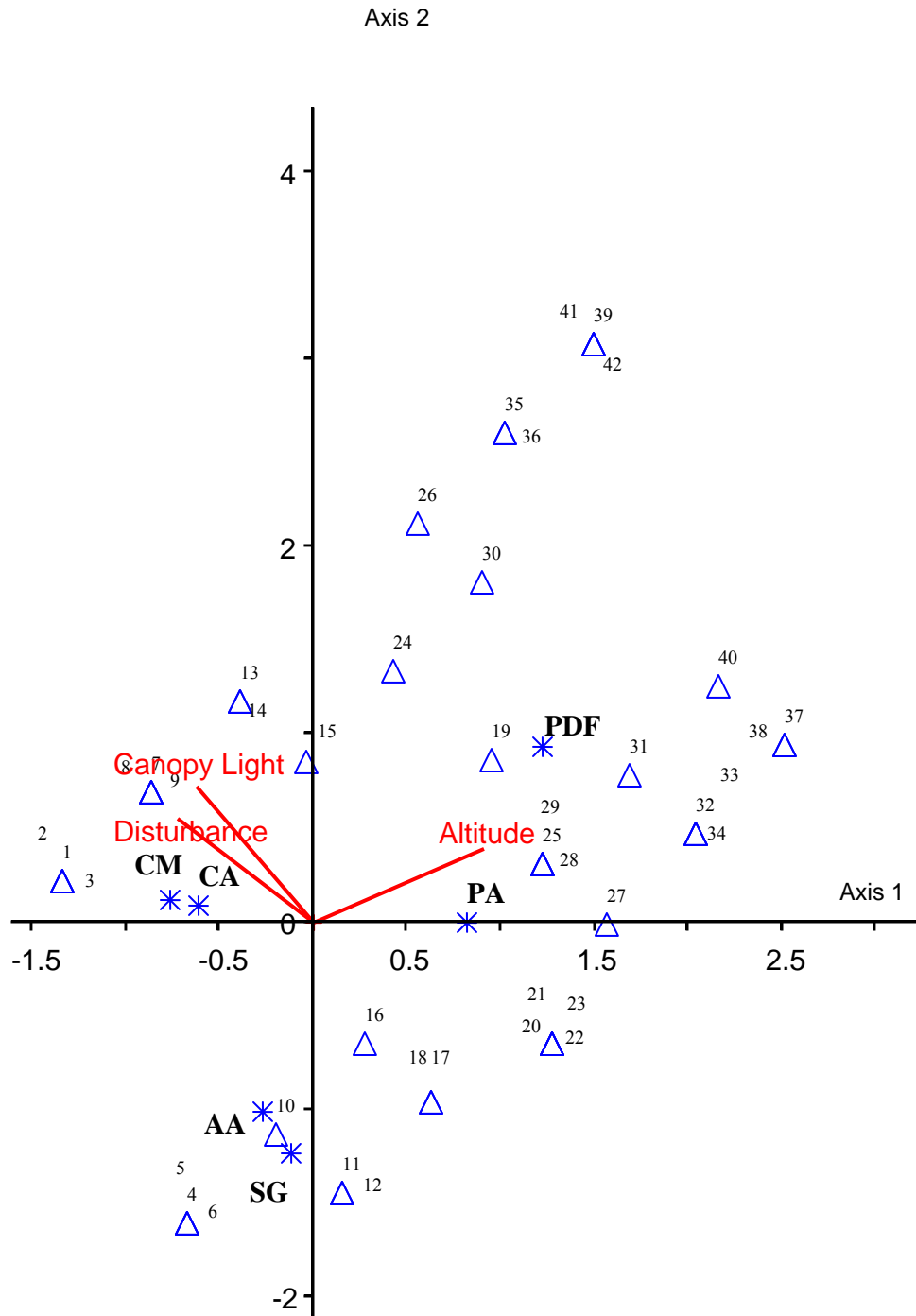


Figure 8: Canonical Correspondence Analysis (CCA) out put showing ordination of number of seedlings of six tree species and their distribution in forty-two quadrats along gradients of altitude, canopy light and disturbance at Munessa-Shashemene Forest (species CM = *Croton*; CA = *Celtis*; PDF = *Podocarpus*; PA= *Prunus*; AA = *Pouteria*; SG = *Syzygium*).

5.3.2. Tree and Sapling Density, and Their Distribution Along the Altitudinal Gradient

The mean density of trees and saplings of the seven study species is shown in Table 9. Average tree and sapling densities of the study species varied between 3 individuals ha⁻¹ (for *Polyscias*) and 102 individuals ha⁻¹ (for *Podocarpus*). The mean tree and sapling densities among species did not exhibit significant variations between *Pouteria* and *Polyscias*; *Croton* and *Podocarpus*; and *Prunus* and *Syzygium* (Table 9). On the other hand, frequency distributions of trees and saplings of the seven study species varied between 15 % (*Polyscias*) and 89 % (*Podocarpus*). Relatively low tree and sapling frequency was observed with *Pouteria*, *Syzygium* and *Celtis*, and high frequency with *Podocarpus*.

Figures 9a-g shows tree and sapling densities and distributions of the studied species along an altitudinal gradient in the Munessa-Shashemene Forest. Trees and saplings of *Celtis* were recorded between 2100 m and 2300 m asl. Tree and sapling density along the altitudes varied slightly between 23 - 30 individuals ha⁻¹. The mean tree and sapling density of *Celtis* was 11 individuals ha⁻¹ of which saplings accounted 16 percent of the population.

Trees and saplings of *Croton* were recorded between 2100 and 2400 m asl. The highest density was recorded at 2200 m (480 individuals ha⁻¹) and the lowest at 2400 m (3 individuals ha⁻¹). The mean density of trees and saplings of *Croton* was 94 individuals ha⁻¹ of which saplings accounted for 29 percent.

Trees and saplings of *Podocarpus* were recorded along the entire altitudinal range of the forest. However, the tree and sapling density varied considerably across the altitudes and range

between 43 - 198 individuals ha⁻¹. The highest tree and sapling density was found at 2600 m and, the lowest at 2300 m and 2700 m asl. The mean density of trees and saplings was 102 individuals ha⁻¹ of which saplings accounted for 64 percent.

Trees *Polyscias* were recorded between 2100 m and 2300 m asl. Tree density along the altitudes remained very low between 5 and 8 individuals ha⁻¹. The highest tree density was recorded at 2100 m asl and the lowest at 2200 and 2300 m asl. The mean density of tree of *Polyscias* was 3 individuals ha⁻¹ and no sapling was recorded.

Trees of *Pouteria* were recorded between 2100 m and 2300 m asl. Tree density showed slight variation across the altitudes and range between 5 - 13 individuals ha⁻¹. The highest density of tree was recorded at 2300 m asl and the lowest at 2200 m asl. The mean tree density of *Pouteria* was 4 individuals ha⁻¹ and no sapling was recorded.

Trees and saplings of *Prunus* were recorded along the entire altitudinal range of the forest. However, tree and sapling density varied remarkably along the altitudes and range between 10 individuals ha⁻¹ (at 2100 m and 2700 m asl) and 63 individuals ha⁻¹ (at 2400 m asl). The mean density of trees and saplings of *Prunus* was 29 individuals ha⁻¹ of which saplings accounted 25 percent of the population.

Trees of *Syzygium* were recorded between 2100 m and 2300 m asl. Tree density along the altitudes varied considerably and ranged between 18 and 63 individuals ha⁻¹. Tree density of *Syzygium* decreased progressively with increasing altitudes. The mean density of trees of

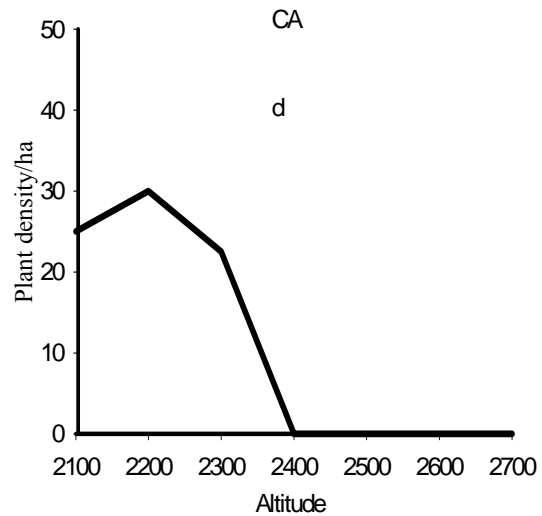
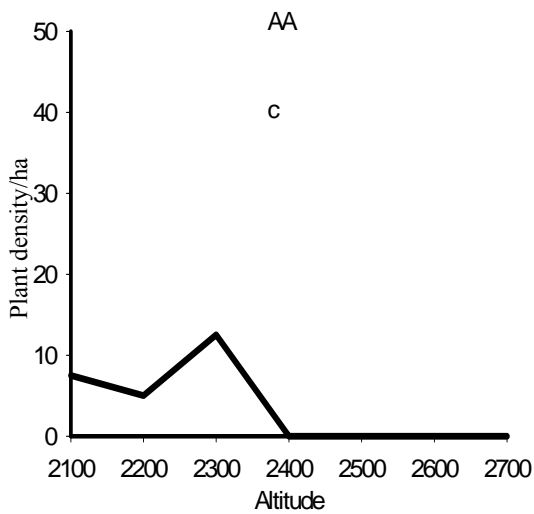
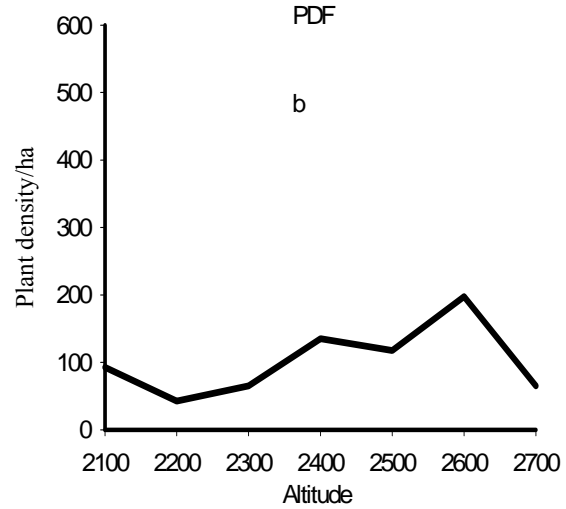
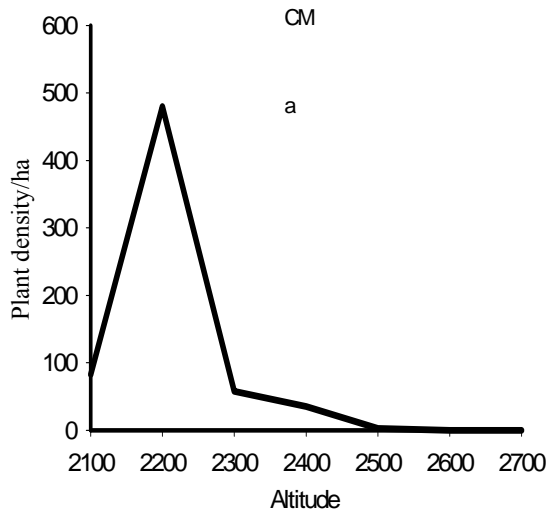
Syzygium was 19 individuals ha^{-1} and no sapling was recorded. On the other hand, the frequency distribution of trees and saplings varied considerably among species (Table 9). The highest frequency of trees and saplings was exhibited by *Podocarpus*, followed by *Prunus* while the lowest by *Polyscias*.

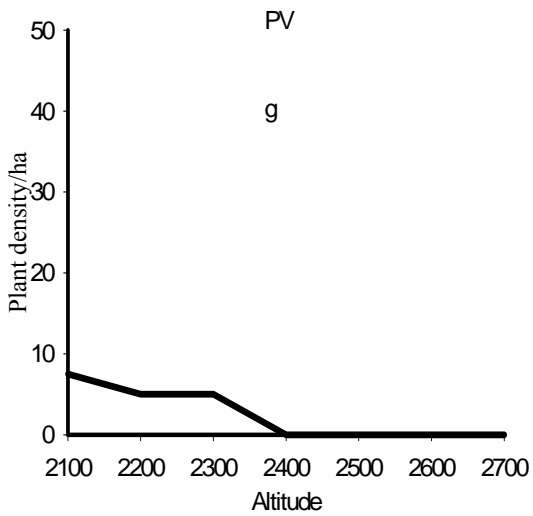
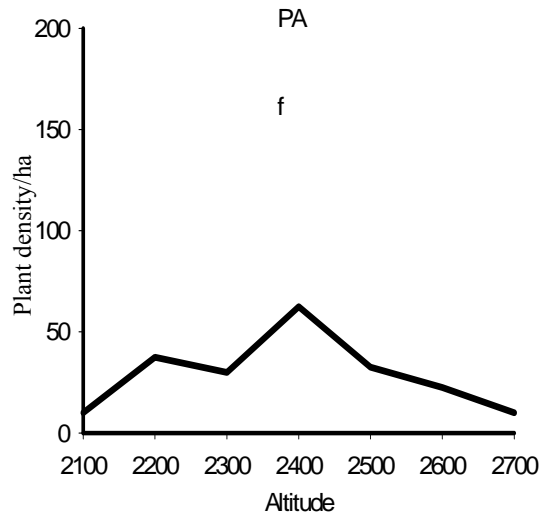
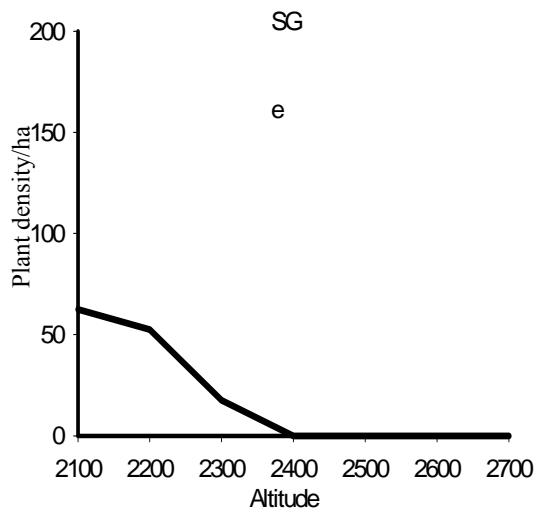
The mean total trees and saplings density of the seven studied species along the altitudes is shown in Figure 10. The total tree and sapling densities of the seven study species peaked at an altitude 2200 m (652 individuals ha^{-1}), followed by 2100 m (288 individuals ha^{-1}) and the lowest at 2700 m (75 individuals ha^{-1}). *Croton*, *Podocarpus* and *Prunus* contributed 74 to 82 percent of the trees and saplings density at 2200 m and 2100 m peaks indicating that majority of the tree and sapling populations in the lower elevations were from this group

Similarly, comparison of the mean total trees and saplings densities of the seven studied species were categorized with respect to altitudinal ranges: the highest tree and sapling density (283 individuals ha^{-1}) was recorded in the lower Munessa-Shashemene Forest between 2100 m and 2300 m asl. With higher altitudes the tree and sapling density declined markedly, amounting to 192 individuals per hectare in the upper range (2600 - 2700 m asl) and, only 148 individuals ha^{-1} in the middle range.

Reproductive performance of the mother trees as measured by the density of seedlings per single reproductive tree showed considerable variation among species. The highest density was found with *Celtis* (423 seedlings), followed by *Prunus* (243 seedlings) and *Pouteria* (215 seedlings). The lowest value was that of *Syzygium* (only 2 seedlings) which also exhibited the

lowest seedling density in the study site. *Podocarpus*, which had relatively low seedling density likewise, had low number of seedlings per reproductive mother tree (5 seedlings). *Croton* was unexpectedly on the lower side (29 seedlings).





