

Regeneration of seven indigenous tree species in a dry Afromontane forest, southern Ethiopia

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ABSTRACT

Regeneration of seven indigenous tree species having significant ecological and economic importance was investigated in the Munessa-Shashemene dry Afromontane forest (MSF), southern Ethiopia. Densities and distributions of seedlings, saplings and trees were assessed along gradients of altitude, light and disturbance using quadrat sizes of 10 × 5 m (for seedlings) and 20 × 20 m (saplings and trees) following line transects. The number of individuals, frequency and height of the study species were recorded in the quadrats at every 100 m drop in altitude. Seedling densities varied markedly among the species and altitudes. Mean densities (number of individuals ha⁻¹) of seedlings ranged from zero (*Polyscias fulva*) to 5334 (*Prunus africana*), and from three (*Polyscias fulva*) to 102 (*Podocarpus falcatus*) for trees and saplings. Canonical Correspondence Analysis revealed that seedlings of *Celtis africana* and *Croton macrostachyus* were highly favored by disturbance and, hence, were concentrated in canopy gaps within the forest. Based on their population structures, the study species could be categorized into three groups: (1) Species that showed the highest proportion of individuals in the lowest height class and with a gradual decrease towards the upper height classes, which suggests good regeneration; *Podocarpus falcatus*, *C. africana*, *C. macrostachyus* and *P. africana* belonged to this group. (2) Species that showed higher proportions of individuals in the lowest height class and with missing individuals in the subsequent middle height classes, indicative of hampered regeneration; *Syzygium guineense* and *Pouteria adolfi-friederici* belonged to this group. (3) Species with no individuals in the lowest and middle height classes but represented by individuals in upper height classes; *P. fulva* belonged to this group. The species categorized in the last two groups exhibited hampered regeneration, and *P. fulva* is in the verge of local extermination. High seedling densities (e.g. *C. africana* and *P. africana*) and/or adaptive defense mechanisms to herbivory (e.g. *P. falcatus* and *C. macrostachyus*) were common attributes of species, which exhibited good regeneration. Regeneration problems were largely attributed to human disturbance, lack of suitable habitat for seed germination or problems associated to seed set (seed predation or abortion). Our study indicated that *P. fulva*, *P. adolfi-friederici* and *S. guineense* require the highest immediate attention for conservation in the MSF.

Introduction

Regeneration is a central component of tropical forest ecosystem dynamics and restoration of degraded forest lands. Sustainable forest utilization is only possible if adequate information on the regeneration dynamics and factors influencing important canopy tree species are available. Tropical forests revealed variation in patterns of regeneration both through

differences in their constituent species and the environmental variables in which they grow (Demel, 1997a; Denslow, 1987; Whitmore, 1996). 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 understory), and coppice (root/shoot sprouts of damaged individuals) (Demel, 1997b; Demel and Granström, 1995; Garwood, 1989; Getachew et al., 2002; Whitmore, 1996).

Studies on population structure and density of major canopy tree species can help to understand the status of regeneration of species, and, thereof, management history and ecology of the forest (Alvarez-Buyalla et al., 1996; Foster, 1980; Harper, 1977; Hubbel and Foster, 1986; Lykke, 1993; Saxena et al., 1984). Plant population structure shows whether or not the population has a

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stable distribution that allows continuous regeneration to take place (Enright and Watson, 1991; Pinerio et al., 1984; Rao et al., 1990). If regeneration was taking place continuously, then, the distribution of species cohorts would show reverse J shape curve, which is an indicator of healthy/good regeneration (Demel, 1997a; Harper, 1977; Silvertown, 1982). Such population structures are common in natural forests where external disturbances are limited (Demel, 1997a; Feyera, 2006; Getachew et al., 2002).

Seedling densities in forest understories are dynamic and rates may vary among species and in gap and shade environments (Bazzaz, 1991). The rates also vary due to mortality, which could include abiotic stresses such as light, drought, and biotic factors that include herbivory, disease or competition (Augsburger, 1984; Janzen, 1971). Information on tree seedling ecology can provide options for forest development through improvement in recruitment, establishment and growth of the desired species (Swaine, 1996). Thus, regeneration studies have significant implications on the management, conservation and restoration of degraded natural forests.

The dry Afromontane forests in Ethiopia, like their tropical counterparts, are among the most threatened ecosystems in the country due to conversion, commercial logging and loss of biodiversity. Several forests and forest tree species in the country have shown decline in their population structure and regeneration due to past and present disturbances, conversion and management. Disturbance such as intensive removal of trees for timber, construction, and forest grazing have placed significant pressure on forest regeneration (Getachew et al., 2002). Important canopy tree species in the dry Afromontane forests of Ethiopia have already been reported to exhibit problems of natural regeneration (Demel, 1997a; Getachew et al., 2002; Simon and Girma, 2004). The present study stems from this understanding. The objectives of the study were to: (1) investigate seedling, sapling and tree population densities, and their distributions along altitudinal, light and disturbance gradients for seven indigenous tree species of a dry Afromontane forest in southern Ethiopia; (2) examine the population structure using height-class distributions; and (3) examine the overall regeneration status and identify major bottlenecks that hamper natural regeneration of the species.

Materials and methods

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 Afromontane forest, hereafter referred to as MSF, and covers an altitudinal range between 2100 and 2700 m. The total area of the forest is 21,000 ha and exotic species plantations cover about 28% of the total forested area. The MSF is one of the major timber supplying forests in the country, and this puts the natural forest under severe pressure from illegal loggers. Logging in this forest started about 50–60 years ago (Lundgren, 1971). In addition, accessibility of the forest to the central market, about 250 km from Addis Ababa, made it highly vulnerable to huge smuggling activities leading to its transformation from a primary to secondary forest. The mean annual rainfall varies between 900 and 1500 mm, and the mean annual temperature is 15 °C. There is a bimodal rainfall pattern where the small unreliable rainy season is from March to May and a major rainy season from July to September. The long dry season is from October–February and the small dry season from May–June. Detail descriptions of the soils, geology, and vegetation of the study site can be found in Asferachew (2004) and Fritzsche et al. (2006).

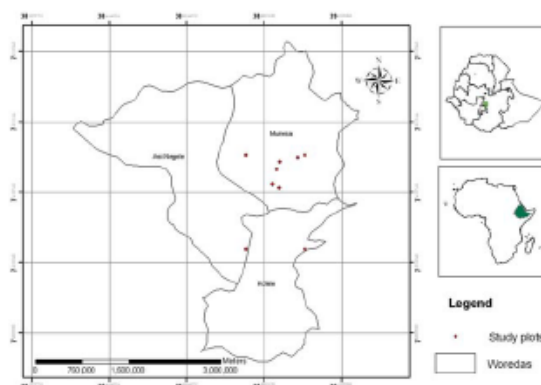


Fig. 1. Map of Ethiopia showing the study site, Munessa-Shashemene forest.

