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Recruitment, survival and growth of *Olea europaea* subsp. *cuspidata* seedlings and juveniles in dry Afromontane forests of northern Ethiopia

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Abstract: Vast areas of Afromontane forests in Ethiopia have been converted to cropland, shrub land or grazing areas. Hence, knowledge and understanding of the factors affecting the regeneration of tree species is of a paramount importance for the restoration of such areas. The natural regeneration of *Olea europaea* subsp. *cuspidata*, a dominant late-successional species, was studied in five sites in the Afromontane zone in Southern Wello (Ethiopia), for two years (1994-1996). Annual seedling establishment showed marked variation between years and among sites. Recruitment rates during the dry season (October-February) were significantly lower than in the moderately wet (February-June) and wet (June-October) seasons. Sites also showed significant differences related to microclimatic conditions. The survivorship of the seedling cohorts established during the long dry, moderately wet and wet seasons differed significantly, with higher survivorship during the wet season. Mortality was higher for small and large seedlings than for juveniles, and decreased with age. The mean annual relative growth rate for the three size classes showed a marked decrease from 1994-95 to 1995-96 with the highest growth rates consistently found for small seedlings. In a field experiment, seed germination was high after the rainy seasons for both intact and mechanically scarified seeds. In both open and shade treatments the scarified seeds showed higher cumulative germination percentage. For seeds sown in February, the seedlings under shade attained significantly higher height than those in the open and also showed a significantly higher number of leaves. Seeds were still germinating 35 months after sowing, indicating long persistence of the seeds. Rainfall seasonality appears to be a dominant factor influencing the establishment, recruitment rate, survival and growth of *Olea europaea* subsp. *cuspidata* populations, particularly during the early life–cycle stages. The results also indicate the importance of shade and protection from disturbance for successful seedling establishment and growth of *Olea europaea* subsp. *cuspidata.*

Resumen: Vastas áreas de bosques afromontanos en Etiopía han sido transformados en tierras agrícolas, matorrales o áreas de pastoreo. Por lo tanto, el conocimiento y la comprensión de los factores que afectan la regeneración de las especies arbóreas es fundamental para la restauración de dichas áreas. Se estudió la regeneración natural de *Olea europaea* subsp. *cuspidata*, una especie dominante sucesional tardía, en cinco sitios de la zona afromontana en Wello del Sur (Etiopía), durante dos años (1994-1996). El establecimiento anual de plántulas mostró una marcada variación entre años y entre sitios. Las tasas de reclutamiento durante la temporada seca (octubre-febrero) fueron significativamente más bajas que en las estaciones moderadamente húmeda (febrero-junio) y húmeda (junio-octubre). También se encontraron diferencias significativas entre sitios relacionadas con las condiciones microclimáticas. La supervivencia de plántulas difirió significativamente entre las cohortes de plántulas

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establecidas durante la larga estación seca, la moderadamente húmeda y la húmeda, con una mayor supervivencia durante la temporada húmeda. La mortalidad fue mayor entre las plántulas pequeñas y grandes que entre los juveniles, y decreció con la edad. La tasa promedio anual de crecimiento para las tres clases de tamaño mostró un claro decremento de 1994-95 a 1995-96, y las tasas de crecimiento más altas fueron encontradas de manera consistente para las plántulas pequeñas. En un experimento de campo, la germinación de semillas fue alta después de las estaciones lluviosas, tanto para las semillas intactas como para las escarificadas mecánicamente. Tanto en el tratamiento abierto como en el de sombra las semillas escarificadas mostraron un mayor porcentaje acumulado de germinación. Para las semillas plantadas en febrero, las plántulas ubicadas bajo la sombra alcanzaron alturas significativamente mayores que las que estaban creciendo en el sitio abierto, y también mostraron un número de hojas significativamente mayor. Las semillas continuaban germinando 35 meses después de haber sido plantadas, lo que constituye un indicio de su larga persistencia. La estacionalidad en la precipitación parece ser el factor dominante que influye en el establecimiento, la tasa de reclutamiento, la supervivencia y el crecimiento de las poblaciones de *Olea europaea* subsp. *cuspidata*, particularmente durante las etapas tempranas del ciclo de vida. Los resultados también indican la importancia que tienen la sombra y la protección contra el disturbio en el establecimiento exitoso y el crecimiento de plántulas de *Olea europaea* subsp. *cuspidata.*