Figures 9a-g: Tree and sapling densities and distributions of the seven studied species along altitudinal gradient in the Munessa-Shashemene Forest (PDF = *Podocarpus falcatus*; AA = *Pouteria adolfi-friederici*; CA = *Celtis africana*; CM = *Croton macrostachyus*; PA = *Prunus africana*; SG = *Syzygium guineense*; and PV = *Polyscias fulva*).

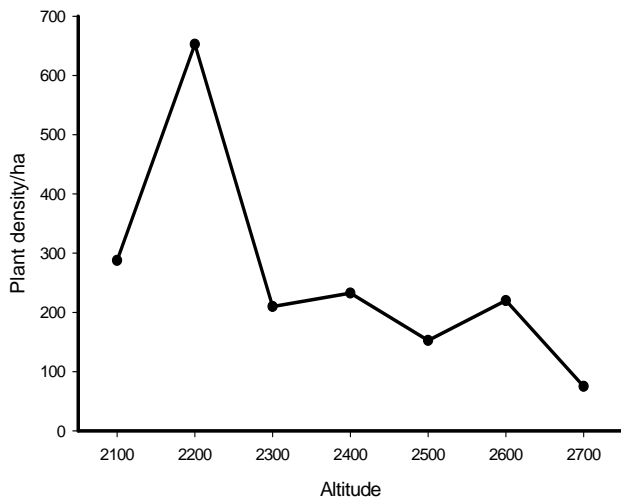


Figure 10: Mean total sapling and tree densities of the seven studied species along altitudinal gradient in the Munessa-Shashemene Forest.

5.3.3. Population Structure of the Seven Tree Species

Population structures provide information on the proportions of size or age classes in the population and thus provide important information for the assessment of the regeneration status. Height and diameter class proportions of the seven study species are shown in Figures 11a-g. The shape of the population curves of the species differs markedly. Both the height class and the diameter class structures of the studied species are presented here for the sake of direct comparison of regeneration status of the species from other afro-montane forests of Ethiopia or elsewhere.

Population structure of *Celtis* showed continuous size-class distribution with progressive decline of the proportion of individuals with increasing height. The proportion of individuals in the lower height classes were significantly higher than the rest of the height classes and

exhibited an inverse J-shape curve. The proportion of individuals in the successive height classes showed an exponential decline ($d = 0.54$, $P < 0.01$).

Population structure of *Croton* showed continuous size-class distribution with progressive decline in the proportion of individuals with increasing height. The proportion of individuals in the lower height classes were significantly higher than the remaining height classes and exhibited a typical inverse J- shaped curve. The proportion of individuals in the successive height classes showed an exponential decline ($d = 0.54$, $P < 0.01$).

In the population structure of *Podocarpus* individuals were represented in all size-classes but a progressive decline of the proportion of bigger individuals was noted resulting in a near exponential population curve ($d = 0.46$, $P < 0.01$). The proportion of individuals in the lowest height class was much higher than the rest of the classes exhibiting an inverted J-shape. About 5 % of the population was mature individuals (above 30 m in height), which also resulted in a longer tail to the right.

Population structure of *Polyscias* showed hardly any regeneration at the lowest and subsequent height classes. Individuals below 10 m in height were totally lacking implying regeneration was hampered and future self-replacement would be less likely. Higher proportion of individuals was represented in the upper most height class.

Population structure of *Pouteria* showed a non-continuous distribution. Higher proportion of individuals in the lowest height class followed by absence of individuals in the subsequent

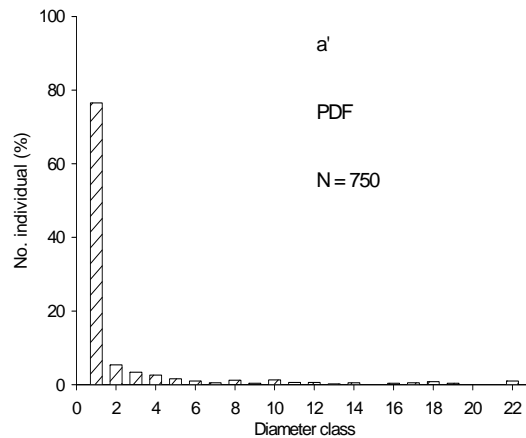
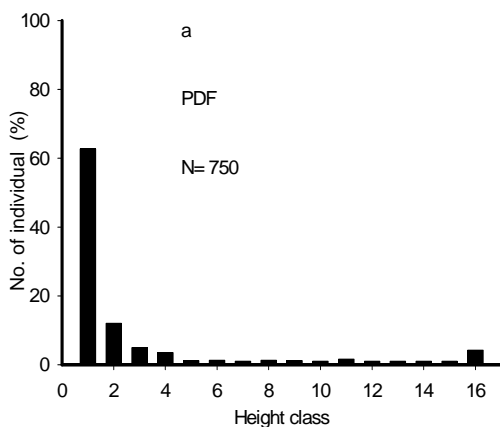
middle height classes and other upper height classes. Such plant population curve implies that regeneration was hampered or obstructed at several growth stages. Plant height between 14 - 30 m sizes are still hunted by loggers that always strive for any single standing trees of *Pouteria*. The over mature individuals (> 30 m in height) constituted larger proportions of the population, which could serve as good sources of seeds for natural regeneration of the species.

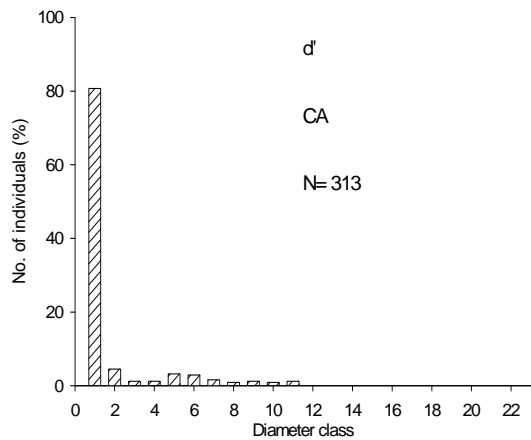
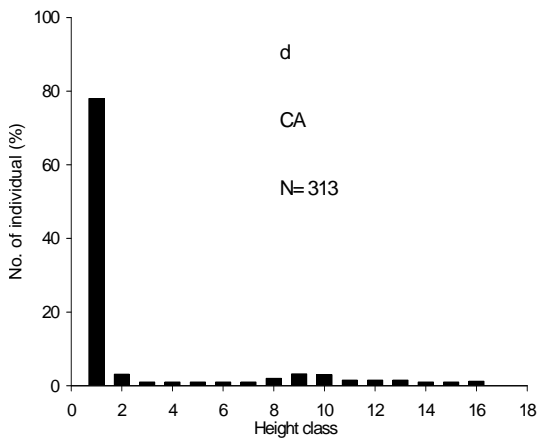
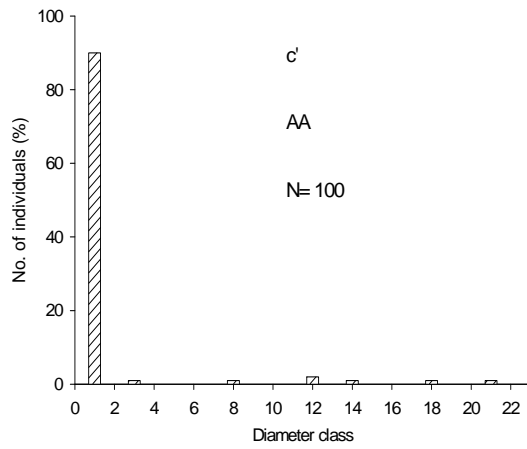
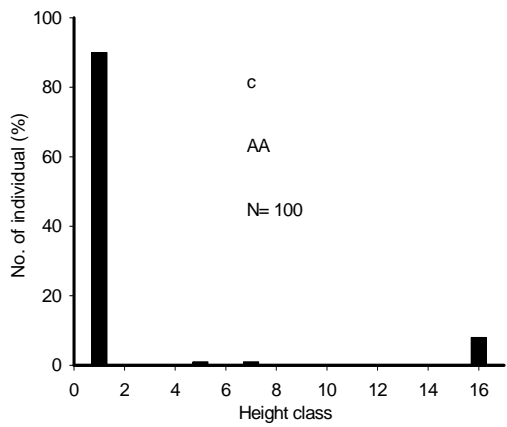
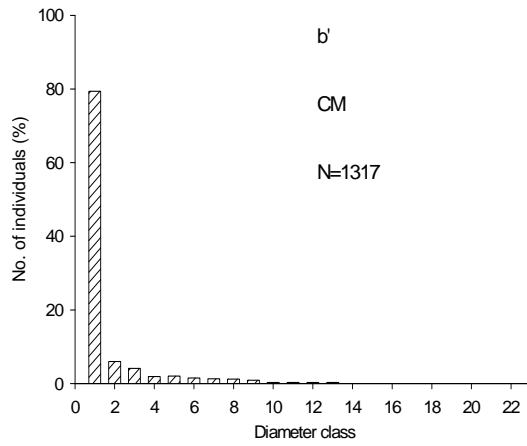
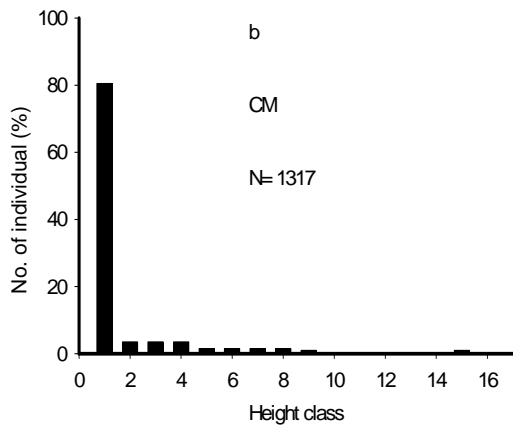
Population structure of *Prunus* showed continuous size class distribution with progressive decline of the proportion of individuals with increasing height. The proportion of individuals in the lower height classes were much higher than the rest of the height classes and exhibited an inverse J shape curve. The proportion of individuals in the successive height classes showed an exponential decline ($d = 0.71$, $P < 0.01$).

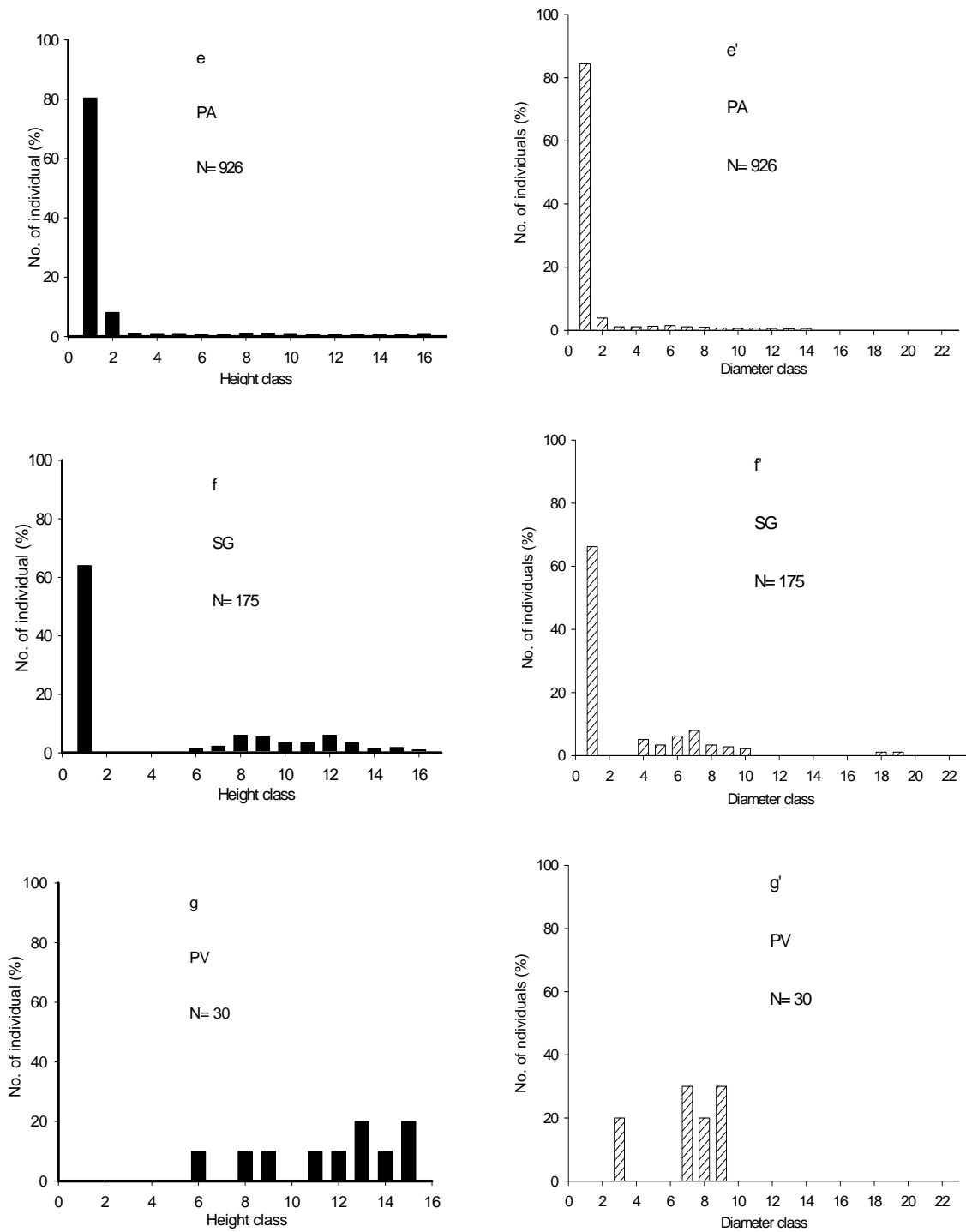
Population structure of *Syzygium* showed non-continuous distribution. Higher proportions of individuals in the lowest height class followed by the absence of any individual in the consecutive middle height classes, and relatively large proportion of mature individuals in the upper most height classes. Such population curve implies the lack of continuity in regeneration of the species as it is hampered somewhere in the middle height classes. The proportions of individuals in the upper height classes (height > 14 m) were quite large and this group could serve as major reproductive sources for natural regeneration of the species.

Spearman rank correlation test of the size class distributions for the seen studied species showed that *Podocarpus*, *Celtis*, *Croton* and *Prunus* had significant negative correlations implying the presence of larger proportions of smaller individuals than larger sized plants;

Pouteria and *Syzygium* had non-significant correlations implying haphazard/fluctuating populations; *Polyscias* had significant positive correlation implying the presence of the larger sized individuals than young plants. Generally, considering size-class distribution curve from regeneration point of view, three major groups can be recognized. These are (1) species with continues size-class distributions also called the inverse J-shape. Such population curve indicates the presence of sufficient and healthy regeneration of species; (2) species with non-continuous size-class distributions. In this group, the population curves showed higher proportions of individuals in the lowest height class, but absence of individuals in the subsequent middle height classes and few mature ones in the upper most height class. Species with such population curves exhibited variable and fluctuating patterns with hampered regeneration and; (3) species that showed hardly any regeneration in the lowest and middle height classes and represented by relatively higher proportions of large sized individuals in the population (e.g. *Polyscias*). Such species have serious problem for self-sustenance and thus at risk of local extermination.