Study species

Seven indigenous tree species, namely, *Podocarpus falcatus* (Thunb.) R.Br. ex Mirb., *Celtis africana* Burm.f., *Croton macrostachys* Hochst., *Pouteria adolfi-friederici* (Engl.) A. Meeuse (synonym: *Aningeria adolfi-friederici* (Engl.) Robyns & Gilbert), *Polyscias fulva* (Hiern) Harms, *Prunus africana* (Hook.f.) Kalkman and *Syzygium guineense* (Willd.) DC. (hereafter referred to by their genus names) having significant ecological and economic importance were selected for the study. Detail descriptions of the habit, geographical distribution, size of propagule and biology of the species can be found in Getachew et al. (2002). Among the study species *Podocarpus*, *Pouteria*, *Prunus* and *Syzygium* are climax species (shade-tolerant) (*sensu* Swaine and Whitmore, 1988) and constituted major proportions in the upperstory of the forest canopy. *Celtis*, *Croton* and *Polyscias* are pioneer species (light demanding) that occupy both the middle and upper canopy strata of the forest. The seven species constituted 91–95% of the total tree basal cover and 58–77% of the Importance Value Index (IVI) of trees at the MSF (Getachew, 2008). Nomenclature of plant names follows Bamps (1989), Friis (1992, 1995, 2003), Gilbert (1995), Hedberg (1989) and Polhill (1989).

Methods

Densities and distributions of seedlings, trees and saplings along the altitudinal gradient

Seedling, tree and sapling survey works were conducted between April and May 2006. For the purpose of this study, terms "seedling", "sapling" and "tree" are defined as plants with heights up to 150 cm, between 150 and 300 cm and above 300 cm, respectively (Demel, 1997a; Getachew et al., 2002). To examine tree and sapling densities and their distribution along the altitudinal gradient, six line transects were established following north-south orientation and with 300 m distance between them. At every 100 m drop in altitude, quadrats with sizes of 20 × 20 m (400 m²) were laid down along the line transects. Forty-two quadrats (16,800 m² = 1.68 ha) were assessed for densities and distributions of saplings and trees. To determine the densities and distributions of seedlings, the same procedures described for trees and saplings were employed, except that the size of quadrats was reduced to 10 × 5 m (50 m²). In each quadrat, the number and height of all seedlings, trees and saplings of the seven species

were recorded. Additional information on the light conditions and disturbance were recorded in the plots. The light levels were measured using a PAR sensor (Li 190 S, Li-COR, Nebraska) and readings were taken at 150 cm above the ground. Measurements were made in the shade and open, and irradiance was expressed in percentage of the open. The degree of human disturbance in each quadrat was recorded using 1–4 scale as follows: 1=no signs of any stump cut left; 2=one stump cut and less frequent wood collection; 3=2–3 stump cut and frequent wood collection; 4=greater than 3 stump cut and frequent wood collection.

Population structure and regeneration status of the study species

'Population structure' refers to the distribution of individuals in different height classes to provide the regeneration profile of the species. Although diameter at breast height (DBH) is the most commonly used size variable in the analysis of population structure, several studies have used height class distribution for the inclusion of seedlings and saplings in studies of population structure of tree species (Breckle, 1997; Demel, 1997a; Geldenhuys, 1993). The inclusion of seedlings and saplings in plant population structures would provide better information on the status of the species at the early stage of regeneration. To examine the population structure of each species, six line-transects were established following a similar procedure as described above. Height was measured using a Suunto Clinometer. All individuals of each species were, then, grouped into different height classes, i.e. 0–2, 2–4, 4–6, 6–8, 8–10, ..., 28–30, and > 30 m.

Data analyses

Seedling density, tree and sapling density and their frequencies were analyzed following Müller-Dombois and Ellenberg (1974). Prior to analysis, data were tested for homogeneity variances and log transformed (Zar, 1996). Analysis of variance was used to determine significance of seedling, sapling and tree densities among the species. Tukey's multiple range tests was used for comparison of means. The seedling densities were also correlated to altitudes. The data from the seedling survey 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 and disturbance. Spearman correlation test was conducted to see the significance of the proportion of individuals per size-class distributions (Zar, 1996). A negative correlation indicates an inverse J-shaped curve and a positive correlation refers to only few small individuals and more of large ones in the population.

Results

Densities and distributions of seedlings along the altitudinal gradient

The mean densities (number of seedlings ha^{-1}) of seedlings of the seven studied species in the MSF showed significant ($P < 0.05$) differences between species, varying between zero (for *Polyscias*) and 5334 individuals ha^{-1} (for *Prunus*) (Table 1). High densities were typical for *Croton* and *Celtis*. On the other hand, frequency of distribution of seedlings varied considerably and ranged between zero (for *Polyscias*) and 78 (for *Podocarpus*). Relatively low seedling frequencies were also observed for *Syzygium*, *Pouteria*, *Celtis* and *Croton*.

Seedlings of *Podocarpus* showed no concentration at any elevation in the forest and occurred along the entire altitudinal range (Fig. 2). However, 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, 67% were less than 50 cm in height.

Seedlings of *Pouteria* showed distinct altitudinal concentration between 2100 and 2300 m (Fig. 2). Seedling densities decreased progressively from 1240 individuals ha^{-1} at 2300 m to 2250 individuals ha^{-1} at 2100 m. The highest seedling density was recorded at 2100 m and the lowest at 2300 m. All of the seedlings were less than 50 cm in height.

Seedling densities of *Celtis* varied between 930–13,310 individuals ha^{-1} across the altitudes (Fig. 2). They showed a distinct altitudinal concentration between 2100 and 2400 m. The highest seedling density was recorded at 2200 m and the lowest at 2400 m. Of all the seedlings, 83% were less than 50 cm in height.

Seedling densities of *Croton* varied between 52 and 7180 individuals ha^{-1} across the altitudinal gradient (Fig. 2). The seedlings showed a distinct altitudinal peak between 2100 and 2400 m. The highest seedling density was recorded at 2200 m and the lowest at 2400 m. The density of seedlings at the lower elevation was relatively higher than further up. Of the total seedlings, nearly half of them (48%) were less than 50 cm in height.