Resumo: Vastas áreas de florestas Afromontanas na Etiópia foram convertidas em áreas de cultura, zonas arbustivas ou pastagem. Assim, o conhecimento e compreensão dos factores que afectam a regeneração das espécies arbóreas são da maior importância para a restauração dessas áreas. Durante 2 anos (1992-1994) a regeneração natural da *Olea europaea* subsp. *cuspidata*, uma espécie dominante nas espécies da fase final da sucessão, foi estudada em cinco estações na zona Afromontana no sul de Wello (Etiópia). O estabelecimento anual de plântulas mostrou uma variação acentuada entre anos e entre estações. As taxas de restabelecimento durante a estação seca (Outubro-Fevereiro) foram significativamente menores do que na estação moderadamente húmida (Fevereiro-Junho) e húmida (Junho-Outubro). As estações também mostraram diferenças significativas relacionadas com as condições micro-climáticas. A sobrevivência dos grupos de plântulas estabelecidas durante a longa estação seca, a moderadamente húmida e a húmida diferem significativamente, com mais elevada sobrevivência durante a estação húmida. A mortalidade apresentou-se mais elevada para as plântulas pequenas e grandes do que para as juvenis, e decresceu com a idade. A taxa média anual relativa do crescimento para as três classes de dimensão mostrou um decréscimo marcado de 1994-95 a 1995-96 com a mais alta taxa de crescimento consistentemente encontrada para as plântulas pequenas. Numa experiência de campo, a germinação das sementes foi maior após a estação chuvosa para as sementes intactas ou mecanicamente estratificadas. Foi mostrado que nos tratamentos, sem ou com sombreamento, as sementes escarificadas apresentaram uma mais alta percentagem de germinação cumulativa. Para as sementes semeadas em Fevereiro, as plântulas sob sombreamento atingem uma altura significativamente mais elevada do que as semeadas a céu aberto e mostram, também, uma número de folhas significativamente mais elevado. As sementes encontravam-se ainda a germinar 35 meses após sementeira, indicando a longevidade das sementes. A sazonalidade da queda pluviométrica parece ser um factor dominante influenciando o estabelecimento, a taxa de restabelecimento, a sobrevivência e o crescimento das populações de *Olea europaea* subsp. *cuspidata*, particularmente durante os primeiros estágios do ciclo de vida. Os resultados também indicam a importância do sombreamento e da protecção sem distúrbio para o estabelecimento das plântulas e o crescimento com sucesso da *Olea europaea* subsp. *cuspidata*.

Key words: Germination, growth rate, mortality rate, natural regeneration, *Olea europaea,* survivorship.

Introduction

The long history of human disturbance in the Afromontane zone of Ethiopia started with the inception of agriculture about 5000 BP (Anonymous 1997). Today, most of the area suitable for cultivation in Ethiopia is found in this zone, i.e. above 1500 m, and this is where the majority of the human population lives. The natural vegetation in this zone is forest, either "undifferentiated Afromontane forest" with *Podocarpus falcatus* and *Juniperus procera* or “dry single dominant Afromontane forest” with *Juniperus procera* and/or *Olea europaea* L. subsp. *cuspidata* (Wall. ex DC.) Ciffieri (Friis 1992).

Destruction of forest in the Afromontane zone in Wello, northeastern Ethiopia has been documented through carbon dating of charcoal as far back as 2450 BP (Hurni 1985). The forests have been replaced by cultivated fields and by various types of shrublands and grassland (Kebrom *et al.* 1997; Mesfin 1991; Pichi-Sermolli 1957). Intensive use and over-use of forest generally result in damage and degradation (e.g. Silver *et al.* 1996). A change in land holding system occurred in northern Ethiopia at the end of the 17th century (Tewolde 1989). This resulted in a total lack of responsibility for uncultivated rural land. Local people could herd their animals and collect firewood and other commodities from uncultivated rural lands without restrictions (Tewolde 1989). This uncontrolled use of uncultivated land, including natural forest, continued until recent government activities to protect the few remaining forests and rehabilitate former forest. Thus, rehabilitation of the natural forest is a very recent development. Restoration of natural Afromontane forest in Ethiopia has been attempted by protection of hill slopes (cf. Kebrom *et al.* 1997). This has given opportunities to study various ecological processes in the course of succession and to evaluate ways to restore degraded forest ecosystems.