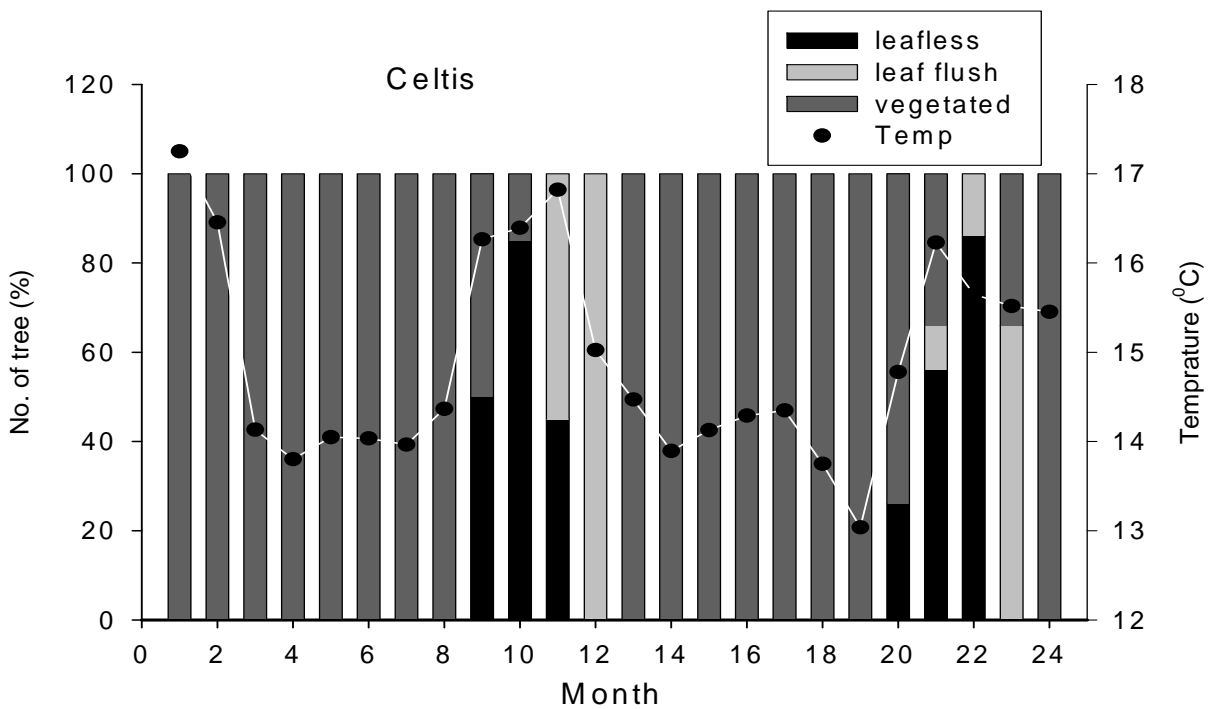
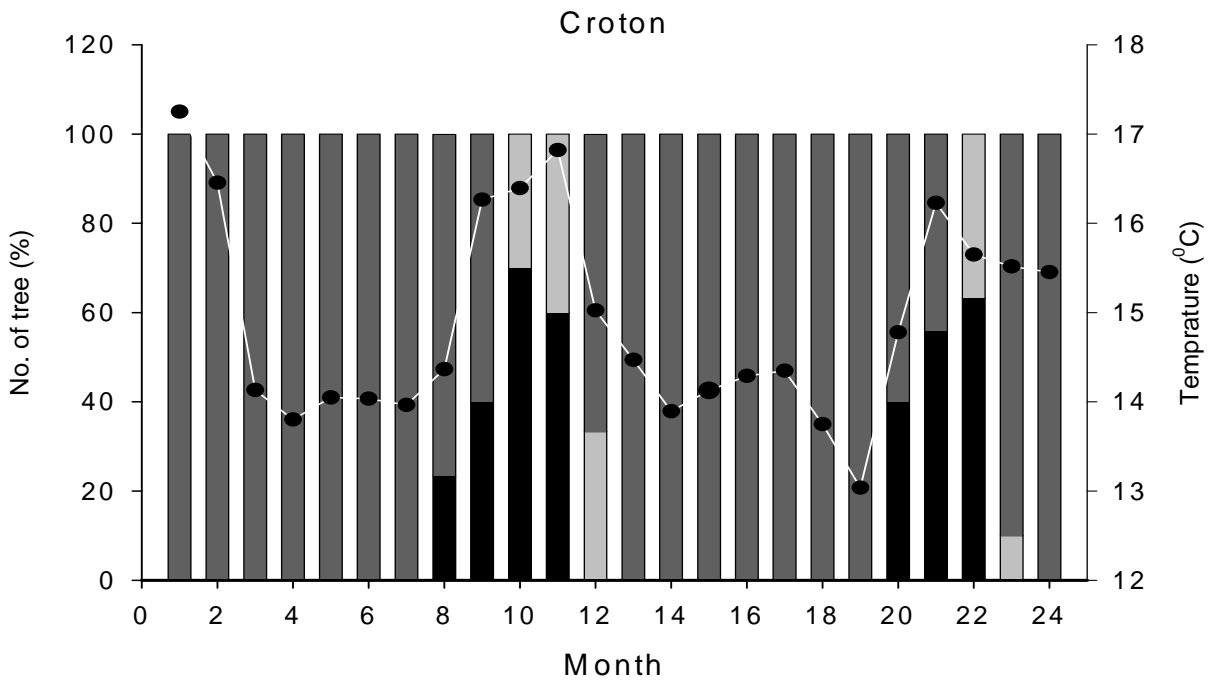
Figures 11a-g: Population structure of seven tree species in height-class distribution (shaded columns) and diameter-class distribution (hatched columns) in the Munessa-Shashemene Forest (species PDF = *Podocarpus falcatus*; AA = *Pouteria adolfi-friederici*; CA = *Celtis africana*; CM = *Croton macrostachyus*; PA = *Prunus africana*; SG = *Syzygium guineense*; and PV = *Polyscias fulva*).

5.4. Phenology of the Study Species

5.4.1. Leaf Phenology

Five of the studied tree species are evergreen with foliage (leaves) all year round. *Celtis* and *Croton* are deciduous and may shed their leaves annually (Figs. 12a-b). Both leaf fall and leaf flush were significantly seasonal ($P < 0.001$, $N = 12$ for both species). Leaf fall ranged between 26 and 86 % for *Celtis* and 23 and 70 % for *Croton* (Figs. 12a-b). Mean leaf fall dates of *Croton* and *Celtis* were non-significantly ($P = 0.19$) different, which also holds for leaf flush ($P = 0.72$) (Table 10). Moreover, leaflessness between *Celtis* and *Croton* were significantly ($r = 0.94$, $P < 0.001$) correlated.

Leaf fall of both *Celtis* and *Croton* began in January/February and continued until March/April. Peak leaf fall was in March towards the end of the long dry season (Table 10). The period of leaflessness was generally three to four months. Leaf fall and mean monthly temperature were significantly correlated for both species (*Croton*: $r = 0.55$, $P = 0.005$ or $R^2 = 0.31$, $P = 0.004$; *Celtis*: $r = 0.55$, $P = 0.005$ or $R^2 = 0.25$, $P = 0.01$). Leaf flush commenced in March for both species (except for *Celtis* in 2005 where new leaf growth started in April). Leaf flushing peaked in April (Table 10) coinciding with the end of the long dry season when the temperature was still high and the small rains started. Surprisingly, leaf flush was not significantly correlated with monthly rainfall ($r = 0.03$; $P = 0.81$ for *Celtis*; and $r = -0.02$, $P = 0.86$ for *Croton*). Leaf flush generally lasts for less than three months.



Figures 12: Leaf phenology of *Croton macrostachyus* and *Celtis africana* between June 2004 (month 1) to May 2006 (month 24) in the Munessa-Shashemene Forest (bars refer to leaf phenophases while line graphs indicate temperature).

Table 10: Mean date of leaf fall and leaf flush (Julian calendar followed by angular mean date), and peak leaf fall and leaf flush of *Croton macrostachyus* and *Celtis africana* (June 2004- May 2006) in the Munessa-Shashemene Forest

Species	Mean date of leaf fall	Mean date of leaf flush	Date of peak leaf fall	Date of peak leaf flush
<i>Celtis</i>	February 6 36.47 ⁰ ± 2.11	March 21 81 ⁰ ± 2.7	1 March	1 April
<i>Croton</i>	February 9 40.05 ⁰ ± 1.66	March 24 84.00 ⁰ ± 1.27	1 March	15 April

5.4.2. Flowering

Flowering phenology of six tree species is shown in Figures 13a-f. Tree species differed with respect to timing, frequency and the duration of the period of flowering. Most species flowered twice while *Polyscias* flowered in four peaks during the two years study period. Most species, therefore, exhibited annual flowering except *Polyscias*, which had shown continuous flowering at the population level. The percentages of flowering individuals between months were not uniform indicating significant seasonality in flowering was exhibited by species of *Pouteria* (P = 0.001), *Celtis* (P = 0.014), *Croton* (P < 0.001), *Prunus* (P < 0.001) and *Podocarpus* (P < 0.001) (Table 11). On the other hand, the percentages of flowering individuals between months were uniformly distributed, i.e. non-seasonal flowering exhibited by *Polyscias* (P = 0.46) and *Syzygium* (P = 0.31) (Table 11). Another test using chi-square analysis revealed that flowering in *Syzygium* had nevertheless significant variation between

months ($\chi^2 = 43.5$, $df = 9$, $P < 0.01$) and therefore significant seasonality can be assumed also for this species. This happened because one of the three populations located at the upper altitude/elevation exhibited a slightly longer/extended flowering period than the other two populations.

Mean dates of flowering of the study species were found to be considerably variable (Table 11). In most species significant variations in mean dates of flowering was observed (Table 11) except for *Polyscias* which flowered continuously. Flowering periods between the years were significantly correlated for *Pouteria* ($r = 0.73$, $P = 0.002$, $N = 12$), *Prunus* ($r = 0.75$, $P = 0.005$, $N = 12$), *Croton* ($r = 0.72$, $P = 0.007$, $N = 12$); strongly correlated but non-significantly for *Syzygium* ($r = 0.54$, $P = 0.05$, $N = 12$); negatively and non-significantly correlated for *Celtis* ($r = -0.36$, $P = 0.25$) and *Polyscias* ($r = -0.11$, $P = 0.72$, $N = 12$). Duration of the flowering periods in most species ranged from 2 to 7 months. Relatively short flowering period were observed for *Pouteria*, *Celtis*, and *Prunus*; whereas long flowering period were recorded for *Croton*, *Polyscias* and *Syzygium* (Table 12).

Flowering in *Celtis* was unimodal and varied between 3 to 73 % of the population (Figs. 13a-f). Flowering lasted from two to four months. The onset and period of flowering duration varied between the years. Flowering took place from July-August and September-December in 2004 and 2005, respectively. The peak of flowering was in August and September in 2004 and 2005, respectively. The onset and peak of flowering coincided with the long rainy season.

Flowering in *Croton* was unimodal and varied between 3 to 63 % of the population (Figs. 13a-f). Flowering lasted four to five months with pronounced single peak at the middle of the flowering period. The onset and peak of flowering period showed slight variation between the years. The onset of flowering coincided with the short dry season and peaked towards the end of the dry season and the beginning of the long rainy season.

Flowering in *Polyscias* was more or less continuous but with a bimodal pattern and varied between 4 to 100% of the population (Figs. 13a-f). Flowering extended for nine to eleven months. The onset of flowering and peaks varied between the years. Major peak flowering was in March and minor peak in November. However, flowering activity was low starting from the end of the long dry season until the middle of the long rainy season.

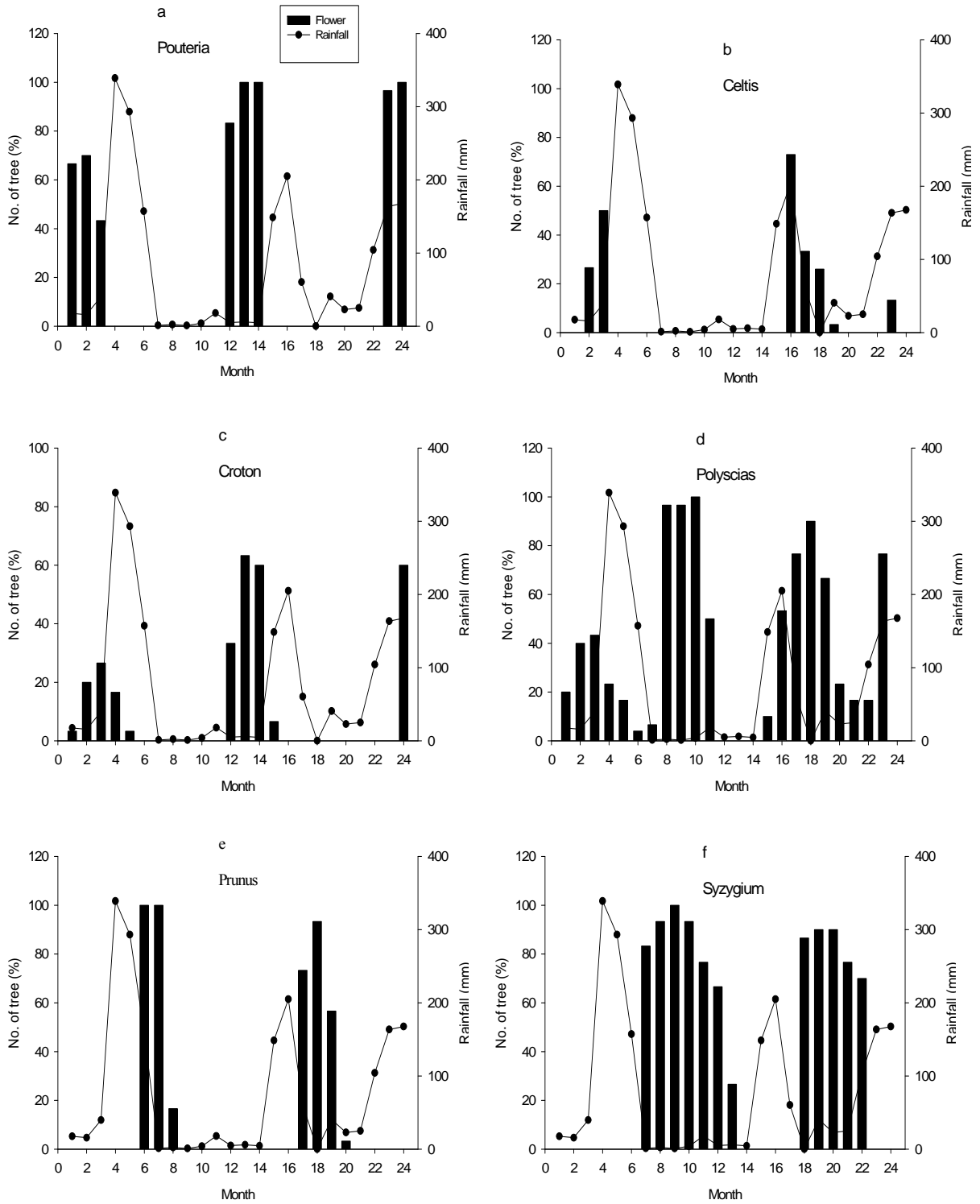
Flowering in *Pouteria* was unimodal and varied between 43 to 100 % of the population (Figs. 13a-f). Flowering lasted for three months and the period had no variation between the years. Onset of flowering was towards the end of the long dry season when the temperature was still high and sporadic small rains commenced. Peak flowering was at the beginning of the long rainy season.