Seedlings of *Prunus* showed no concentration at any elevation and occurred along the entire altitudinal range (Fig. 2). However, seedling densities varied considerably with altitudes ranging between 1060 individuals ha^{-1} at 2700 m and 7900 individuals ha^{-1} at 2500 m. Seedling densities increased progressively with increasing altitude except at the uppermost elevation. Of the total seedlings, 93% were less than 50 cm in height.

Seedling densities of *Syzygium* varied between 40 and 160 individuals ha^{-1} across the altitudinal gradient (Fig. 2). The seedlings showed a distinct altitudinal concentration between 2100 and 2300 m. The highest seedling density was recorded at 2200 m and the lowest at 2300 m. All of the seedlings were less than 50 cm in height.

Table 1
Mean densities of seedlings (\pm SE), trees and saplings of the study species and their frequencies of distribution in the Munessa-Shashemene Forest.

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

Similar letters in each column are not significantly different at $P=0.05$; *mean seedling density ha^{-1} ; **percentage of quadrats occupied.

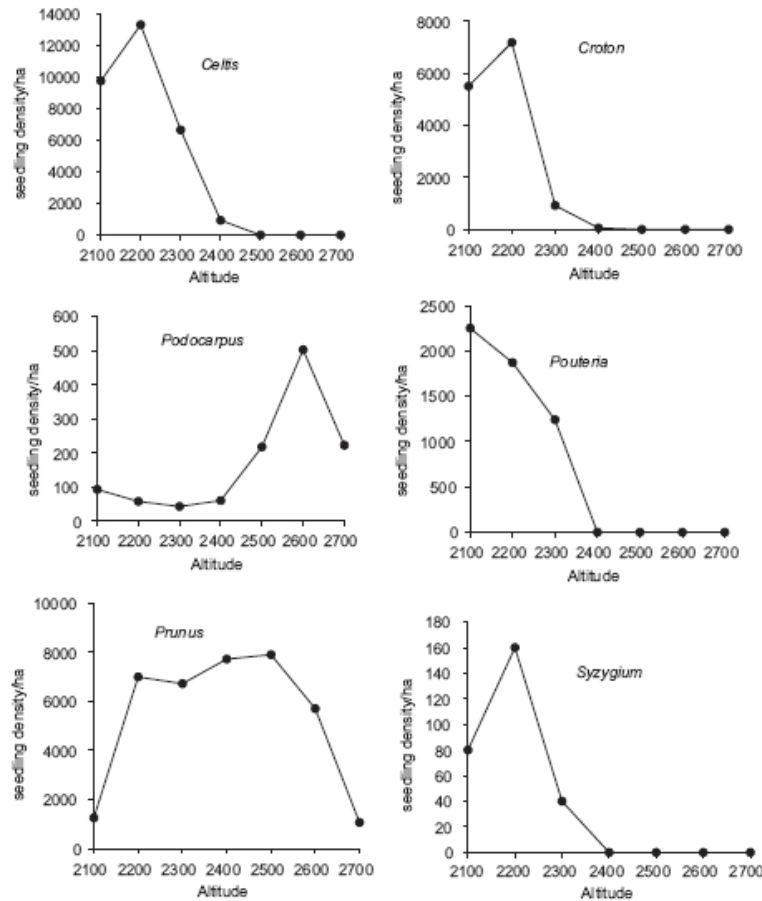


Fig. 2. Densities and distributions of seedlings of the study species recorded along the altitudinal gradient in the Munessa-Shashemene forest.

Surprisingly, not even a single seedling of *Polyscias* was recorded along the entire altitudinal range in the MSF. In general, seedling densities and distributions strongly correlated to altitudes except for *Prunus* ($r=0.1$; $p=0.7$) for which no significant correlation with altitude could be established. Seedlings of *Pouteria* ($r=-0.9$; $p<0.001$), *Croton* ($r=-0.9$; $p<0.001$), *Celtis* ($r=-0.9$; $p<0.001$) and *Syzygium* ($r=-0.8$; $p=0.01$) showed strong significant negative correlation with elevation, whereas *Podocarpus* ($r=0.7$; $p=0.07$) exhibited a strongly positive but non-significant correlation with altitude.

The total seedling density of all the species peaked at 2200 m (29,567 seedlings ha^{-1}) followed by 2100 m (18,922 seedlings ha^{-1}), and the lowest at 2700 m (1282 seedlings ha^{-1}) (Fig. 3). *Celtis*, *Croton* and *Prunus* contributed 77–93% of the seedlings at 2100 and 2200 m.

Result from the Canonical Correspondence Analysis (CCA) ordination of seedling distributions along gradients of altitude, light and disturbance revealed that the three environmental variables explained 54% of the total variation for six of the seven studied species (Fig. 4). Axes 1 and 2 of the CCA (Eigenvalues 0.52 and 0.08, respectively) accounted for 53% of the total variation while the third canonical axis explained only an additional 1% of the variation. The variance in species data explained 46%, 7% and 1% for the canonical axes 1, 2 and 3, respectively. Altitude strongly

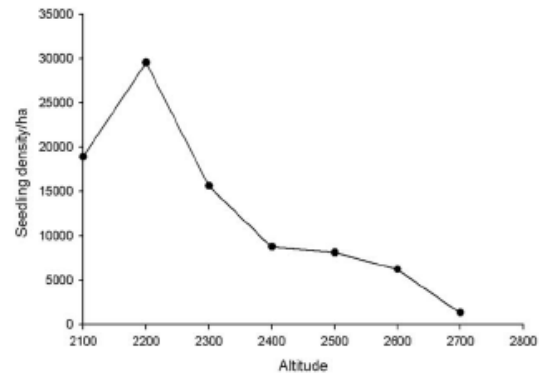


Fig. 3. Total seedling densities of the study species recorded along the altitudinal gradient in the Munessa-Shashemene forest.

correlated with the seedling abundance on Axis 1 ($r=0.91$), while both canopy gaps/light ($r=0.72$) and disturbance ($r=0.55$) were strongly correlated with the seedling abundance on Axis 2. Altitude was correlated negatively but non-significantly to