The formation of a seedling bank under the forest canopy is a major regeneration route in dry tropical forest, especially for species of mature forest (Demel 1997). Knowledge of factors influencing seedling and juvenile mortality, survival and growth in natural populations will, therefore, lead to a better understanding of the regeneration processes of trees and has practical applications in the sustainable management of forest tree species (Still 1996).

Olea europaea subsp. *cuspidata* (hereafter referred to as *Olea*) is a dominant late-successional species in the Afromontane zone. *Olea* is a highly esteemed tree in Ethiopia and elsewhere and has a great variety of uses (cf. Dale & Greenway 1961; Jones 1991; Legesse 1995). Because of this importance in combination with the continued degradation of the Afromontane forests, a situation is created where the existence of *Olea* is threatened. The consequence is that its population is dwindling. This work documents recruitment, survival and growth of the seedling and juvenile stages in populations of *Olea* in four secondary dry Afromontane forests in Southern Wello, Ethiopia. A demographic approach was used to examine establishment, recruitment, survival and growth of *Olea* in natural populations and in a field experiment. The following questions were addressed: How do establishment, survival, growth and recruitment rates vary in space and time? How is germination affected by light conditions and seed scarification? Which biotic and abiotic factors influence recruitment, growth and survivorship?

Materials and methods

Study area

Topography and soils

The study was carried out in Southern Wello, Ethiopia, (11° 00′ - 11° 30′ N and 39° 30′ - 40° 00′ E). Southern Wello (Fig. 1) is generally characterised by rough topography (up to 3500 m) with mountains, deeply incised valleys, escarpments and plateaus. Volcanic rocks, mainly basalts of Tertiary age, cover the major part of the study area. The major soil types are Pheozems, Cambisols, Lithosols and Vertisols (Anonymous 1988).

Climate

The altitudinal range of the study sites is 2230 - 2590 m, and the field germination experimental site is 2110 m. The altitude has a decisive influence on temperature and rainfall. Rainfall generally increases and temperature decreases with altitude (Daniel 1990), but rainfall also depends much on local topography. The mean

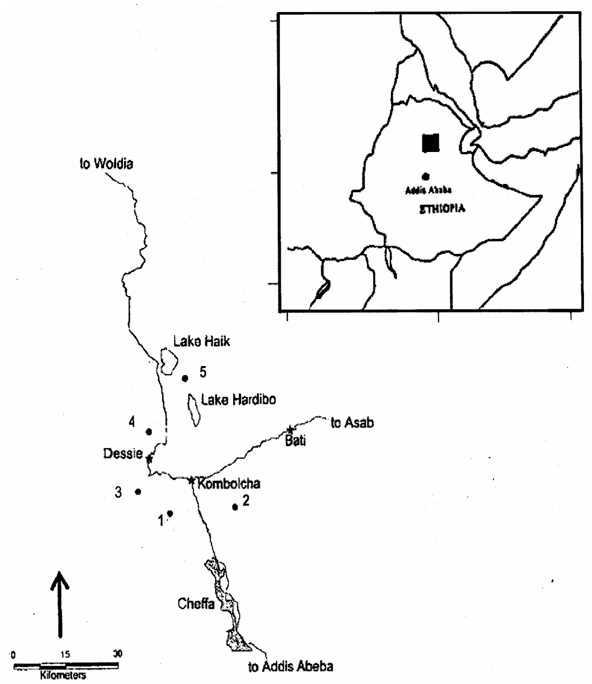

Fig. 1. Location of the study sites.