Flowering in *Prunus* was unimodal and varied between 3 to 100 % of the population (Figs. 13a-f). Flowering lasted for three to four months. The onset and peak of flowering period was either simultaneously or had a lag period of one month after flower initiation. The onset and peak of flowering coincided with the long dry season.

Flowering in *Syzygium* was unimodal and the proportion varied between 26 to 100 % of the population (Figs. 13a-f). Flowering lasted for five to seven months duration. The peak of flowering was in February, and December- January in 2005 and 2005-2006, respectively. The onset and peak of flowering periods both coincided with the long dry season.

Expectedly, flowering and fruiting periods of each species were highly correlated in time. Flowering preceded fruiting significantly by four months for *Pouteria* ($r = 0.45$, $P = 0.04$), for *Polyscias* ($r = 0.57$, $P = 0.004$), and for *Celtis* ($r = 0.47$, $P = 0.01$); by three months for *Prunus* ($r = 0.52$, $P < 0.01$), and for *Syzygium* ($r = 0.40$, $P = 0.03$); and finally by two months for *Croton* ($r = 0.69$, $P < 0.01$). These time-spans are apparently caused by species-specific traits that, however, may be controlled by climate. Flowering was significantly positively correlated with mean monthly temperature with different time lag for *Pouteria* and *Polyscias* but significantly negative for *Celtis*, *Croton*, *Podocarpus*, *Prunus* and *Syzygium* (Table 13). Moreover, flowering was significantly positively correlated with monthly rainfall at different time lag for *Polyscias* and *Prunus* but significantly negative for *Pouteria*, *Croton* and *Syzygium* (Table 13).

Shannon diversity index showed that flowering pattern was diverse (less synchronized) among individuals of species of *Croton* (2.7) and *Polyscias* (2.7), whereas less diverse (highly synchronized) among the individuals of species *Celtis* (1.54) and *Prunus* (2.05), and intermediate for *Pouteria* (2.31) and *Syzygium* (2.41). High similarity is observed between *Pouteria* and *Croton* in synchronization of proportion of individuals flowering (Figs. 14).



Figures 13a-f: Percentage of flowering individuals of six tree species from June 2004 (month 1) to May 2006 (month 24) in the Munessa-Shashemene Forest (the bars refers to flowering while the line graphs to rainfall).

Table 11: Mean date of flowering and fruiting (Julian calendar followed by mean angular date $a \pm$ S.E.), Z- test for seasonality and concentration around the mean (r), in flowering and fruiting patterns of seven tree species in the Munessa-Shashemene Forest.

Species	Mean date of flowering		Mean date of fruiting	
	Mean angular date (a)	Z- test P-value and r	Mean angular date (a)	Z – test P-value and r
<i>Pouteria adolfi-friederici</i>	May 12 $162.51^0 \pm 2.2$ A	P < 0.001 $r = 0.75$	October 1 $301.4^0 \pm 3.8$ A	P = 0.718
<i>Celtis africana</i>	August 1 $245.0^0 \pm 4.0$ B	P = 0.001 $r = 0.94$	February 6 $36.62^0 \pm 2.9$ B	P = 0.393
<i>Croton macrostachyus</i>	May 27 $178.14^0 \pm 3.9$ C	P = 0.002 $r = 0.48$	February 9 $39.63^0 \pm 3.7$ BC	P = 0.053
<i>Syzygium guineense</i>	February 6 $66.0^0 \pm 2.9$ D	P = 0.139 $r = 0.45$	April 15 $137.5^0 \pm 3.1$ F	P = 0.002 $r = 0.001$
<i>Podocarpus falcatus</i> (female trees)	December 26 $356.6^0 \pm 2.2$ F	P < 0.001 $r = 0.9$	May 3 $155.36^0 \pm 5.5$ E	P = 0.329
<i>Prunus africana</i>	October 6 $306.29^0 \pm 1.9$ E	P < 0.001 $r = 0.9$	February 7 $67.71^0 \pm 5.9$ D	P = 0.005 $r = 0.22$
<i>Polyscias fulva</i> (population level)	May 18 $168.7^0 \pm 6.8$ AC	P = 0.893	May 12 $162.3^0 \pm 7.1$ EG	P = 0.203
Cycle 2 Individual level			March 2 $92.3^0 \pm 4.9$	
Cycle 1 Individual level			October 3 $303.65^0 \pm 3.3$	

(Different letters across columns show significant mean variation at P < 0.001)

Table 12: Onset, duration and peak of flowering and fruiting of seven tree species in the Munessa-Shashemene Forest

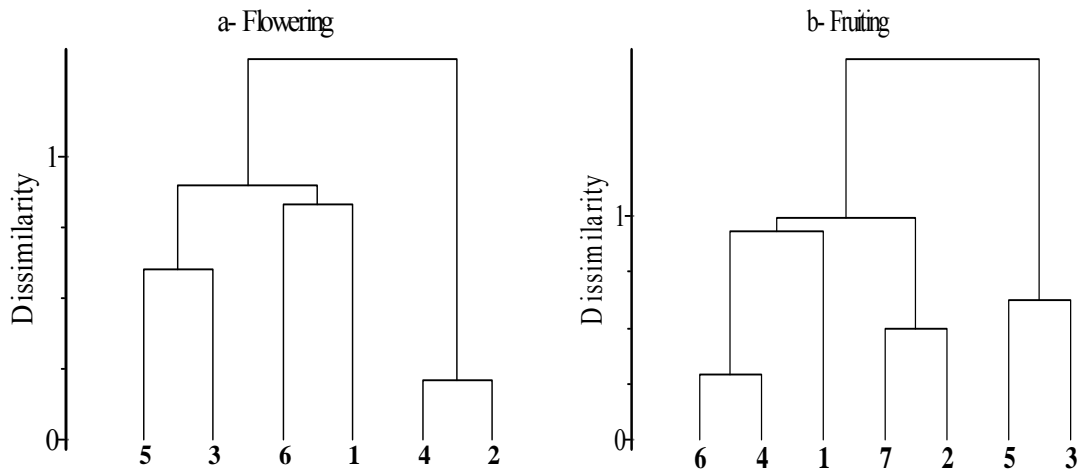
Species	Flowering			Fruiting		
	Date of first flowering	Duration of flowering (month)	Date of peak flowering	Date of first fruiting	Duration of fruiting (month)	Date of peak Fruiting
<i>Pouteria</i> (133 cm)	15 April	15 April-15 July (3)	1 May	15 September	15 September- July (6-11)	15 February
<i>Celtis</i> (49 cm)	1 August	1 August- November (2-4)	15 August	1 September	1 September-April (6-9)	15 January
<i>Croton</i> (53 cm)	1 May	1 May- September (4-5)	15 May	1 August	1 August -April (6-11)	1 January
<i>Podocarpus</i> (135cm)	1 November	1November- December (2)	1 November	1 June	1 June - May (12)	1 January
<i>Polyscias</i> (62 cm)	1 August	1 August - May (9-10)	1 April	1 September 1 March	1September– December (4) 1 March- July (4-5)	1December 1 May
<i>Prunus</i> (74 cm)	1 October	1 October- January (3-4)	1 November	15 December	15 December- May (4-5)	1 January
<i>Syzygium</i> (65 cm)	15 November	15 November- May (5-7)	1 January	1 March	1 March-August (4-7)	1 May

- Average DBH of the focal trees are given in parenthesis in the first column

Table 13: Cross correlation and time-lag for the highest significant correlation coefficient between flowering, fruiting and climate factors (June 2004 – May 2006) in the Munessa-Shashemene Forest (the highest correlation coefficients are highlighted).

Species	Flowering						Fruiting					
	Temperature			Rainfall			Temperature			Rainfall		
	Time lag month	r	p	Time lag month	r	p	Time lag month	r	p	Time lag month	r	p
<i>Pouteria</i>	2	0.62	P< 0.01	5	-0.55	0.01	2	0.62	0.001	0	-0.65	P< 0.01
<i>Celtis</i>	1	-0.43	0.03	ns	ns	ns	8	0.60	0.01	5	0.52	0.01
<i>Croton</i>	2	-0.56	P< 0.01	5	-0.48	0.03	10	-0.58	0.02	8	0.65	P< 0.01
<i>Podocarpus</i>	0	-0.44	0.02	ns	ns	ns	5	-0.60	P< 0.01	11	-0.78	P< 0.01
<i>Polyscias</i>	12	0.49	0.04	6	0.58	0.03	ns	ns	ns	10	0.75	P< 0.01
<i>Prunus</i>	1	-0.55	P< 0.01	2	0.64	P<0.01	1	0.72	P< 0.01	ns	ns	ns
<i>Syzygium</i>	4	-0.62	P< 0.01	0	-0.65	P<0.01	2	0.54	P< 0.01	8	0.78	P< 0.01

ns: non significant



Figures 14a & b: Cluster analyses showing flowering and fruiting similarities among seven indigenous tree species in the Munessa-Shashemene Forest (species: 1 = *Celtis*; 2 = *Croton*; 3 = *Syzygium*; 4 = *Pouteria*; 5 = *Polyscias*; 6 = *Prunus*; 7 = *Podocarpus*).

5.4.3. Fruiting

Results of fruiting patterns of the seven examined tree species presented in Figures 15a-g. Fruiting patterns as documented on annual basis were even more diverse among the species than patterns of flowering. One explicit fruiting period per year was recorded with *Prunus* and *Syzygium* while fruits were seen all year round or extended over several months in *Pouteria*, *Croton*, *Celtis*, *Podocarpus*; an exception again was *Polyscias* with two fruiting cycles per year. Fruiting periods were significantly correlated between the years for *Prunus* ($r = 0.53$, $P = 0.07$), *Polyscias* ($r = 0.50$, $P = 0.09$) and, strongly but not significantly for *Croton* ($r = 0.52$, $P = 0.078$). However, the fruiting periods of most species did not significantly correlated between the years due to the variations in the duration and the proportion of fruiting individuals.

Most species fruited twice while *Polyscias* fruited four times during the two years study period. The percentages of fruiting individuals between months were not uniform indicating significant seasonality in fruiting of *Prunus* ($P = 0.005$) and *Syzygium* ($P = 0.001$) (Table 11). On the other hand, the percentages of fruiting individuals between months were uniformly distributed indicating non-seasonal fruiting of *Pouteria*, *Celtis*, *Croton*, *Podocarpus* and *Polyscias* (Table 11). The mean dates of fruiting among the investigated species showed significant and considerable variations (Table 11).

Most species fruited from February to May (Table 12). Fruiting duration varied considerably between the species (Table 12). However, most species bore fruits for extended period exceeding six months and *Podocarpus* exhibited the longest fruiting period (Table 12). Fruiting significantly correlated with mean monthly temperature and positively for *Pouteria*, *Celtis*, *Prunus* and *Syzygium*; and negatively for *Croton* and *Podocarpus* (Table 13). On the other hand, fruiting correlated significantly with monthly rainfall positively for *Celtis*, *Croton*, *Polyscias* and *Syzygium*; and negatively for *Pouteria* and *Podocarpus* (Table 13). Similar patterns of fruiting and time-setting was observed with *Pouteria* and *Prunus* (Figs. 14). Fruiting in *Celtis* varied between 10 and 93 % of the population and a slight shift in fruiting period was observed between the years (Figs. 14). Fruiting was unimodal and lasted for 8-10 months. The peak fruiting period was in September in 2004 and in December in 2005 coinciding with the end of the long rainy season and the beginning of the long dry season, respectively.

Fruiting in *Croton* varied between 6 and 63 % of the population and had duration of six and eleven months in 2004-2005 and 2005-2006, respectively (Figs. 15). Fruiting was unimodal with a single extended peak in 2004-2005 and bimodal with pronounced two peaks in 2005-2006. Fruiting peaks coincided with the long dry season.

Fruiting in *Podocarpus* varied between 20 and 66 % of the population (Figs. 15). *Podocarpus* bore fruits year round with at least 20 % of the population in fruit at any one time. Fruiting was bimodal and the major peak was in January coinciding with the long dry season (Figs. 15). The percentage of individuals fruiting during the long dry season was relatively higher than during the long rainy season.

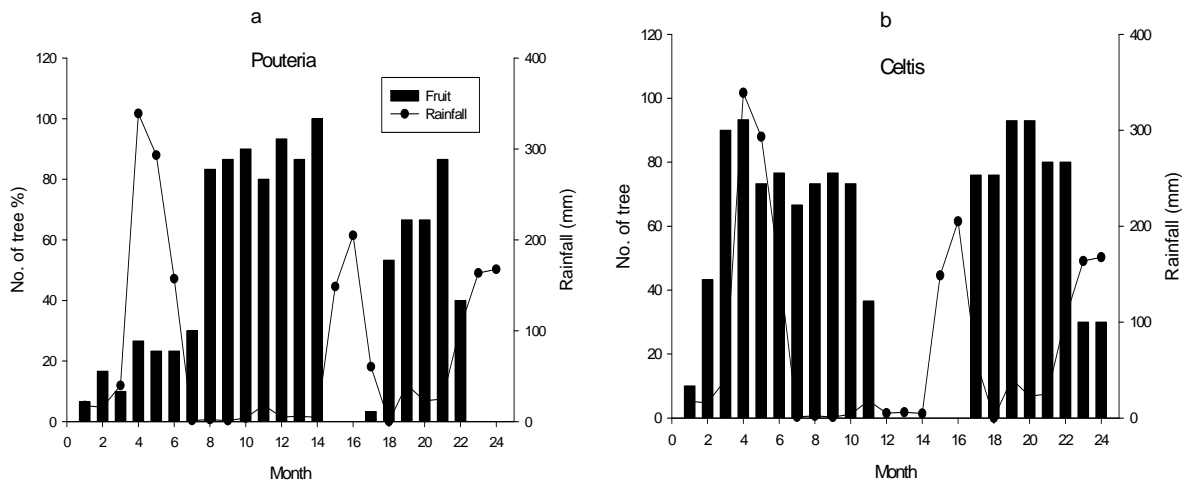
Fruiting in *Polyscias* varied between 26 and 93 % of the population (Figs. 15). Fruiting period lasted 4 to 5 months and exhibited four major fruiting events/cycles in two years period. The first cycle was from September to December 2004; the second from March to July 2005; the third from December to March 2005-2006 and the fourth commenced in April 2006. The transition from one fruiting cycle (episode) to the next cycle lasted for 1-3 months. Fruiting patterns were mix of both unimodal and bimodal. Fruiting occurred mainly during the long dry season and towards the beginning or end of the long rainy season.