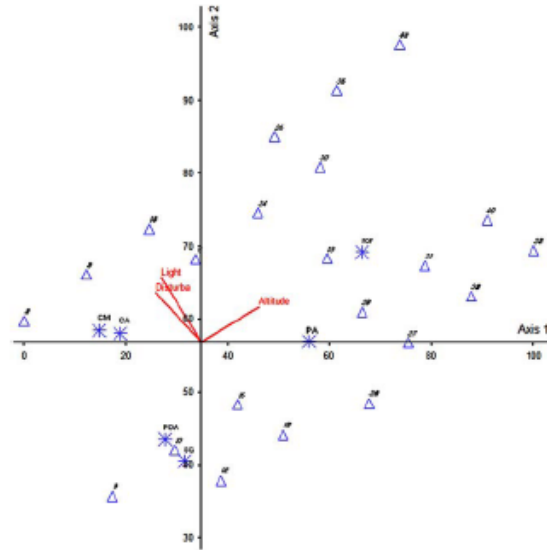


Fig. 4. Output of the Canonical Correspondence Analysis (CCA) showing ordination of the numbers of seedlings of the six species and their distributions in forty-two quadrats along gradients of altitude, canopy light and disturbance in the Munessa-Shashemene forest (CM=*Croton macrostachys*; CA=*Celtis africana*; PDF=*Podocarpus falcatus*; PA=*Prunus africana*; POA=*Pouteria adolfi-friederici*; SG=*Syzygium guineense*; the triangles and asterisks refer to quadrats and species, respectively; Eigenvalues 0.61; explained total variance 54.1%).

canopy gap/light ($r=-0.31$) and disturbance ($r=-0.39$). Expectedly, canopy gap/light and disturbance were strongly correlated ($r=0.73$). The CCA clearly showed that *Celtis* and *Croton* were favored by disturbance and concentrated in plots with canopy gaps while the rest of the species were concentrated in plots of shaded/closed canopy. In addition, the CCA revealed that seedlings of *Podocarpus* dominated over the other species at the upper forest ranges while those of *Prunus* prevailed in the middle ranges. *Croton*, *Pouteria* and *Syzygium* dominated at the lower portion of the forest.

Densities and distributions of trees and saplings along the altitudinal gradient

The mean densities of trees and saplings of all the species varied between 3 individuals ha^{-1} (for *Polyscias*) and 102 individuals ha^{-1} (for *Podocarpus*) (Table 1). Comparable mean densities of trees and saplings were recorded for *Pouteria* and *Polyscias*, *Croton* and *Podocarpus* as well as *Prunus* and *Syzygium*. On the other hand, frequency of distributions of trees and saplings varied between 15% (for *Polyscias*) and 89% (for *Podocarpus*). Relatively low frequencies of distributions were exhibited by *Pouteria*, *Syzygium* and *Celtis* while *Podocarpus* had the highest frequency.

Trees and saplings of *Croton* were recorded between 2100 and 2400 m (Fig. 5). 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 was 94 individuals ha^{-1} of which saplings accounted for 29%.

Trees and saplings of *Podocarpus* were recorded along the entire altitudinal range of the forest (Fig. 5). However, the densities varied considerably along the altitudes and ranged between 43 and 198 individuals ha^{-1} . The highest density was found at 2600 m and the lowest at both 2300 and 2700 m. The

mean density of trees and saplings was 102 individuals ha^{-1} of which saplings accounted for 64%.

Trees of *Pouteria* were recorded between 2100 and 2300 m and no sapling was found (Fig. 5). The densities showed slight variation across the altitudes and ranged between 5 and 13 individuals ha^{-1} . The highest density was recorded at 2300 m and the lowest at 2200 m. The mean density was 4 individuals ha^{-1} .

Trees and saplings of *Celtis* were recorded between 2100 and 2300 m (Fig. 5). The densities varied slightly along the altitudes between 23 and 30 individuals ha^{-1} . The mean density was 11 individuals ha^{-1} of which saplings accounted for 16%.

Trees of *Syzygium* were recorded between 2100 and 2300 m and no sapling was found (Fig. 5). The densities varied considerably along the altitudes and ranged between 18 and 63 individuals ha^{-1} . The density decreased progressively with increasing altitude. The mean density was 19 individuals ha^{-1} .

Trees and saplings of *Prunus* were recorded along the entire altitudinal range of the forest (Fig. 5). However, the densities varied remarkably along the altitudes and ranged between 10 individuals ha^{-1} (both at 2100 and 2700 m) and 63 individuals ha^{-1} (at 2400 m). The mean density was 29 individuals ha^{-1} of which saplings accounted for 25%.

Trees of *Polyscias* were recorded between 2100 and 2300 m and no sapling was encountered (Fig. 5). Tree densities remained very low along the altitudes, i.e. between 5 and 8 individuals ha^{-1} . The highest density was recorded at 2100 m and the lowest at both 2200 and 2300 m. The mean density of trees was three individuals ha^{-1} .

The mean total densities of trees and saplings peaked at 2200 m (652 individuals ha^{-1}) followed by 2100 m (288 individuals ha^{-1}) and the lowest density was found at 2700 m (75 individuals ha^{-1}). *Croton*, *Podocarpus* and *Prunus* contributed 74%–82% of the densities of trees and saplings at 2200 and 2100 m peaks.

Comparison of total mean densities of trees and saplings of all the species along the altitudinal gradient revealed that the highest density (283 individuals ha^{-1}) was recorded at the lower altitudes, i.e. between 2100 and 2300 m (Fig. 6). As altitude increased, the densities declined markedly, amounting to 192 individuals ha^{-1} in the upper range (2600–2700 m) and only 148 individuals ha^{-1} in the middle range.

Population structure of the study species

The population structures of the species differed markedly (Fig. 7). In four of the seven studied species (*Podocarpus*, *Celtis*, *Croton* and *Prunus*) the structures showed continuous height-class distributions with progressive decline in the proportions of individuals with increasing height. They exhibited inverse J-shaped distributions. The proportion of individuals in the successive height classes showed an exponential decline in the four species ($d=0.56$, $P < 0.01$, for four species). In *Podocarpus*, about 5% of the population had a height of more than 30 m, which also resulted in a longer tail to the right.

Population structures of *Syzygium* and *Pouteria* showed non-continuous distributions, i.e. higher proportions of individuals in the lowest height class followed by the absence of individuals in the successive middle height classes and a relatively large proportion of mature individuals in the uppermost height classes. This implies that regeneration was hampered at one or several stages of growth. However, the proportions of individuals in the upper height classes were quite large and these groups could still serve as major seed sources for natural regeneration of the species. Individuals of *Pouteria* with heights between 14 and 30 m are still poached by loggers.