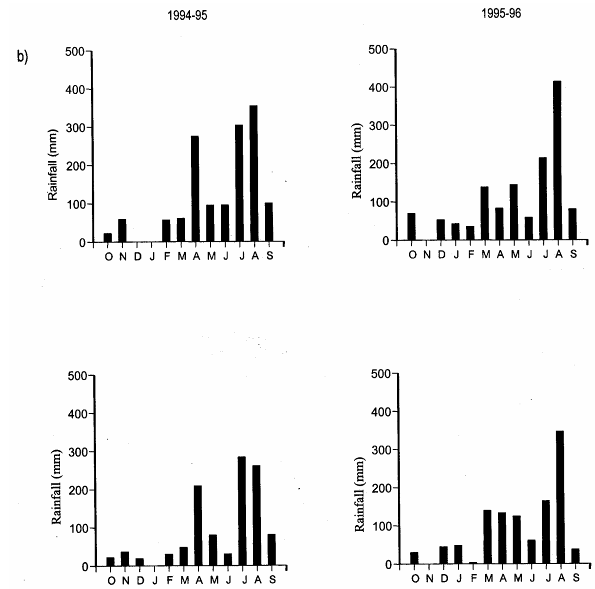

Fig. 2. Monthly rainfall at Dessie (a) and Kombolcha (b) during 1994-95 and 1995-96. Data were obtained from the National Meteorological Services Agency, Addis Ababa.

annual precipitation at Dessie station (2540 m) is 1175 mm year^{-1} (18 years) and at Kombolcha station (1903 m) 1055 mm per year (29 years). The mean annual temperature is 14.9°C at Dessie (9 years) and 18.7 °C at Kombolcha (19 years) (data from National Meteorological Service Agency). The distribution of rainfall is seasonal with one long dry period from October to February and one usually short dry spell from mid May to June. Wet seasons occur from July to the end of September ("big rainy season") and from February to the end of May ("small rainy season"). Total rainfall and the timing of the rains vary considerably, during the small rainy season in particular. The seasonal and inter-annual climatic variation in northern Ethiopia in general and in Wello in particular has been discussed by different authors (Abebe 1977; Daniel 1990; Helldén & Eklundh 1988). Climatic diagram for Dessie and Kombolcha meteorological stations in the proximity of the study sites is presented in Fig. 2.

Description of the sites

The vegetation in Southern Wello is characterized by shrubland, grasslands, regenerating areas with pioneer species such as *Dodonaea angustifolia* and *Euclea racemosa*, degraded areas with little vegetation or devoid of vegetation cover and areas with remnants of Afromontane forests dominated by *Juniperus procera* and *Olea europaea* (Kebrom *et al.* 1997). The permanent plots established for this study were located within the remnant Afromontane forests. The altitude, protection and habitat condition varied among these sites. Demographic data were collected from four populations of *Olea* censused in permanent plots from the natural vegetation (hereafter referred to as "forest sites"). The site had the following characteristics:

1. *Yegof.* Dense forest, including old trees on Mt. Yegof, dominated by *Juniperus procera* and *Olea.* It was protected in 1973 by the Ministry of Agriculture. Human disturbance is small.
2. *Abule.* Small patch of *Juniperus procera-Olea europaea* forest. It is protected, but cutting of trees and cattle grazing were observed.
3. *Harego.* Dense secondary regrowth of *Juniperus procera* and *Olea* along the Dessie - Kombolcha road. This previously degraded and barren land was protected in 1974. The plot was fenced in 1991.

4. *Korke*. Within a site protected in 1974 with scattered *Juniperus procera* and *Olea* located between Dessie and Haik.

Field germination data were collected from the experimental site at *Aloma.* At this site, germination experiment was established within two-fenced plots (30 x 30 m = 900 m^2). There were no mature trees within and around the plot to avoid the possibility of seed rain on the experiment. The area had been protected from human activities and cattle grazing since 1983, and was fenced for the purpose of the experiment in 1993.

Study species

Olea europaea L. ssp. *cuspidata* (Wall. ex DC.) Ciffieri (synonym: *Olea africana* Mill.), the wild olive tree, is widely distributed in dry forests of Ethiopia. It usually reaches 15 m (seldom 25 m) in height and is found in dry forests and forest margins at 1250 - 3100 m (Friis 1992; Legesse 1993). *Olea* is a long-lived tree. It shows strong xeromorphic characteristics and can survive as an adult tree in dry microclimatic conditions (Coetzee 1978). It is eagerly browsed and can withstand heavy browsing. Under favourable conditions, it may flower within 4 - 5 years (Legesse 1995). The fruits are fleshy and eaten by birds, leaving the seed with its hard endocarp.