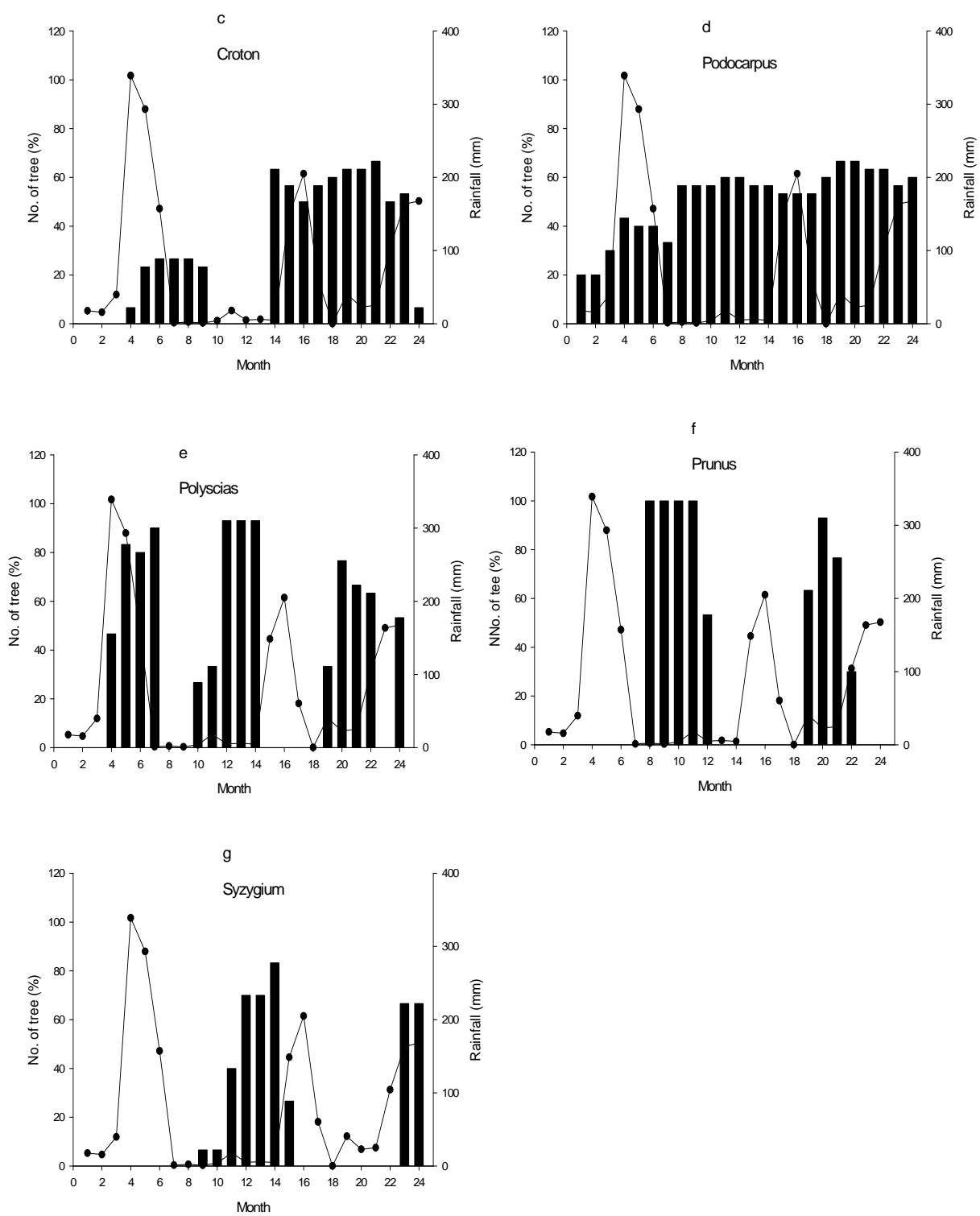
Fruiting in *Pouteria* varied between 3 and 100 % of the population and there was pronounced variation in durations of fruiting between the years (Figs. 15). Mature trees bore fruits for 12 months/all year round in 2004-2005, but only for five months in 2005-2006. Fruiting was bimodal in 2004-2005 and unimodal in 2005-2006. Fruiting peaked in February and the

proportion of fruiting individuals was relatively higher in the dry season and low or absent in the major rainy season.

Fruiting in *Prunus* varied between 30 to 100 % of the population and the duration was 4-5 months (Figs. 15). Fruiting was unimodal and the peak was in January. The peak fruiting and the first fruiting periods were either in the same month or the latter preceded by one month. The peak fruiting period coincided with the long dry season.

Fruiting in *Syzygium* varied between 6 and 83 % of the population and the duration was 4- 5 months (Figs. 15). Fruiting was unimodal, commenced in February i.e. around mid of the long dry season and continued until August- the long rainy season. The peak of fruiting was in May towards the end of the long dry season when temperature was still high and the small rains commenced.





Figures 15a-g: Percentage of fruiting individuals of seven tree species from June 2004 (month 1) to May 2006 (month 24) in the Munessa-Shashemene Forest (the bars refers to fruiting while the line graphs to rainfall).

6. DISCUSSION

6.1. Survival and Growth of Planted Seedlings Along a Light Gradient

6.1.1. Seedling Survival (or Mortality)

Striking differences were observed in survivorship of seedlings between light conditions and among species at the Munessa-Shashemene Forest. In five out of the six studied species, survival was negatively related to light and large proportion of seedlings survived in low- than in high- light. In a related study, Poorter and Hayashida-Oliver (2000) had reported higher rate of seedling survival in the understory shade than canopy gaps of a tropical forest in Bolivia due to dryness of the soils. Soil moisture content in tropical forest can be lower in gaps due to higher radiation loads, which leads to desiccation of the top soils through evaporation (Ashton, 1992; Poorter and Hayashida-Oliver, 2000). In contrast, seedling survival of pioneer species had been much lower in the understory of tropical forests than in forest gaps (Boot, 1996; Poorter and Hayashida-Oliver, 2000). Similarly, in the present study, the survival of *Croton* (one of the two pioneer species the other being *Celtis*) was low in low-light than in high-light. According to King (1994), the reason for poor survival of pioneer species in shaded understory of tropical forests is that leaf life-spans are too short to maintain a positive whole-plant carbon budget. Seedlings of *Celtis* had shown less survival in high light than in low light, survival rates being 78 % and 90 %, respectively. Seedlings grown in high light might have suffered from water stress.

Tree seedling mortality generally ranges between 3 and 96 % in tropical forests (Swaine, 1996). In an Ethiopian montane forest Getachew Tesfaye *et al.* (2002) reported upto 27 % seedling mortality. Seedling mortality of the present study (i.e. 31 % for all species) is thus

very close to what has been reported earlier. Causes of seedling mortality in tropical forests are diverse including, light and soil moisture/water limitations, herbivory and disease pathogens (Burselm, 1996; Poorter, 1999).

6.1.2. Seedling Growth

6.1.2.1. Relative importance of light, species and biomass

In tropical forest ecosystems, light is a highly variable and often limiting resource (Chazdon *et al.*, 1996; Souza and Valio, 2003). In the present study, all species had shown some degree of plasticity in terms of morphological and physiological traits in response to light, but species varied greatly in the amplitude and rate of change of particular traits. Other than RMR, all measured plant variables were significant between light conditions and among species. Size related variables such as total biomass, height, total leaf area and root length were more influenced by light. Leaf traits such as LMR, SLA, and LAR were significant between light conditions and among species, but inherent differences among species accounted for more variation than did light responses. Moreover, RGR and NAR were significant between light, species and plant biomass, which imply that relative growth was dependent on and change with plant size.

6.1.2.2. Light effects and intra-specific variation in growth

Seedling growth in tropical forests is enhanced by increased light (Denslow, 1987; Swaine, 1996; Chazdon *et al.*, 1996; Chandrashekara and Ramakrishanan, 1993; Souza and Valio, 2003). It is important to emphasize here that none of the studied six species grew better under

low light environment. For all species but *Pouteria* plant variables such as total plant biomass, height, total leaf area were largest in high light and the result agrees with other studies (King, 1994; Masresha Fetene and Yonas Feleke, 2001). For example, total plant biomass in high light for species of *Croton* was 165 and 58 fold greater than in low- and medium- light grown plants of the same species, respectively. Similarly, biomass increase for *Celtis* in high light was 33 and 15 fold greater than in low and in medium light, respectively. In addition, RGR and NAR were also highest in high light for species of *Prunus*, *Celtis* and *Croton*. The increased plant growth was expected because increased light results in increased assimilation rates and photosynthesis (Kitajima, 1994; Chazdon *et al.*, 1996; Poorter, 1999; Shulze *et al.*, 2002).

On the other hand, RGR and NAR were highest in medium light than in high light for species of *Podocarpus*, *Syzygium* and *Pouteria*. Again the result agrees with an earlier work of Poorter (1999) where RGR in most seedlings reached optimum at intermediate light level (25-50%), above which it declined. The possible explanations for the observed pattern, first, very high irradiance levels may lead to irreversible damage to the photosynthetic system (Poorter, 1999). Second, high irradiance around midday may lead to stomata closure, turgor loss and wilting of leaves (Chiariello *et al.*, 1987). This may have such an impact that even late in the afternoon light-saturated photosynthetic rates can be considerably lower compared to the morning (Poorter and Oberbauer, 1993). Although *Podocarpus* and *Syzygium* had shown highest RGR in medium light, their total plant biomasses were greatest in high light and the possible explanation for this unexpected deviation could be that the seedlings might have started at different initial biomass.

Leaf and root growth morphology in the present study followed the trends so characteristically found for sun and shade plants (Pompa and Bongers, 1988; Poorter, 1999). In a low light where light becomes a limiting factor, light interception per unit plant biomass would be increased by the production of relatively thin leaves with a high SLA (Poorter and Remkes, 1990; Reich *et al.*, 1998; Veneklass and Poorter, 1998). In the present study, SLA was more sensitive to change in light environment, i.e. higher SLA in low light that decreased with increased light condition. According to Lambers and Poorter (1992) and Poorter (1999), SLA was more determinate of leaf area than leaf weight in explaining inherent variation in relative growth rates. In a high light, water may become a limiting factor due to higher radiation loads, and therefore plants have to invest larger on root system in order to compensate for transpiration losses (Pompa and Bongers, 1988; Veneklaas and Poorter, 1998). In the present study, all the studied species increased their root length with increased light, hence greater plasticity in root morphology, which allowed the plants to explore a larger surface area and deeper soil layers for water.

On the other hand, light was not closely related in biomass allocations to leaf, stem, and root of some of the studied species. For example, light was not related to LMR, RMR and SMR in *Prunus*, *Croton* and *Syzygium*; LMR or SMR and RMR in *Celtis* and *Pouteria*; and RMR in *Podocarpus*. Reich *et al.* (1998), and Veneklaas and Poorter (1998) also found similar results from seedling growth studies in tropical rainforests. This may happen because in natural system variation in the allocation of biomass among plant tissue types may occur in response

to variation in the balance between the availability of several resources (water, nutrient, light) and in response to several stress factors (Grime, 1979 & 1994).

6.1.2.3. *Inter-specific variation in growth (RGR, NAR, LAR and SLA)*

Tree seedlings may differ in relative growth rate caused by habitat related variation (light, temperature, water and nutrients) or by biotic factors (competition, disease or herbivory) (Kitajima, 1994). Nevertheless, even when grown under identical conditions large interspecific variation in RGR exists (Poorter and Remkes, 1990). Relative growth rates of the studied species changed with change in light conditions. In high light, *Celtis* had the highest RGR, followed by *Croton*; in medium light *Syzygium* had the highest RGR, followed by *Celtis*; and in low light again *Celtis* showed the highest RGR, followed by *Syzygium*. *Prunus* maintained the same (third) ranking position under all light conditions. The lowest RGR were displayed by *Pouteria* and *Podocarpus*, with a slightly higher rate by *Syzygium* in high light. In medium- and low- light, lowest RGR were displayed by *Croton* and *Pouteria*, with a slightly higher rate by *Podocarpus*. Although a species with high RGR in low light also maintained high RGR in high light, there were changes in rank growth rates of the species. In a comparison of 15 rain forest tree species Poorter (1999) found that the species with highest growth rate at high light levels also showed the highest growth rates at low light levels, but Agyeman *et al.* (1999) found a negative correlation between growth rates at low and high light among different group of 15 tropical tree species. Cross-over effects in seedling growth rates studies can be strongly influenced by seedling size/ontogeny, selection of species, duration of growth and the selected range of light gradient (Kitajima and Bolker, 2003; Balderrama and Chazdon, 2005). The co-variations in growth rates between light conditions may have played a role in the co-existence

of the species in the study forest and related to their ecology of regeneration. *Celtis* and *Croton* are pioneer species with abundant seedlings successfully established in the edges of the forest and in relatively larger gaps than the rest of the study species (Gemedo Dalle and Masresha Fetene, 2004).

The changes observed in relative growth rates of the species were due to the interplay between the two major components- NAR (physiological plasticity) and LAR (morphological plasticity). In high light, *Croton* had two fold higher NAR than *Celtis*, but the latter grew faster than the former. This was perhaps due to higher LAR, as *Celtis* had three fold greater LAR than *Croton*, thus overriding the possible effect of higher NAR. In medium light, *Syzygium* grew faster than *Celtis* and the RGR of the former was two fold greater than that of the latter, and this might be mainly due to its high NAR. Here, the interspecific difference in RGR was more explained by NAR. However, in low light, *Celtis* grew faster than *Syzygium* largely because of its higher leaf morphological plasticity (higher SLA and LAR as well). Indeed, *Celtis* exhibited the highest SLA in all light conditions. The change in rank growth rate and shifting competitive hierarchy between these two species in low- and medium- light condition is of particular interest from gap regeneration point of view. Accordingly, during small gap colonization *Syzygium* would grow fastest because of its distinctive ability in accelerating its NAR five fold higher (as compared to the understorey seedlings of the same species), when *Celtis* accelerates its NAR only by two fold. The accumulation of seedling bank in the forest understorey by *Syzygium* (coupled with high survival in low light condition - 90 %) is advantageous to benefit from increased light during gap formation. Nevertheless, *Celtis* seems

to be the most successful competitor in terms of both relative growth (across a range of light gradient) and seedling abundance within the study forest.

Moreover, among studied species seedlings of *Celtis* had shown the highest plasticity that responded to ten out of the twelve morphological variables measured while seedlings of *Pouteria* responded the least. Indeed, *Pouteria* exhibited the least RGR among the shade tolerant species in all light conditions. According to Riddoch *et al.* (1991), and Bazzaz (1991), pioneer species can demonstrate a higher plasticity response to light during growth than shade tolerants. It is generally assumed that species with high phenotypic plasticity have a growth advantage under heterogeneous conditions such as in tropical forest ecosystems (Rice and Bazzaz, 1989). However, the expression of plasticity at any given time may be constrained by ontogeny, resource availability or by losses to herbivores and damage caused by falling branches (Bloom *et al.*, 1985).

Negative RGR was recorded only for *Croton* in low light and this was mainly due to low NAR and LAR, which imply that the understorey low light was below compensation point to maintain a positive carbon balance. In addition, RGR can be negative due to loss of carbon, leaf and stem parts (Poorter, 1990; Kitajima, 1994). I have no good explanation why *Croton*, the pioneer-deciduous species, had shown the lowest LAR in all light conditions, which is contrary to expectation. According to Reich *et al.* (1991) species with short leaf life spans tend to have higher LAR (also SLA and RGR) than those with long leaf life spans.

On the other hand, RGR of *Croton* was positive which increased by three and seventeen fold in medium- and in high- light in relation to its low-light grown plants, respectively. Similarly, NAR also increased by thirteen and seventeen fold in medium and high light, respectively. Such a remarkable increase in growth rates (RGR and LAR) by pioneer species across light gradient have been reported elsewhere from tropical forests (Pompa and Bongers, 1988; Boot, 1996). Such a drastic increase in RGR in high light for pioneers is advantageous because they can quickly preempt space and resources from shade tolerant species. In montane forests of Ethiopia, *Croton* mainly occupies gaps, roadsides and large clearings formed because of fire or logging disturbances (Getachew Tesfaye *et al.*, 2004; Getachew Tesfaye and Demel Teketay, 2005 b).