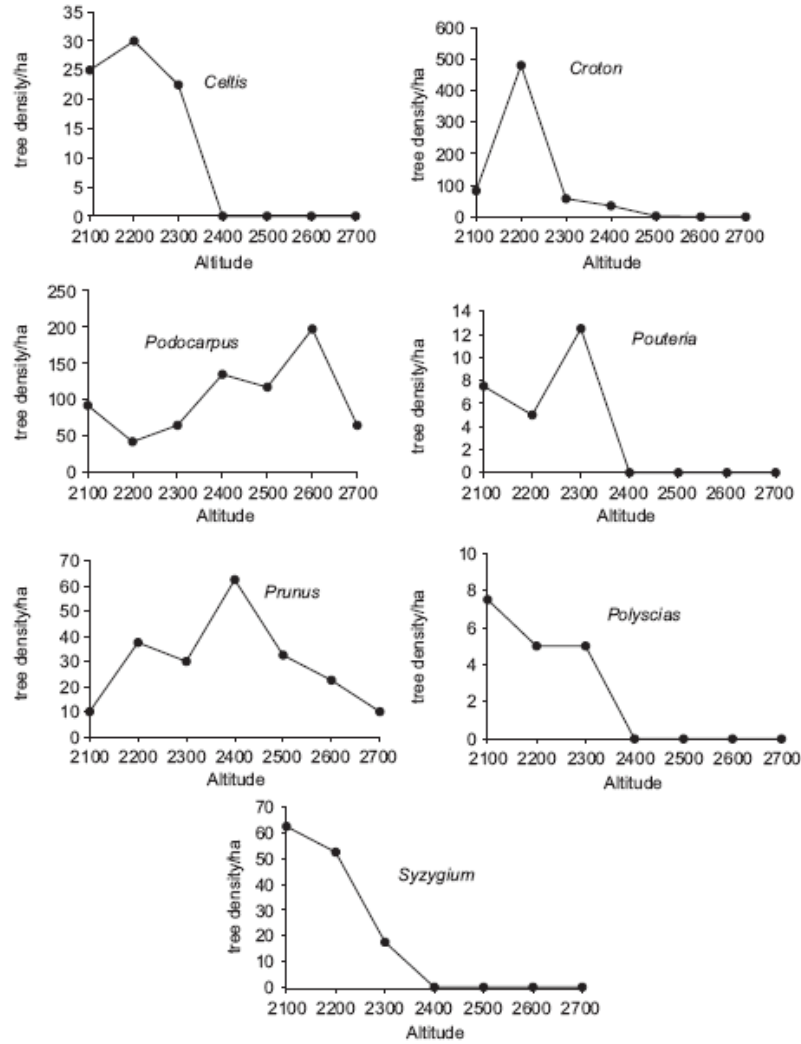


Fig. 5. Densities and distributions of trees and saplings of the study species along altitudinal gradient in the Munessa-Shashemene forest.

The population structure of *Polyscias* exhibited absence of individuals in the lowest and subsequent middle height classes suggesting that regeneration was hampered and self-replacement in the future would be extremely difficult.

Spearman rank correlation test of height-class distributions of the species showed that *Podocarpus* ($r = -0.6$; $p = 0.01$), *Celtis* ($r = -0.6$; $p = 0.01$), *Croton* ($r = -0.9$; $p < 0.001$) and *Prunus* ($r = -0.5$; $p = 0.02$) had significant negative correlations implying the presence of larger proportions of smaller than larger individuals. *Pouteria* ($r = -0.1$; $p = 0.5$) and *Syzygium* ($r = 0.2$; $p = 0.4$) had non-significant correlations implying fluctuating populations. *Polyscias* ($r = 0.7$; $p < 0.001$) had significant positive correlation implying the presence of older than younger individuals.

Based on their population structures, the study species could be categorized into three groups: (1) Species that showed the highest proportion of individuals in the lowest height class and with a gradual decrease towards the upper height classes, which suggests good regeneration; *Podocarpus*, *Celtis*, *Croton* and *Prunus*

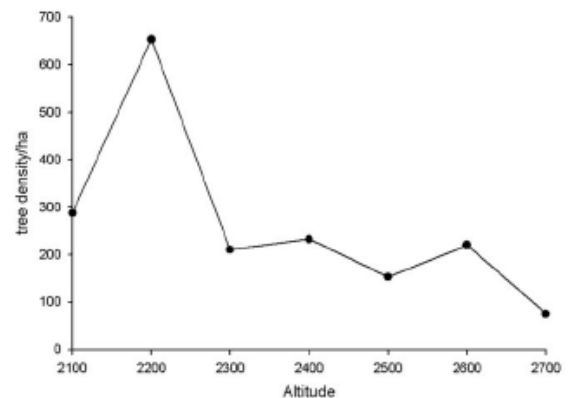


Fig. 6. Total sapling and tree densities of the study species along the altitudinal gradient in the Munessa-Shashemene forest.

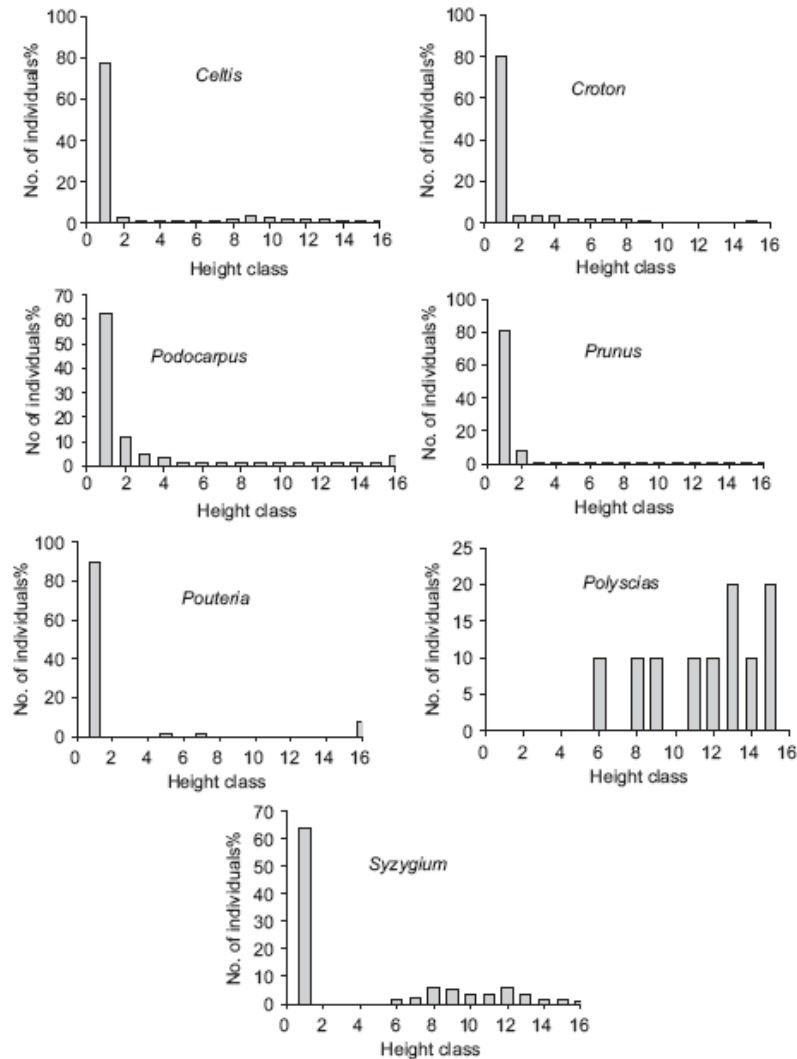


Fig. 7. Plant population structures of the study species in the Munessa-Shashemene forest (height classes: 1=0-2, 2=2-4, 3=4-6, 4=6-8, 5=8-10, ... 15=28-30 and 16 > 30m).