Methods

Natural populations

Demographic data on establishment, survival and growth were collected from plots of 6 x 15 m at the four forest sites. These sites were subdivided into nine subplots of 2 x 5 m each. Five of these subplots (corners and centre of the plot) were censused seven times from October 1994 to October 1996. At the first census, all *Olea* plants in each subplot were numbered, mapped and categorised in terms of size class (see below). At the following censuses, plants were relocated with the aid of the map and any new seedlings were numbered and added. At each census, the height of each individual was measured to the nearest centimetre and any damage was noted.

The censuses were conducted in October after the big rainy season, in February after the long dry season (which extends from five to six months) and in June after the small rainy season. These sampling months are characterised by the rainfall availability during the census interval and are hereafter referred to as wet (June to October), long dry (October to February) and moderately wet (February to June), respectively.

Size categories

The *Olea* plants were classified in three size categories. Cut-off points between categories were determined by inspecting the frequency distributions of plant heights. The following three categories were defined: Small seedlings (Sd): individuals still bearing cotyledon leaves or attaining a maximum height of 5 cm; Large seedlings (Ls): individuals 5-15 cm high; and Juveniles (Ju): individuals 15-200 cm high. Individuals higher than two meters were not included in this study.

Recruitment rate

Recruitment rate (r_i) was calculated according to Hall & Bawa (1993) as:

$$r_i = 100\ [\ln((N_0+a_i)/N_0)/\ t_i]$$

where, N_0 is the number of individuals at the first census; a_i is number of recruits added to the population at the time of the second census, and t_i is the length of the time interval. Seasonal recruitment rates (t_i = c. 4 months) and annual recruitment rates (t_I = 12 months) were calculated and tested for differences between sites, years and seasons and their interactions using factorial GLM (ANOVA) with resampling (Manly 1997). Seasonal recruitment rates were calculated separately for each subplot.

Transition probabilities

The transition probabilities of growth into higher size classes, remaining in the same class or retrogression into lower classes were calculated by dividing the frequency of transitions from size class *j* to size class *i* over the census period *t* to *t* + 1 (Caswell 1989). The transition periods were from October 1994 to October 1995 and from October 1995 to October 1996. The transition probabilities were examined for the three size categories in each site and year. Stage specific mortality rates were also calculated as 1- the $\sum$ (survival probabilities) for each size category (Bierzychudek 1982).

Seedling survivorship

The survival of newly germinated seedlings was analysed by pooling seedlings from all forest sites. Only the cohorts established in October 1994 - February 1995, February - June 1995 and June - October 1995 were included for survivorship analysis because the remaining cohorts were maintained over only up to three time intervals. The cohorts thus represent establishment during the long dry, moderately wet and wet seasons. Seedlings from the first recording were also excluded from the seedling survivorship analysis, since their age was unknown. Survivorship curves were drawn and differences between the curves were statistically tested with a log-rank test procedure (see Hutchings *et al.* 1991; Pyke & Thompson 1986). The survival of seedlings could not be compared among sites because of limited sample sizes. The survival of small seedlings, large seedlings and juveniles through the dry, moderately wet and wet seasons were examined.

Growth rate

Growth rates were calculated from the difference in height measured in successive censuses. Relative growth rate (RGR), the change in height relative to initial height (cf. Still 1996), was calculated for each size class as follows:

$$RGR = 100(\ln H_2 - \ln H_1) / t$$

where, H_1 is the initial height, and H_2 is the height at time (t+ 1). Annual RGR (t = 1 year) were estimated for each size category.

Field germination experiment

To examine the effects of light conditions and scarfication on seed germination of *Olea,* I conducted a field experiment. In this experiment, I sowed seeds in four experimental plots of 1 x 2.5 m on each of three occasions (February, June and October 1995; hereafter refered to as cohorts). Two plots were under shade (mesh with the size of 5 x 5 mm) and two were in open. In each plot, there were two subplots in which untreated and treated seeds were sown. The seed treatment was mechanical scarification with sand paper. The number of seeds sown in each subplot was 66. The seeds were obtained from the Ministry of Agriculture in the study area and had been collected around site 2 in 1995. Germination, survival, height and number of leaves produced by established seedlings were recorded in June, October and February from February 1995 to October 1996. The experimental period covered 20 months for the February cohort, 16 months for June cohort and 12 months for October cohort. In addition, a final census was also done in January 1998.