6.1.2.4. Growth predictors/determinants of relative growth rates

Contrasting results in relation to the determinants of RGR have been found in several earlier reports on tropical forests. According to Watling *et al.* (1997), Pompa and Bongers (1988), RGR in seedlings of rainforest species correlated better with NAR than LAR. On the other hand, RGR was correlated with LAR in some rainforest pioneer species (Pompa and Bongers, 1988). In related studies, Osunkoya *et al.* (1994) and Reich *et al.* (1998) found that RGR was correlated not only with NAR but also with LAR. Poorter (1999) reported that the different components of RGR become important at different irradiances or light levels. In the present study, considering all species there was stronger relationship between RGR and NAR in low- and high- light grown plants, indicating that differences in RGR were explained by the physiological component largely determined by photosynthetic activity of the plants. However, in medium light there was strong relationship between RGR and LAR indicating

that differences in RGR was better explained by the morphological plant trait. This positive correlation (in the latter case) was mainly due to leaf mass ratio, the fraction of plant biomass allocated to leaves and the specific leaf area, the ratio between leaf area and leaf weight. Nevertheless, in all light conditions NAR was strongly related to SLA as well as LMR indicating that both leaf morphology and leaf weight were important factors in determining growth. Similarly, Souza and Valio (2003) in their study of seedling growth of 15 Brazilian tropical tree species, reported that RGR was significantly related to NAR for plants grown in low light (natural shade) and in high light (full sun). So, based on our results it can be concluded that seedling RGR in tropical forest understorey is determined by NAR in low- and high- light environments and by LAR in medium light level.

The present study results suggest that species with highest growth rate in high light environment are also adapted higher plastic traits to grow fastest in low light. This was mainly due to the high plasticity responses in leaf morphology (LAR and SLA). While species that accumulate seedling bank in the understorey had traits to grow fastest in an intermediate light environment (small gap) due to its high plasticity in NAR. Further studies are needed to document the role of resource heterogeneity including soil moisture and nutrients in determining the observed patterns of seedling regeneration of these and other species. This study was limited to less than five months growth period of seedlings under natural conditions in degraded montane forest of Ethiopia. Further, long-term field data on tree seedling survival and growth could provide further insights into species regeneration responses during secondary succession and options for sustainable forest management.

6.2. Survival and Herbivory Damage on Naturally Regenerated Seedlings in Munessa-Shashemene Forest

6.2.1. Seedling Survival (or Mortality)

Seedlings of the study species showed pronounced variation in their survival rates. In other words, seedling mortality ranged between 11 and 67 percent per year. According to Becker (1983), seedling mortality in tropical forests can range between 16 and 19 percent per year. In Hawaiian rain forest seedling mortality through physical disturbance accounted 11 to 31 percent per year (Drake and Pratt, 2001). In a related study, Swaine (1996) reported that seedling mortality in tropical forests generally vary between 3 and 96 %. Similarly, Getachew Tesfaye *et al.* (2002) reported that seedling mortality in Harenna Forest from Ethiopia ranged between 11 and 50 %. The results of the present study are, therefore, comparable to what has been reported earlier from montane forest in Ethiopia and elsewhere in tropical forests.

The cause of seedling mortality was not investigated independently for every species as it was found difficult to differentiate the factor responsible for the death of every seedling. Seedling mortality was attributed to drought/soil moisture stress, low light/shade, and physical disturbances (such as tree/branch falls, trampling, and animal digging). Seedling mortality was higher during the dry season than in wet season, and this was attributed largely to drought (or soil water availability). Seedlings are more sensitive to drought, because they are shallow rooted and thus do not have access to lower soil layers with higher water potentials. In the study site, solar radiation was high during the dry season as a result plants were exposed to considerable soil moisture stress and vapor pressure deficit (Fritzsche *et al.*, 2006). Soil water stress in dry season was also indicated by low leaf water potentials in trees (Fetene and Beck, 2004; Fritzsche *et al.*, 2006). The insufficient soil moisture coupled with increased

transpiration due to high leaf area could result in the death of seedlings during the dry season since several dead, dried otherwise intact or normally rooted seedlings were observed. From other field studies, it is known that seedling mortality rates peak during the dry season in dry, moist and even wet tropical forests (Howe, 1990; Turner, 1990; Poorter and Hayashida-Oliver, 2000). Furthermore, seedling death during dry season can occur both as a direct result of drought stress, or because drought can exacerbate the effects of non-drought factors such as pathogens, herbivores, or competitors (e.g. Turner, 1990; Veenendaal *et al.*, 1995; Condit *et al.*, 1995).

In addition, the importance of drought (or soil water stress) in seedling survival was further supported by the experiment with transplanted seedlings at the study site, which showed consistently higher seedling mortality in high light environment than in low light condition. Accordingly, seedling mortality of the study species increased with increasing light environment (where there is high radiation load and soil moisture stress) except for *Croton*. Other factors such as seedling density and age are likely to magnify the impact of drought on seedlings (Poorter and Oliver, 2000). In the present study, however, seedling mortality rates were not correlated to their densities within the forest.

Tree species exhibit differential characters in response to soil moisture variation in tropical forests and this can be explained by species-habitat associations (e.g. ridge, slope, river banks, and altitude) (Webb and Peart, 2000). In the forest understorey, *Syzygium* showed the highest mortality that accounted for 67 percent of its seedling population. In a related study, Getachew Tesfaye *et al.* (2002) in their study of 14 tree species in a montane forest from Ethiopia

reported that the same species accounted the highest seedling mortality rate (50 % of its population). The high seedling mortality in *Syzygium* could be accounted to its high moisture loving character (or low drought tolerance) since the mother trees are naturally associated to riverbanks where the soil moisture is relatively high. In addition, the low-light grown seedlings of *Syzygium* showed the highest survival and the converse is true. Some authors (e.g. Friis, 1992) recognized *Syzygium* as riverine species of the montane forests of Ethiopia. On the other hand, low seedling mortality in *Podocarpus* may be explained with its capacity to withstand dry conditions. This may include, reducing sap flow in the stem and transpiration during the dry season through low stomatal conductance and shifting water uptake to deeper soils layer at times of drought (Fetene and Beck, 2004; Fritzsche *et al.*, 2006).

Seedling mortality can also be affected by inter-annual fluctuation of rainfall in tropical montane forests (Garwood, 1983). In the present study, seedling mortality varied significantly between the years and, mortality was higher during the first year than in the second year. The total annual rainfalls at the study site were about 900 mm and 1000 mm during the first and the second years, respectively. More importantly, in the earlier year the dry season lasted for about eight months whereas in the following year it lasted only for five months (monthly rainfall < 25 mm). In general, drought (soil water availability), physical disturbance, and understorey light environments were found to be the major factors responsible for the death of tree seedlings in the forest understorey.

6.2.2. Seedling Herbivory

Herbivory plays an important role in seedling dynamics and its impacts have become an issue of concern in many places (Crawley, 1997). In some instances, like the Harena forest in southeastern Ethiopia, livestock grazing have been regarded as a major factor affecting tree seedling population (Getachew Tesfaye *et al.*, 2002). Mammalian herbivory can reduce or even eliminate woody plant seedling regeneration through removal of leaf and stem tissue. Herbivory involves browsing and trampling which both cause leaf losses that can lower growth and increase mortality of seedlings (Hendrix, 1988). Primary herbivore damages weaken an individual, increase its susceptibility to drought, insects, or pathogens, and decrease its competitive abilities.

In the present study, stumps of all tagged seedlings were examined and those individuals that had shown partial or complete defoliation were considered as damage by herbivores. Most of the species investigated were found to be prone to herbivory. In most cases browsed/grazed seedlings recovered from herbivore damage, others were repeatedly browsed and several others were unable to recover. In addition to defoliation of the individual plants in most cases, the growing tips of the seedlings were consumed/removed together with their leaves. Majority of the defoliated individuals that survived decreased in size. Seedlings of *Celtis*, *Pouteria*, *Prunus* and *Syzygium* species exhibited some kind of re-growth behavior after herbivory damage. The extent of re-growth following herbivory are usually proportional to the amount of tissue lost, and for many species there is a threshold level below which re-growth can be adversely hampered (Hendrix, 1988). The re-growth behavior suggests that the plants have developed the ability to compensate to the selection pressure. However, opinion varies about

the degree to which plants can compensate for or tolerate loss of vegetative tissue, and therefore about the impact of herbivory on plant performance (Hendrix, 1988; Horvitz and Schemske, 2002). The effect is strong for individuals from which all leaves are removed, and after repeated leaf removals.

Herbivory rate varied pronouncedly among species and ranged from 0 to 56 % at the Munessa-Shashemene Forest. Similarly, Getachew Tesfaye *et al.* (2002) have reported herbivory rates between 0 and 83 % from the Hareenna Forest. The rate of herbivory in tropical forests can be highly variable and in some season and places, the whole cohorts or a significant proportion of the population can be lost to herbivory while in others the effect may seem unimportant (Crawley, 1997). According to Pietrzykowski *et al.* (2003), many factors affect the extent to which seedlings are eaten that include structure, morphology, primary and secondary metabolites, all of which influence whether a plant is a potential food item and the probability of it being visited. Seedlings of *Podocarpus* and *Croton* remained unaffected by herbivory and this can be accounted to their characteristic tough leaves that deter animals from browsing.

In the present study, herbivory was significantly higher in the dry season than in the wet season. The high herbivory rate in the dry season can be accounted to the huge grazing activities by livestock. The local people graze their livestock deep into the forest during the dry season when palatable grasses become highly scarce from the surrounding. In wet season as the people are engaged in crop farming activities, livestock are often kept around homestead and in peripheral areas. Currently more than 25,000 livestock are grazing through the portion of the Munessa-Shashemene Forest where the study was conducted (MoARD, Personal

communication). Wet season herbivory in the forest was attributed to both wild animals (e.g. Gazelle, Bushbuck and Mountain Nyala) and insect herbivores (personal observation). Massive infestation of *Celtis* trees by insect herbivores during rainy season was noted in several occasions within the forest. All infected trees became leafless soon after the invasion.

Among studied species, *Celtis* had shown the highest seedling herbivory damage, which accounted nearly 55 percent of its populations. *Prunus* and *Syzygium* had also considerably high proportion of seedling damage accounting 49 and 42 percent, respectively. Similarly, these species had shown comparable herbivory rate from the Harenna Forest (Getachew Tesfaye *et al.*, 2002). The study result supported that herbivory can influence seedling survival directly or indirectly as 38 to 50 percent of the browsed/grazed seedlings died after initial exposure. Herbivory may directly increase mortality by providing entry for pathogens (Pietrzykowski *et al.*, 2003)

In conclusion, herbivory was a major factor affecting seedling population dynamics in the study forest. The species exhibited either an adaptive defense mechanism or compensatory regrowth to herbivory damage. The species ability to develop defense mechanism or response to herbivory damage could influence the population dynamics and ultimately the composition and structure of the forest through differential attrition in seedling populations.

6.3. Density, Distribution and Population Structure of the Study Species

6.3.1. Seedling Density and Distribution Along the Altitudinal Gradient

The investigated tree species had numerous seedlings in the Munessa-Shashemene Forest except for *Polyscias*. The lack of any seedling of *Polyscias* may partially attributed to limitation of environment conducive for the seeds to germinate such as severe disturbance of the canopy together with the forest soil. *Polyscias* was among eleven tree species that regenerated on disturbed soils of logged fields at the Haremma Forest (Getachew Tesfaye and Demel Teketay, 2005b). In the present study, seedling densities varied significantly among species. The presence of abundant seedlings on the forest floor is in consistence with previous reports from other afro-montane forests in Ethiopia (Demel Teketay, 1997; Getachew Tesfaye *et al.*, 2002) and tropical rain forests (Swaine, 1996; Whitmore, 1996). The accumulation of seedling bank under forest canopy is known to be the major regeneration route of climax tree species (Demel Teketay, 1997). In the present study, large numbers of seedlings were observed for the climax species (*Prunus* and *Pouteria*) in the shaded forest canopy suggesting that seedling bank accumulation is the major regeneration strategy. The ripe seeds of most climax species germinate shortly after dispersal and thereafter show slow growth rates in the forest understorey. According to Demel Teketay and Granstorm (1995), these species lack the reserves for longevity as seeds in the soils (soil seed banks). Similarly, several other tree species of afro-montane forests in Ethiopia (e.g. *Ocotea*, *Filicium*, *Olea capensis*, *Pouteria altissima*, *Teclea*) follow seedling bank regeneration pathway for canopy replacement (Getachew Tesfaye *et al.*, 2002; Kumelachew Yeshitela and Taye Bekele, 2003).

According to Swaine and Whitmore (1988), pioneer/light demanding species accumulate their seeds in the soil to germinate and establish only after gap formation within the canopy. The two pioneers, *Celtis* and *Croton* having seed bank densities of 28 - 31 seeds/m² (data not shown) in the Munessa-Shashemene Forest regenerated in gaps. At lower elevation of the forest canopy gaps were more frequent with quite a number of patchy successional development due to selective tree felling for the purposes of timber and construction.

Seedling density was highest for *Prunus* and *Celtis* due to the high reproductive potential of the mother trees. However, about 42- 61 % of the seedling population of these species were lost on annual basis because of drought or soil moisture stress, disturbance and herbivory damage. *Syzygium* had shown the lowest seedling density, which could be accounted to the low survival rate in the forest understorey (only 33 % year⁻¹). The low seedling density in *Podocarpus* can be attributed to its seed dormancy and reserve seed accumulation in the soils (Demel Teketay and Granstorm, 1995). According to Legesse Negash (1995), the hard seed coat in *Podocarpus* prevents high seed germination. In the present study, *Podocarpus* seeds were found highly dormant where only 2 % germination rate (data not shown) was achieved over two years period. Unlike the many other shade-tolerant species that lacks seed reserves in forest soils, *Podocarpus* was found as one of the major seed bank forming species with a density of 355 seeds/m² (data not shown) in the Munessa-Shashemene Forest. The relatively low seedling density of *Podocarpus* in the Munessa-Shashemene Forest is compensated by its highest seedling survival rates (88 % per year) and its characteristic defenses to herbivory.

The distribution of seedlings along the altitudinal gradient showed marked variations among species. *Podocarpus* and *Prunus* showed wider distribution and occurred along the entire altitudinal range within the forest. On the other hand, *Pouteria*, *Celtis* and *Syzygium* had narrow distribution and occurred in lower elevation of the forest. At the upper altitudes of the Munessa-Shashemene Forest humid climate conditions (low temperature, rainfall and high humidity) prevails which may restrict the distribution of some of these species.

6.3.2. Tree and Sapling Density, and Their Distribution Along the Altitudinal Gradient

Tree and sapling densities varied significantly among species. *Podocarpus* showed the highest tree and sapling density, followed by *Croton*. *Podocarpus* is the dominant tree species of the dry afro-montane forests in Ethiopia (Friis, 1992). Although most of the standing trees are buttressed and over-matured ones, *Podocarpus* constituted the largest proportion of trees in the Munessa-Shashemene Forest across the entire range of altitude. *Podocarpus* has comparable tree densities in forests of Munessa-Shashemene, Harena (Getachew Tesfaye and Demel Teketay, 2005a) and Dindin (Simon Shibru and Girma Balcha, 2004), but lower than forests of Wof-Washa and Chilimo (Tamrat Bekele, 1994). In the present study, *Polyscias* and *Pouteria* showed the lowest tree densities. Spatial distances between the mother trees on average were 63 m and 60 m (data not shown) for *Polyscias* and *Pouteria*, respectively, implying high fragmentation among the reproductive individuals. *Polyscias* had also low tree density in forests of Wof-Washa (Tamrat Bekele, 1994) and Dindin (Simon Shibru and Girma Balcha, 2004). *Prunus* had a higher tree density in the Munessa-Shashemene than in forests of Menagesha, Chilimo and Jibat (Tamrat Bekele, 1994), and Dindin (Simon Shibru and Girma Balcha, 2004). On the other hand, *Syzygium* had shown low tree density in Munessa-

Shashemene than the Jibat forest (Tamrat Bekele, 1994). *Celtis* had comparable tree density in forests of Munessa-Shashemene and Dindin (Simon Shibru and Girma Balcha, 2004). *Croton* had higher tree density in Munessa-Shashemene than Dindin forest (Simon Shibru and Girma Balcha, 2004). The variation in species densities among the dry afro-montane forests of Ethiopia indicates the level of utilization of the species, nature of disturbance and ecology. In general, the tree densities reported in the present study are within the broad range reported from the other dry afro-montane forests of Ethiopia.