belonged to this group. (2) Species that showed higher proportions of individuals in the lowest height class and with missing individuals in the subsequent middle height classes, indicative of hampered regeneration; *Syzygium* and *Pouteria* belonged to this group. (3) Species with no individuals in the lowest and middle height classes but represented by individuals in upper height classes; *Polyscias* belonged to this group. The species categorized in the last two groups exhibited hampered regeneration, and *Polyscias* is in the verge of local extermination.

Discussion

The investigated tree species in the MSF had numerous seedlings except *Polyscias*. The presence of abundant seedlings on the forest floor is consistent with previous reports from other Afromontane forests in Ethiopia (Demel, 1997a; Getachew et al.,

2002) and tropical rain forests (Cesar, 1992; Swaine, 1996; Whitmore, 1996). The accumulation of a seedling bank under the forest canopy is known to be the major regeneration route of climax tree species (Demel, 1997a; Whitmore, 1996). In the present study, large numbers of seedlings were observed for the climax species (*Prunus* and *Pouteria*) in the understory shade suggesting that seedling bank is their major regeneration strategy. The seeds of most climax species germinate shortly after dispersal and, thereafter, show slow growth rates in the shaded understory of forests (Demel, 1997a; Masresha and Yonas, 2001; Whitmore, 1996). Significant proportions (60–89%) of seeds of *Prunus* and *Syzygium* germinated in a period of less than 1 year after dispersal mainly during the wet season in the studied forest (Getachew, 2008).

The lack of seedlings of *Polyscias* may be partially attributed to the absence of a conducive environment for germination of its seeds, such as severe disturbance of the canopy and forest soils. In

a previous similar study, *Polyscias* was among those eleven tree species that regenerated well on disturbed soils of logged fields at Harena forest in Ethiopia (Getachew and Demel, 2005b).

Seedling densities varied significantly among species. Seedling densities were highest for *Prunus* and *Celtis* due to the high reproductive potential of the mother trees. However, about 42–61% of the seedling populations of these species were lost annually due to drought, disturbance or herbivory damage (Getachew, 2008). *Syzygium* had the lowest seedling density, which could be attributed to low reproductive performance of the mother trees (only two seedlings per reproductive tree) (Getachew, 2008). The two pioneer species, *Celtis* and *Croton*, were concentrated in the lower elevation of the forest where disturbance is high because of tree felling (Gemede and Masresha, 2004).

The distribution of seedlings along the altitudinal gradient also showed marked variations among species. *Podocarpus* and *Prunus* showed wide distributions and occurred along the entire altitudinal range in the forest. On the other hand, *Pouteria*, *Celtis* and *Syzygium* had shown narrow distribution ranges and were concentrated at lower elevation of the forest. At the upper altitudes, relatively humid climate conditions (low temperature, rainfall and high humidity) would restrict the distribution of some species.

Tree and sapling densities also varied significantly among species. *Podocarpus* showed the highest tree and sapling density followed by *Croton*. *Podocarpus* is known to be the single most dominant tree species of dry Afromontane forests in Ethiopia (Fris, 1992). The tree density reported in this study was comparable to earlier reports from the Harena forest (Getachew and Demel, 2005a, b), but was slightly lower than in forests of Wof-Washa and Menagesha (Tamrat, 1994). Both *Podocarpus* and *Croton* constituted 78–82% of the tree basal area and 37–55% of the Importance Value Index in the MSF (Getachew, 2008). *Pouteria* and *Polyscias* showed the lowest tree densities, which is in agreement with previous results from other dry Afromontane forests in Ethiopia (Tamrat, 1994; Simon and Girma, 2004).

Tree species examined had shown considerable variations in their height-class distributions, which also imply differences in the overall regeneration status among species. Four of the seven studied species exhibited continuous height-class distributions with an inverse J shape curve implying healthy regeneration (Demel, 1997a; Feyera, 2006; Geldenhuys, 1993). Such population structures are typical characteristics of many tropical forest tree species (Cesar, 1992; Poorter et al., 1996). *Podocarpus* displayed healthy regeneration in several Afromontane forests in Ethiopia, including MSF, though it is still under pressure from selective logging (Chaffey, 1979; Getachew et al., 2002). The tree population of *Podocarpus* is likely to decrease in the future, as it is the only remaining target species of loggers in the MSF. Similarly, *Croton*, *Celtis* and *Prunus* exhibited good regeneration status in the MSF but not in other Afromontane forests in Ethiopia (Demel, 1997a; Getachew et al., 2002). The three species were not preferred much for commercial timber in MSF. Unlike in many other African countries, the bark of *Prunus* has not been, as yet, extracted for medicinal or industrial purposes in Ethiopia.

Plant population structure of *Pouteria* and *Syzygium* had shown that regeneration was hampered in these species at the MSF, and similar results were reported from other Afromontane forests in Ethiopia (Getachew et al., 2002). In similar studies, Bongers et al. (1988) and Breckle (1997) have also described a similar discontinuous height-class distribution pattern from tropical rain forests. The lack of good regeneration in *Pouteria* can be attributed to the excessive selective cutting of the species for commercial timber. The few standing trees of *Pouteria* in the MSF were left only because they are highly buttressed, difficult to cut manually

and saw in the dark, thus making an escape of poachers from the attention of forest guards impossible. *Pouteria* ranks as the number one priority timber species and the second most harvested in Ethiopia only surpassed by *Podocarpus* (Getachew and Demel, 2005a, b; Legesse, 1995; von Breitenbach, 1963). The overall regeneration status of *Pouteria* is alarming because those few old and over-mature trees are standing on fragile lands and marginal environment with a narrow altitudinal range. In addition, seedlings of *Pouteria* showed the lowest growth rates (relative and absolute growths) and least plasticity responses (to ten out of eleven plant morphological growth traits measured) (Getachew, 2008), which probably indicates the low adaptation potential of the species to future environmental change or forest degradation. If the current pressure from illegal loggers on *Pouteria* in the MSF continues unabated, coupled with the problems mentioned above, the species will disappear from the forest in the near future. It is highly recommended, therefore, to protect those few remaining mature individuals as potential seed sources for any conservation efforts in the future to rescue the species. *Syzygium*, having the least seedling density and highest mortality rate in the MSF, is another priority species that needs conservation attention.

Polyscias lacks representation of individuals in the lower and intermediate height classes in the studied forest. Although the species flowered and fruited regularly and abundantly (Getachew, 2008), the absence of seedlings in the forest leads to the question whether or not the reproductive trees are providing viable seeds. Unfortunately, our attempts to collect ripe seeds directly from the trees during the study period were unsuccessful. The lack of naturally regenerated seedlings, young trees and seeds stored in the soil (Getachew, 2008) may aggravate the local extermination of the species from the forest in the near future.

Species that require high conservation priority at the MSF were *Polyscias*, *Pouteria* and *Syzygium*. Regeneration problems were largely attributed to human disturbance, lack of suitable habitats for seeds to germinate or problems associated with producing matured and fertile seeds. On the other hand, high seedling densities (e.g. *Celtis* and *Prunus*) or adaptive defenses to herbivory (e.g. *Podocarpus* and *Croton*) were common attributes to healthy regenerating species.

Based on our results, the following recommendations are forwarded as options for sustainable forest management of the MSF: (i) initiate *in-situ* conservation efforts for *Polyscias*, *Pouteria* and *Syzygium*, including strict protection of the remaining mother trees; (ii) promote sustainable utilization of trees of *Podocarpus*, *Celtis*, *Croton* and *Prunus* through knowledge-based decision systems such as population growth models of each species; (iii) study the reproductive ecology of the species including pollination, seed production, dispersal and germination.

Acknowledgments

This study is part of the Ph.D. work of the first author. The African Forest Research Network (AFORNET) (Grant # 10/2004) and The German Research Foundation (DFG) (Project # BE-473/35) are gratefully acknowledged for funding the study. We thank Feyiso Meko and Deksiso Bulcha for their field assistance. The Institute of Biodiversity Conservation, Ethiopian Institute of Agricultural Research, and The Shashemene Forest Enterprise are highly acknowledged for their support during the study. The scientific and technical staff members of the Munessa Project are also gratefully acknowledged. We thank the two anonymous reviewers for their comments on the previous version of the manuscript.