6.3.3. Population Structure of the Seven Tree Species

The pattern of size-class distribution of seedlings, saplings and mature individuals can provide good indication about the overall regeneration status of a species and the level of disturbance in the forest. Tree species examined showed considerable variations in their size-class distributions. Plant population structure of *Celtis* had shown highest proportion of individuals at the lowest height class and missing of individuals in the middle height classes at Gara-Ades Forest (Demel Teketay, 1997). On the other hand, *Celtis* exhibited highest proportion of individuals at the lowest height class and a gradual decrease towards the upper height classes in the Munessa-Shashemene Forest. The good representation of individuals in all size classes coupled with its high seedling density and growth rate would enable *Celtis* to be another potential expanding species in the Munessa-Shashemene Forest. However, possible problems in regeneration of *Celtis* may come from excessive browsing/grazing of the understorey seedlings. The fruits from trees of *Celtis* were also important food sources for at least 13 bird species in the Munessa-Shashemene Forest (Getachew Tesfaye, unpublished data). All the thirteen bird species picked the fruits and swallowed the pulp with the seeds inside. The role of

frugivore animals to seed germination and regeneration of the species need further investigation.

Plant population structure of *Croton* had higher proportion of individuals in the lower height classes and missing of individuals in the middle and towards upper height classes in forests of Gara-Ades and Harena (Demel Teketay, 1997; Getachew Tesfaye *et al.*, 2002). On the other hand, *Croton* showed continuous representation of individuals in all height classes at Munessa-Shashemene Forest. Such good regeneration of the pioneer species may suggest that the forest has been severely disturbed in the past due to past logging activities (Lundgren, 1971). *Croton* seems to be one of the most expanding species as evidenced from its seedling and tree densities, and the population structure.

Podocarpus exhibited continuous size-class distribution and an inverted J-shaped curve in several montane forests (Geldenhyus, 1993; Demel Teketay 1997; Feyera Senbeta and Demel Teketay, 2003; Feyera Senbeta, 2006). Similarly, *Podocarpus* showed highest proportion of individuals in the lowest height class and a gradual decrease towards the larger size classes in the Munessa-Shashemene Forest. *Podocarpus* therefore generally displays a healthy regeneration in afro-montane forests in Ethiopia, though individual trees of middle and upper height classes are still under pressure from selective cutting and logging (Getachew Tesfaye *et al.*, 2002). The low seedling density coupled with its low seed germination rate (data not shown) of *Podocarpus* in the Munessa-Shashemene Forest probably indicates that it may not be able to maintain the current tree population level sufficiently in the future. However, detailed evaluation of the population projection matrix is necessary before arriving to concrete

conclusion. In any case, tree population in *Podocarpus* is likely to decrease in the future, as it is the only remaining target species hunted by illegal loggers (after *Pouteria*). Nevertheless, the longer tail to the right in its size-class distribution suggests the presence of good proportion of reproductive individuals that can actively supply seeds for regeneration of the species.

According to Getachew Tesfaye *et al.* (2002), the population structure of *Polyscias* had the highest proportion of individuals at the lowest height class and missing of individuals at one of the intermediate height class at Harena Forest. On the other hand, *Polyscias* lacks representation of individuals at the lowest and intermediate height classes in the Munessa-Shashemene Forest. The lack of seedlings and young individuals in the forest coupled with the low tree density would probably aggravate the local extermination of *Polyscias* from the forest interior, if not from the forest margins. In addition, the absence of any germinated seeds of *Polyscias* from soil seed banks of the Munessa-Shashemene Forest provoked the question whether the reproductive individuals are producing viable seeds or not. Unfortunately, the attempts to collect ripe/mature seeds directly from the trees were unsuccessful and ended up in removal of unripe fruits/seeds.

Plant population structure of *Pouteria* had highest proportion of individuals at the lowest height class and missing of individuals in the middle height classes at Harena forest (Getachew Tesfaye *et al.*, 2002). Similarly, *Pouteria* showed highest proportion of individuals at the lowest height class and missing of individuals at several intermediate classes in the Munessa-Shashemene Forest. Regeneration of the species appears to be hampered (obstructed) as there was no sapling or young trees (between 14- 30 m height) encountered in the forest.

This was attributed to the excessive selective hunting of trees for commercial timber. The few remaining trees of *Pouteria* in the Munessa-Shashemene Forest were left standing there only because they are extremely buttressed, difficult to cut manually and to saw them through the dark, thus making it impossible to smuggle or escape the attention of the forest guards. *Pouteria* stands as the number one (priority) timber species and the second most harvested in the country only surpassed by *Podocarpus* (Breitenbach, 1963; Legesse Negash, 1995; Getachew Tesfaye and Demel Teketay, 2005b). The overall regeneration status of *Pouteria* is alarming because those few old and over-mature trees are standing on highly fragile land, fragmented and with narrow altitudinal range. The seedling density in the understorey was relatively low due to high mortality and grazing effect. In addition, seedlings of *Pouteria* showed the lowest relative growth rate and plasticity response to changing light environment. If the current pressure from illegal loggers on *Pouteria* in the Munessa-Shashemene Forest continues unabated, coupled with problems mentioned above, the species will disappear locally from the forest in near future. It is highly important, therefore, to protect those few remaining mature individuals of the species as a potential seed sources for any conservation effort deemed in the future.

Plant population structure of *Prunus* had highest proportion of individuals in the lowest height class and no individuals in the subsequent middle and upper height classes in forests of Menagesha and Harena (Demel Teketay, 1997; Getachew Tesfaye *et al.*, 2002). On the other hand, *Prunus* showed highest proportion of individuals at the lowest height class and a gradual decrease towards the upper height classes in the Munessa-Shashemene Forest. The level of utilization of this species in the Munessa-Shashemene Forest may be attributed to the good

regeneration status exhibited by *Prunus* to the fact that it was not (at least so far) the favorite species of illegal loggers. Unlike many other localities, the bark or any usable part from this species has not been extracted for commercial purposes.

According to Getachew Tesfaye *et al.* (2002) population structure of *Syzygium* had the highest proportion of individuals at the lowest height class and missing of individuals at several intermediate and upper height classes at Harena forest. A similar population structure was recorded for *Syzygium* in the study site. This was attributed to tree cutting for timber, construction and other household activities. In addition, *Syzygium* was recognized as having major problems of regeneration in the Munessa-Shashemene Forest as evidenced by its low seedling density, high seedling mortality and herbivory damage, and low number of seedlings per mature tree.

The population structure of tropical forest tree species have been found variable depending on the level of utilization and history of the forest (Saxena *et al.*, 1984). The inverse J-shape curve observed in *Podocarpus*, *Prunus*, *Celtis* and *Croton* in the Munessa-Shashemene Forest indicates that there exists healthy regeneration. Such population structure is typically characteristics of many tropical forest tree species (Cesar, 1992; Poorter *et al.*, 1996). In contrast, the patterns of population structure exhibited by *Pouteria*, *Syzygium* and *Polyscias* indicated a discontinuos or hampered regeneration. Bongers *et al.* (1988) have also described a similar size-class distribution pattern from tropical rain forests.

In parts of the Munessa-Shashemene Forest where natural gaps comprise a small proportion and disturbance was limited, such as the middle elevation, tree species exhibited strong negative correlation to size-class distribution thus successfully regenerating. On the other hand, at the lower elevation due to past and current human disturbance effect (past logging took place about 50-60 years ago) (Lundgren, 1971), tree populations exhibited weak negative correlations to size-class distributions indicating poor regeneration. Thus, human influence in this region goes to an extent that regeneration of major canopy tree species have been substantially altered, and the legacy of this continues today. The lower elevation part of the forest zone has mainly given way from primary forest to secondary type.

6.3.4. Comparison of Seedling Densities and Distributions between Munessa-Shashemene and Three Other Afromontane Forests of Ethiopia

Table 14 shows the mean seedling densities of the investigated species in four dry afromontane forests in Ethiopia. The direct comparison of seedling densities *per se* in the different forests would be difficult, as the minimum size of seedlings recorded was not reported by the different sources. In the present study, seedling investigation was carried out to plant size above 5 cm in height. Seedling densities of *Celtis*, *Croton* and *Prunus* were relatively higher in munessa-shashemene than the three other forests. The presence of higher seedling densities of *Celtis* and *Croton* is an indicative of the magnitude of disturbance in the munessa-shashemene. As the forest is located very close to high way road for market outlets, illegal tree cutting and logging which in turn resulted in large canopy disturbance have been the norm.

Table 14: Comparison of mean seedling densities in Munessa-Shashemene and three other afro-montane forests of Ethiopia

Species	Menagesha	Gara-Ades	Harena	Munessa-Shashemene
<i>Croton</i>	100	2	496	3412
<i>Podocarpus</i>	874	616	1065	171
<i>Prunus</i>	-	627	373	5333
<i>Celtis</i>	-	122	-	7660
<i>Pouteria</i>			284	766

(Source: Demel Teketay, 1997; Getachew Tesfaye *et al.*, 2002)

Table 15 shows the distribution of seedlings along an altitudinal gradient in forests of Menagesha, Gara-Ades, Harena and Munessa-Shashemene. Seedlings of *Pouteria* and *Syzygium* showed more or less similar altitudinal distributions in forests of Harena and Munessa-Shashemene. Seedlings of *Croton* showed a wider range of altitudinal distribution in the Harena than in the other three Forests and this is attributed to the broad variation in altitudinal elevation between the sites. Seedlings of *Celtis* occupied slightly higher altitudes in Gara-Ades than in Munessa-Shashemene Forest and this can be attributed to the variations in rainfall between the sites. Seedlings of *Podocarpus* occupied lower elevations in the Harena Forest than in the Munessa-Shashemene Forest and this can be attributed to the relatively moist or humid environment prevailing in the upper portion of the Harena Forest (Lisanework Nigatu and Mesfin Tadesse, 1989).

Table 15: Comparison of seedling distributions along altitudes in Munessa-Shashemene and Three Other Afromontane Forests of Ethiopia.

Species	Gara-Ades	Menagesha	Harena	Munessa-Shashemene
<i>Celtis</i>	2250- 2450 m	-	-	2100- 2300 m
<i>Croton</i>	2250- 2500 m	-	1500- 2300 m	2100- 2400 m
<i>Podocarpus</i>	2250- 2500 m	2350- 2750 m	1500- 2100 m	2100- 2700 m
<i>Pouteria</i>	-	-	2100- 2300 m	2100- 2300 m
<i>Prunus</i>	-	2400- 2750 m	2000- 2400 m	2100- 2700 m
<i>Syzygium</i>	-	-	2000- 2200 m	2100- 2300 m

(source: Demel Teketay, 1997; Getachew Tesfaye *et al.*, 2002; the figures indicated are altitudinal range).

6.4. Phenology of the Study Species

6.4.1. Leaf Phenology

Trees of the Munessa-Shashemene Forest belong to two life-forms: evergreen and deciduous. Such a mixture of evergreen and deciduous species is also known from other tropical forests e.g. the Malagasy littoral forest. The latter though dominated by evergreen trees, had few deciduous species with annual patterns and marked seasonality in their leaf phenology (Bollen and Giuseppe, 2005). Leaf fall and leaf flush of the (facultative) deciduous species are annual and strictly seasonal, and leaf fall peaks during the long dry season when the temperature is high. The mean dates of leaf fall and leaf flush did not vary significantly between the deciduous tree species. Annual pattern and strong seasonality in leaf fall accords with leaf fall

phenology of deciduous trees from tropical forests in Bolivia (Justiniano and Fredericksen, 2000) and cloud forest in Hawaii (Berlin *et al.*, 2000). Leaf fall of deciduous species in a Bolivian dry forest began at the beginning of the dry season and continued until the beginning of the rainy season. The significant correlation between leaf fall and mean monthly temperature at the Munessa-Shashemene Forest suggests that leaf fall is an adaptation to reduce the effect of water stress in the dry season. The seasonality pattern of peak leaf fall also agrees with reports from the Atlantic Rain Forest Trees (Morellato *et al.*, 2000) where leaf fall consistently peaked during dry seasons when there was high water stress (Anderson *et al.*, 2005). Borchert (1984) argued that the timing of leaf fall is controlled by the water status of the plant.

Leaf flush peaked in April towards the end of the long dry season and the beginning of the small rains. A similar leaf flush pattern was observed in a forest from Tai National Park, Cote de Ivoire (Anderson *et al.*, 2005). Leaf flush during the end of dry season, when water stress is still high, was interpreted as a strategy to minimize herbivory of young vulnerable leaves (Aide, 1993; Coley and Baroney, 1996; Anderson *et al.*, 2005). During the long rainy season of 2004 massive attack of mature leaves in trees of *Celtis* by herbivore insects and subsequent complete shedding of all leaves by the infested plants were noted. Others have also reported that herbivorous insect biomass and therefore plant leaf damage were greatest in the wet season (Aide, 1993; Murah and Sukumar, 1993).

6.4.2. Flowering

Flowering patterns at the Munessa-Shashemene Forest were predominately annual, unimodal and seasonal in all examined species except in *Polyscias* which showed continuous, bimodal and non-seasonal flowering. Such strong seasonality and annual flowering pattern was reported for trees in other dry tropical forests (Justiniano and Fredericksen, 2000). According to Berlin *et al.*, (2000) annual flowering is predominant in a tropical Cloud Forest of the Hawaii and also in a humid tropical mountain forest of southern Ecuador (Bendix *et al.*, 2006). Frankie *et al.* (1974) reported a similar flowering phenology in dry tropical forest trees at La Selva, Costa Rica.

Continuous flowering is very rare in tropical forests and constituted less than 12 % of the species (Frankie *et al.*, 1974; Berlin *et al.*, 2000). In the Malayan forest sub-canopy species displayed continuous flowering (Appanah, 1990). Continuous flowering by sub- canopy species would increase seed production and distribution all year round thus taking the advantage of colonization of new gaps in the forest (Appanah, 1990). *Polyscias*, which contributes to the sub canopy at Munessa-Shashemene Forest, showed continuous flowering (at least at the population/species level) with two major peaks in one year. Each peak was recognized as one complete flowering cycle also at the individual tree level thus classifying *Polyscias* as a sub-annual type. One species can therefore behave differentially in its flowering pattern as continual flowering at the population/species level and sub-annual flowering at the individual/tree level (according to the level of the information analyses).