References

- Alvarez-Buyalla, E.R., García-Barríos, R., Lara-Moreno, C., Martínez-Ramos, M., 1996. Demographic and genetic models in conservation biology: application and perspectives for tropical rain forest tree species. *Ann. Rev. Ecol. Syst.* 27, 387–421.
- Asferachew Abate, 2004. Biomass and nutrient studies of selected tree species of natural and plantation forests: implications for a sustainable management of the Munessa-Shashemene forest, Ethiopia. Ph.D. thesis, University of Bayreuth, Bayreuth, Germany.
- Augsburger, C.K., 1984. Pathogen mortality of tropical tree seedlings: experimental studies of the effects of dispersal distance, seedling density and light conditions. *Oecologia* 61, 211–217.
- Bamps, P., 1989. Araliaceae. In: Hedberg, L., Edwards, S. (Eds.), *Flora of Ethiopia*, vol. 3. Addis Ababa University, Addis Ababa and Uppsala University, Uppsala, pp. 537–543.
- Bazzaz, F., 1991. Regeneration of tropical forests: physiological responses of pioneer and secondary species. In: Gomez-Pompa, A., Whitmore, T., Hadley, M. (Eds.), *Rainforest Regeneration and Management*. Parthenon Publishing, UNESCO, Paris, pp. 91–118.
- Bongers, F., Pompa, J., Meave del Castillo, J., Carabias, J., 1988. Structure and floristic composition of the low land rain forests of Los Tuxtlas, Mexico. *Vegetatio* 74, 55–88.
- Breckle, S.W., 1997. Population studies on dominant and abundant tree species in the montane tropical rain forests of the biological reserve North of San Ramon, Costa Rica. *Trop. Ecol.* 38, 259–272.
- Cesar, S., 1992. Regeneration of tropical dry forests in Central America, with examples from Nicaragua. *J. Veg. Sci.* 3, 407–416.
- Chaffey, Y.D., 1979. South-west Ethiopia Forest Inventory Project: A Reconnaissance Inventory of Forest in South-West Ethiopia. Land Resources Development Center, England.
- Demel Teketay, 1997a. Seedling populations and regeneration of woody species in dry Afromontane forest of Ethiopia. *For. Ecol. Manage.* 98, 149–165.
- Demel Teketay, 1997b. The impact of clearing and conversion of dry Afromontane forests into arable land on the composition and density of soil seed banks. *Acta Ecol.* 18, 557–573.
- Demel Teketay, Granström, A., 1995. Soil seed banks in dry Afromontane forests of Ethiopia. *J. Veg. Sci.* 6, 777–786.
- Denslow, S., 1987. Tropical tree fall gaps. *Ann. Rev. Ecol. Syst.* 17, 430–441.
- Enright, N.J., Watson, A.D., 1991. A matrix model analysis for the tropical tree *Araucaria cunninghamii*. *Aust. J. Ecol.* 16, 507–520.
- Feyera Senbeta, 2006. Biodiversity and ecology of Afromontane rain forests with wild *Coffea arabica* L. populations in Ethiopia. Ecology and Development Series, Cuvillier Verlag, Gottingen 38, 1–152.
- Foster, R.B., 1980. Heterogeneity and disturbance in tropical vegetation. In: Soule, M.E., Wilcox, B.A. (Eds.), *Conservation Biology*. Sinauer, Sunderland, MA, USA, pp. 75–92.
- Friis, I., 1992. *Forests and Forest Trees of Northeast Tropical Africa*. Kew Bulletin, London.
- Friis, I., 1995. Myrtaceae. In: Edwards, S., Mesfin, Tadesse, Hedberg, L. (Eds.), *Flora of Ethiopia and Eritrea*, vol. 2 (2). The National Herbarium, Addis Ababa University, Addis Ababa and Uppsala University, Uppsala, pp. 71–106.
- Friis, I., 2003. Sapotaceae. In: Hedberg, L., Edwards, S., Sileshi, Nemomissa (Eds.), *Flora of Ethiopia and Eritrea*, vol. 4 (1). The National Herbarium, Addis Ababa University, Addis Ababa and Uppsala University, Uppsala, pp. 54–63.
- Fritzsche, F., Abate, A., Fetene, M., Beck, E., Weise, S., Guggenberger, G., 2006. Soil-plant hydrology of indigenous and exotic trees in an Ethiopian montane forest. *Tree Physiol.* 26, 1043–1054.
- Garwood, C., 1989. Tropical soil seed banks: a review. In: Leck, M., Simpson, R., Parker, V. (Eds.), *Ecology of Soil Seed Banks*. Academic Press, San Diego, pp. 149–209.
- Geldenhuis, C.J., 1993. Reproductive biology and population structures of *Podocarpus falcatus* and *P. latifolius* in southern Cape forests. *Bot. J. Linn. Soc.* 112, 59–74.
- Gemedo Dalle, Masresha Fetene, 2004. Gap-fillers in Munessa-Shashemene forest. *Ethiop. J. Biol. Sci.*, 3, 1–14.
- Getachew Tesfaye, 2008. Ecology of regeneration and phenology of seven indigenous tree species in a dry Afromontane forest of Ethiopia. Ph.D. thesis, Addis Ababa University, Addis Ababa, Ethiopia.
- Getachew Tesfaye, Demel Teketay, 2005a. Distribution of *Podocarpus falcatus* along environmental gradients and its regeneration status in Harena forest, Southeastern Ethiopia. *Ethiop. J. Nat. Res.* 7, 111–129.
- Getachew Tesfaye, Demel Teketay, 2005b. The influence of logging on natural regeneration of woody species in Harenne montane forest, Ethiopia. *Ethiop. J. Biol. Sci.* 4, 59–73.
- Getachew Tesfaye, Demel Teketay, Masresha Fetene, 2002. Regeneration of fourteen tree species in Harena forest, southeastern Ethiopia. *Flora* 197, 461–467.
- Gilbert, M., 1995. Euphorbiaceae. In: Edwards, S., Mesfin, Tadesse, Hedberg, L. (Eds.), *Flora of Ethiopia and Eritrea*, vol. 2 (2). The National Herbarium, Addis Ababa University, Addis Ababa and Uppsala University, Uppsala, pp. 265–380.
- Harper, J.L., 1977. *Population Biology of Plants*. Academic Press, London.
- Hedberg, O., 1989. Rosaceae. In: Hedberg, L., Edwards, S. (Eds.), *Flora of Ethiopia*, vol. 3. The National Herbarium, Addis Ababa University, Addis Ababa and Uppsala University, Uppsala, pp. 31–44.
- Hubbel, P., Foster, B., 1986. Biology, chance and history and the structure of tropical rainforest communities. In: Diamond, J., Case, J. (Eds.), *Community Ecology*. Harper and Row, New York, pp. 314–329.
- Janzen, M., 1971. The effect of defoliation on fruit bearing branches of the Kentucky Coffee tree, *Gymnocladus dioica* (Leguminosae). *Am. Midl. Nat.* 95, 474–478.
- Legesse Negash, 1995. *Indigenous Trees of Ethiopia. Biology, Uses and Propagation Techniques*. Addis Ababa University, Addis Ababa, Ethiopia.
- Lundgren, B., 1971. Soil studies in a montane forest in Ethiopia. Royal College of Forestry, Department of Forest Ecology and Forest Soils, Research Notes no. 11, Stockholm. 35 pp.
- Lykke, A.M., 1993. Assessment of species composition change in savanna vegetation by means of woody plants' size class distributions and local information. *Biodiv. Conserv.* 7, 1261–1275.
- Masresha Fetene, Yonas Feleke, 2001. Growth and photosynthesis of seedlings of four tree species from a dry tropical Afromontane forest. *J. Trop. Ecol.* 17, 269–2834.
- Müller-Dombois, D., Ellenberg, H., 1974. *Aims and Methods of Vegetation Ecology*. Wiley, New York.
- Pinerio, B., Martínez-Ramos, M., Sarukhan, J., 1984. A population model of *Astrocaryum mexicanum* and a sensitivity analysis to its finite rate of increase. *J. Ecol.* 71, 977–991.
- Polhill, R.M., 1989. Ulmaceae. In: Hedberg, L., Edwards, S. (Eds.), *Flora of Ethiopia*, vol. 3. Addis Ababa University, Addis Ababa and Uppsala University, Uppsala, pp. 266–269.
- Poorter, L., Bongers, F., van Rompaey, A.R., Klerk, M.D., 1996. Regeneration of canopy tree species at five sites in West African moist forest. *For. Ecol. Manage.* 84, 61–69.
- Rao, P., Barik, S.K., Pandey, H.N., Tripathi, R.S., 1990. Community composition and tree population structure in a sub-tropical broad-leaved forest along a disturbance gradient. *Vegetatio* 88, 151–162.
- Saxena, A.K., Singh, S.P., Singh, J.S., 1984. Population structure of forests of Kuman Himalaya. Implications for management. *J. Environ. Manage.* 19, 307–324.
- Silvertown, J., 1982. *Introduction to Plant Population Ecology*. Longman, New York.
- Simon Shibru, Girma Bakcha, 2004. Composition, structure and regeneration status of woody species in Dindin natural forest. *Ethiop. J. Biol. Sci.* 3, 15–35.
- Swaine, M.D., 1996. *Ecology of Tropical Forest Tree Seedlings*. Parthenon Publishing, UNESCO, Paris.
- Swaine, M., Whitmore, T.C., 1988. On the definition of ecological species groups in tropical rain forests. *Vegetatio* 75, 81–86.
- Tamrat Bekele, 1994. *Studies on remnant Afromontane forests on central plateau of Shewa, Ethiopia*. Ph.D. thesis. Uppsala University, Uppsala, Sweden.
- Ter Braak, F., 1995. Ordination. In: Jongman, G., Ter Braak, F., Van Tongeren, R. (Eds.), *Data Analysis in Community and Landscape Ecology*. Cambridge University Press, Cambridge, pp. 91–173.
- von Breitenbach, F., 1963. *The Indigenous Trees of Ethiopia*. Ethiopian Forestry Association, Addis Ababa.
- Whitmore, T., 1996. A review of some aspects of tropical rainforest seedling ecology with suggestions for further enquiry. In: Swaine, M. (Ed.), *The Ecology of Tropical Forest Tree Seedlings*. Parthenon Publishing, Paris, pp. 3–9.
- Zar, J.H., 1996. *Biostatistical Analysis*. Prentice-Hall, Englewood Cliffs, NJ.