Several studies in other semi-arid tropical forests reported that flower peaks were concentrated in the dry season (Frankie *et al.*, 1974; Fredericksen and Justiniano, 2000; Berlin *et al.*, 2000). Most of the study species had flower peaks during the long dry season. Dry season flowering in tropical forests may be enhanced by the higher radiation as there was a significant positive correlation with mean monthly temperatures. Flowering in most species examined was significantly correlated to mean monthly temperature. In the examples reported here, a significant positive relationship between flowering and the increase of air temperature in the dry season was noted for *Pouteria* allowing for a time lag of two months, between flower induction and onset of flowering. On the other hand, a significant negative relationship of flowering and temperature in the dry season with a time lag of four months was found for the proportion of flowering individuals of *Syzygium*. A significant negative correlation between temperature and flowering with lag time of one month was observed for *Celtis*, which corresponded with the long rainy season. The significant decrease in temperature in the rainy season was followed by significant increase in the flowering individuals one month later. On the other hand, flowering phenology of tropical tree species can also be triggered by the humidity (Augspurger, 1981; van Schaik *et al.*, 1993; Sakai, 2001; Anderson *et al.*, 2005) which has also been noticed for *Croton* and *Polyscias* in the Munessa-Shashemene Forest. For example, there was significant negative correlation between rainfall and flowering with lag time of five months for *Croton*, which corresponded with the end of the long rainy season. The significant decrease in rainfall at the end of the rainy season was followed by a significant increase in the proportion of individuals flowering five months later. On the other hand, there was a significant positive correlation between rainfall and flowering with a time lag of two months for *Prunus*. Similarly, another significant one observed with a lag time of six months

with *Polyscias*, which corresponded to the long rainy season. The significant increase in rainfall in the rainy season was followed by significant increase in the proportion of individuals flowering six months later. Such strong correlations show the importance of climate factors in regulating flowering of trees in Munessa-Shashemene Forest.

According to Frankie *et al.* (1974) wet season flowering in tropical dry forests (e.g. at La Selva, Costa Rica) is rather low. It was also reported for *Shorea affinis* in the tropical wet forests of south Asia (Dayanandan, 1990). As an exception in the present study, *Celtis* flowered profusely during the rainy season after the development of new foliage.

Several tree species in tropical forests that share pollinators exhibit sequential flowering (Appanah, 1985; Ashton, 1992). Such temporal segregation in flowering is an adaptation of plant species that share common pollinators to minimize interspecific overlapping in flowering times and thus ineffective pollination or competition for pollinators (Appanah, 1985; Ashton *et al.*, 1988; Sakai, 2001). The mean dates of flowering in the Munessa-Shashemene Forest varied markedly among the study species and these differences segregated flowering temporally.

Flowering is generally highly synchronized within populations and frequently of short duration in tropical forests (Bawa and Ng, 1990). Such large flowering display by strict synchronization within and among individuals is important to attract pollinators through increase resource density (Sakai, 2002), escaping from predators and spreading the risk of uncertain pollinators

(Augspurger, 1981). Flowering was synchronized (up to 100 %) within and among the populations of *Pouteria*, *Celtis*, *Prunus*, and *Syzygium*.

6.4.3. Fruiting

Phenological patterns of tropical forest trees are diverse and complex (Bawa and Ng, 1990). Fruit production at the Munessa-Shashemene Forest was predominantly annual except for *Polyscias* that exhibited sub-annual fruiting. Most annual fruiting species of tropical forest exhibit non-seasonal fruiting i.e. extended fruiting over several months of the year or produce fruits year round (Frankie *et al.*, 1974; Berlin *et al.*, 2000). Individuals within a population that produce mature fruits asynchronously cause extended fruiting (Bawa and Ng, 1990). Extended fruiting patterns over several months show the availability of fruit resources for frugivore animals in tropical forests for most parts of the year (Justiniano and Fredericksen, 2000). Nevertheless, in tropical dry forests, fruit production remains low during the major rainy season (Justiniano and Fredericksen, 2000). Similarly, few tree species fruited during the rainy season at the Munessa-Shashemene Forest. Plant reproduction in the dry season would facilitate pollination and seed dispersal and free resources for vegetative growth in the wet season, thereby enhancing competitive ability (Frankie *et al.*, 1974; van Schaik *et al.*, 1993).

Although fruiting period extended over several months, fruiting peaked for most species during the mid to late dry season. Such pronounced dry season fruiting peaks have been reported from dry tropical forest in Costa Rica (Frankie *et al.*, 1974), and Cote d'Ivoire (Anderson *et al.*, 2005). Fruiting in the dry season in tropical forests may have evolved to disperse seeds when soil moisture conditions are favorable for seed germination, seedling

growth and survival (van Schaik *et al.*, 1993). Seedling recruitment (of *Pouteria*, *Celtis*, *Croton*, *Prunus* and *Syzygium*) during the major rainy season of 2005 and 2006 in Munessa-Shashemene Forest was 21 fold higher than during the dry seasons (data not shown). Moreover, the survival and growth of the seedlings were largely affected by severe drought and animal herbivory in the dry season (87 % mortality). These observations strongly support (with the exception of *Podocarpus*) the idea that fruiting phenology in tropical dry forests have evolved in relation to rainfall seasonality, the timing of favorable conditions for seed germination and survival, and hence reproductive success of the plant.

The timing of fruiting in tropical trees is highly correlated to temperature and rainfall (Muhanguzi *et al.*, 2003; Anderson *et al.*, 2005). In the present study, for example, a significant positive correlation between fruiting and increase in monthly mean temperature in the dry season was recorded for *Prunus* allowing for a time lag of one month between fruit induction and fruiting. On the other hand, a significant positive correlation between fruiting and the increase of rainfall in the rainy season was recorded for *Celtis* with lag time of five months. The significant rise in rainfall in the rainy season was followed by significant increase in the proportion of individuals fruiting five months latter. A significant positive correlation between fruiting and the increase in rainfall in the rainy season with a time lag of eight months was recorded for the proportion of fruiting individuals of *Syzygium*. A significant negative correlation between fruiting and the decrease in the monthly rainfall in the dry season was recorded for *Pouteria* with no time lag between induction and fruiting. Fruiting of trees in the Munessa-Shashemene Forest, therefore, can be said to be regulated by climate factors.

Pioneer species in tropical forests start reproduction early in life, fruit abundantly and frequently, and have small seeds that can effectively dispersed by wind (Whitmore, 1993). *Polyscias*, having seeds dispersed by wind, is one of the three pioneer species examined that displayed sub-annual fruiting pattern. Although *Polyscias* flowered and fruited frequently and abundantly, it was noted for lacking good regeneration in the Munessa-Shashemene Forest. The other two pioneer species, *Celtis* and *Croton* displayed a similar fruiting phenology with that of the climax species. Large proportions of gaps within the Munessa-Shashemene Forest were colonized by these two pioneer species (Gemedo Dalle and Masresha Fetene, 2006).

A reproductive cycle of the genus *Podocarpus* lasts about 18 months from cone initiation to seed maturity (Wilson and Owens, 1999). In Munessa-Shashemene Forest the female *Podocarpus* trees (56 % of the population) flowered between November-December 2004 and the same individuals required a period of 12 months (from June 2005 -May 2006) to complete the fruiting period, i.e. the development of green (unripe) fruit to mature (yellow) fruit and finally fruit dispersal. The complete reproductive cycle in *Podocarpus* i.e. from female tree flowering to the development of ripe fruit and then dispersal took about 18 months, which is similar to the report of Wilson and Owens (1999) from New Zealand. *Podocarpus* fruits year round and may serve as the only available food source at times of food scarcity to frugivore animals in the forest.

Fruiting followed flowering in all the study species although the time elapsed between flowering and fruiting was species-specific. All the studied species at the Munessa-Shashemene Forest flowered and produced fruits, which may not be always the case in other

tropical forests (Yap and Chan, 1990). Similarly, more than 97 % of the individuals/populations that flowered in the Munessa-Shashemene Forest produced fruits although the intensity may vary from species to species. Such significant proportions of fruit production by the studied species imply that fruit production due to limitations by pollinators might be less significant in the Munessa-Shashemene Forest. However, in *Pouteria* significant number of immature aborted fruits (unripe fruits) had been observed in most branches and under the crowns of the trees (Personal observation), which indicates reduced reproductive success in this species. *Polyscias* also exhibited similar reproductive problem. This may partially attributed to fragmentation of the reproductive trees, which could limit out-crossing among the different individuals of the same species. Abortion of immature fruits or non-viable seed set due to selfing (self-pollination) among out-crossing populations have been reported in several tropical tree species (Sakai *et al.*, 1999).

Fleshy fruits predominate in tropical and subtropical forests and are adaptations for dispersal by birds and mammals (van der Pijl, 1982). Most of the examined species in the present study had fleshy fruits that are dispersed by animals or gravity. More than 25 fruit eating animal species were recorded (Getachew Tesfaye, unpublished data) in the Munessa-Shashemene Forest in 2006. The existence of relatively large number of frugivore species in the forest implies the importance of these animals in seed/fruit dispersal. Regenerated young seedlings on the forest floor within the Munessa-Shashemene Forest were located far away from the crown of the mother trees (average distance was about 10 - 15 m from the crown and some up to 50 m). Fruiting phenology and reproductive success of trees in the Munessa-Shashemene Forest, therefore, influenced by both abiotic (climate) and biotic (dispersal) factors.

In conclusion, flowering phenology of the study species at the Munessa-Shashemene Forest can be categorized as annual flowering where most species flower during the dry season, and still few species flower in the rainy season; or continuous where few species flower year round with brief sporadic break. Moreover, fruiting phenology can be categorized as annual fruiting where most species fruit during the long dry season and, still few species fruit in the rainy season; or continuous fruiting where few species fruit all year round; or sub-annual fruiting where still few species fruit two times a year. The fact that in most species both flowering and fruiting were significantly correlated with temperature and rainfall shows that climate factors could control the reproductive phenology of trees sometimes concurrently or at different times of the year. However, leaf phenology was influenced by temperature.

7. SYNTHESIS AND RECOMMENDATIONS

The present study results showed that natural regeneration of tree species at the Munessa-Shashemene Forest are under the strong influence of various ecological factors. The findings in Section 5.1 had shown that there occur significant intra- and inter-specific variations in survival, growth and biomass allocations of seedlings under different light conditions. All seedlings showed higher growth rates in high light than in low light conditions, which implies light is the limiting factor for growth in the shaded understorey of the forest. Seedlings of *Celtis*, which showed highest growth rate in high light, adapted also higher plastic traits to grow fastest in low light. This was mainly due to its high plasticity in leaf morphology (LAR and SLA). While in medium light, fastest growth was shown by *Syzygium* due to the higher plasticity response in its physiological component (NAR). This finding revealed that natural

regeneration (forest regrowth) in relatively small and large gaps or forest clearings in the Munessa-Shashemene Forest would follow different successional pathways and species replacement pattern. However, seedling growths in the forest were generally determined by NAR both in high and low light environments, and by LAR in medium light level.

The restoration of degraded forest sites through enrichment plantation of indigenous plants needs the careful selection of the appropriate species for planting in the understorey shade-gap-edge environments within the forest. This requires knowledge of the seedling ecology such as seedling survival and growth together with the habitat preferences of the desired tree species. Based on the study results, enrichment plantations within big canopy gaps or afforestation of forest edges/clearings may preferably be planted with seedlings of *Celtis*, *Croton* and *Prunus*, whereas small gaps should be planted with seedlings of *Syzygium*, *Celtis* and *Prunus*. Forest understories should preferably be planted with seedlings of *Podocarpus*, *Pouteria* and *Syzygium*. Other than seedlings of *Croton* and *Podocarpus*, the rest of the species need protection from livestock grazing after planting.

The findings in Section 5.2 revealed that other than the light environment, both drought (soil moisture stress) and livestock browsing (herbivory damage) affected strongly seedling population dynamics in the forest understorey. Understorey seedling mortality and herbivory rates were higher in dry than in wet season. The findings in Section 5.3 revealed that plant population densities varied among species, along gradients of altitude and disturbance. *Prunus* and *Celtis* had highest seedling densities due to the high reproductive performances by the mother trees. *Podocarpus* and *Croton*, the two species whose seedlings developed defense to

herbivores, exhibited the highest tree densities. Reproductive problems (unripe fruit/seed set) were observed in *Pouteria* and *Polyscias*, the two species that exhibited the least tree densities and the greatest spatial distance between the reproductive individuals. The studied species showed variable size-class distributions or regeneration status. The inverse J-shape population structure shown by *Podocarpus*, *Prunus*, *Celtis* and *Croton* revealed healthy regeneration in these species. Thus, high reproductive performances and/or adaptive defences to herbivory were common attributes of healthy regenerating species at the Munessa-Shashemene Forest. On the other hand, the patterns of size-class distributions exhibited by species of *Pouteria*, *Syzygium* and *Polyscias* indicated discontinuous or hampered regeneration. Human disturbances such as illegal logging and tree removal (that involves mature and pole-sized individuals) for construction and other household purposes have contributed much to the regeneration problems. The removal of mature trees coupled with high seedling mortality and herbivory effects in the forest would further complicate regeneration of the species in the future since the reproductive individuals may not be replenished. In general, differences among species in their adaptations or responses to the different ecological factors play an important role in the dynamics of species regeneration and ultimately the composition and structure of the forest.

The findings in Section 5.4 revealed that the study tree species flowered and fruited regularly and abundantly, which shows the study site to be ideal for collection of gene bank seeds. Both rainfall and temperature were found to be strongly affecting the reproductive phenology, whereas temperature affected the leaf phenology of the study species. This implies climate is the environmental factors that triggered the plant phenological cycles. Leaf fall coincides to

the period of peak in temperature while leaf flush coincides to the beginning of the small rains. Flowering phenology of the species was either annual or continuous, while fruiting phenology is rather diverse as continuous, annual, or sub-annual. Flowering mainly occurs during the long dry season. In most species, peak fruiting period was concentrated around mid to late of the long dry season. Reproduction in the dry season enhanced seed germination, seedling establishment, survival and growth during the long rainy season, thereby enhancing competitiveness of the individual and over all regeneration of the species.

The study results showed clear pictures about the over all regeneration status of the species and areas of future management interventions. Thus, species of *Pouteria* and *Polyscias* needs high conservation activities in the immediate future, while species of *Celtis*, *Croton* and *Prunus* are encouraged for sustainable utilization options. The findings have also demonstrated major ecological factors and bottlenecks that involved in shaping the regeneration status of the species at the different growth stages. In conclusion, the understorey light environment, drought or soil water stress, grazing/herbivory damage, reproduction and human disturbance are the major ecological factors governing regeneration of tree species at the Munessa-Shashemene Forest. In the case of *Polyscias* problems of regeneration may partially attributed to the fragmentation of the tree population, which might have reduced its reproductive success/fitness. In addition, lack of suitable habitat for seeds to germinate or seed predation could be the possible sources of regeneration failure in this species.

Based on the study results the following recommendations are forwarded as options for sustainable management, conservation, and research.

I. Recommended options for sustainable management, restoration and conservation of the Munessa-Shashemene Forest in general and the studied tree species in particular are:-

1. Initiate enrichment plantation program of those species, which have already shown regeneration problems within the forest (e.g. *Pouteria*, *Syzygium* and *Polyscias*) through nursery-grown seedlings.
2. Reduce the intensity of livestock grazing during the dry season and establish protected area in the central portion of the forest to minimize human disturbance.
3. Strict protection/conservation of cutting trees of *Pouteria* and *Polyscias* remaining in the forest and carry on in-situ conservation for these two species.
4. Promote the sustainable utilization of trees of *Prunus*, *Croton* and *Celtis* for local consumptions by the inhabitants and other commercial purposes that may be envisaged in the future from the natural forest.
5. The Munessa-Shashemene Forest can be an ideal site for collection of tree seeds (of indigenous species) for gene banks as the mature trees produce fruits regularly and abundantly.

II. Research priority needs for better understanding of the regeneration dynamics:-

1. Further investigations on seedling growth and survival under wide range light environment (with the inclusion of other species) and soil moisture stress. The interactive effects of light and soil moisture stress should also be investigated.

2. Study on reproductive ecology of the species including pollination, seed production, dispersal and germination.
3. Modeling population growth (projection matrix analysis) for species of *Podocarpus*, *Prunus*, *Celtis* and *Croton* to support knowledge based decisions for sustainable forest management including tree harvest for timber, non-timber forest products and local consumptions.

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