Analysis of variance (split-plot) was performed separately for each cohort to examine the effects of light, seed treatment and the interaction between these treatments on germination, survival, growth and number of leaves.

Results

Natural populations

Seedling establishment

A total of 1183 seedlings were found in the forest plots during the study period. Of these, 576 seedlings were present at the time of the first census while 607 were new recruits. Seedlings established in all seasons during the two years except in site 2 (Fig. 3). At site 1, seedling establishment was relatively evenly distributed throughout the study period, which probably reflects the constant fairly moist conditions in the shade under the forest at this site. Seedling establishment at site 2 was the most variable and the lowest among the sites (Fig. 3). The establishment at site 3 showed a tendency to be associated with the moderately wet season of 1995 and the wet season of 1996. At site 4, the establishment was relatively high in the moderately wet season of 1995, but decreased through the rest of the study period with a slight tendency of rising in the wet season of 1995-96 (Fig. 3).

The annual seedling establishment was 0.56, 0.22, 1.84 and 3.32 seedlings per m^2 in 1994-95 for sites 1, 2, 3, and 4, respectively. The establishment for 1995-96 for these sites was 0.72, 0.16, 4.72 and 0.60 seedlings per m^2.

Recruitment rate

Recruitment rates differed significantly among the seasons ($p < 0.001$) and among sites ($p < 0.05$; Table 1). There were also significant season x site and season x site x year interactions. The annual recruitment rate ranged between 11% in site 2 in 1994-95 and 104% in site 3 in 1995-96. The mean

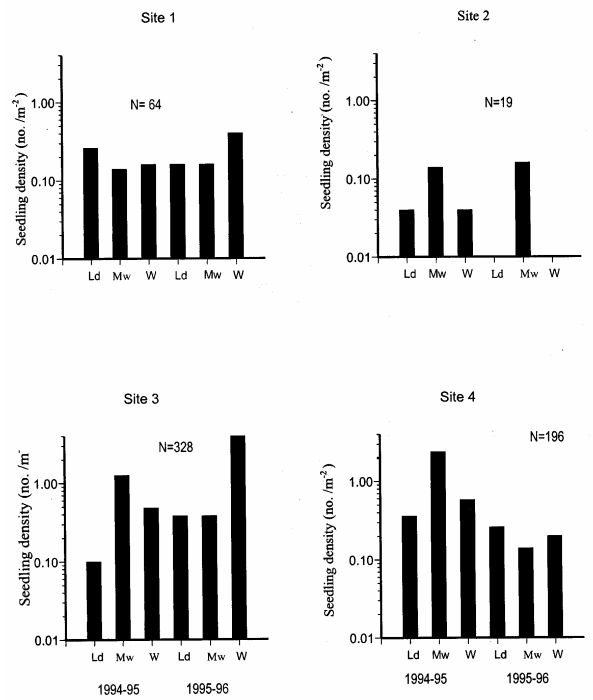

Fig. 3. Establishment of seedlings (no./ m $^{-2}$) of *Olea europaea* ssp. *cuspidata* from plots of 50 m^{-2} each, in Southern Wello (Ethiopia). The establishment was during the long dry (October to February, 'Ld'), moderatly wet (February to June, 'Mw') and wet (June to October 'W') seasons from Oct. 1994 to Oct. 1996 at site 1, site 2 , site 3 and site 4

seasonal recruitment rate was 28.0 ± 15.1 SE for the long dry season, which was significantly lower than 70.8 ± 15.1 SE for the moderately wet and 86.7 ± 15.7 SE for the wet seasons.

Mortality

Mortality was higher among small and large seedlings than among juveniles (Table 2). Site 2 had the highest seedling mortality (94%) of all sites in both years. Retrogression to previous stage was observed in sites 1 and 3 in the second year but was not observed during the first year.

Density and transition probability

The density of *Olea* individuals in different size classes and in each of the four sites is illustrated in Fig. 4. Small seedlings dominated at all sites in 1994-95 and at sites 3 and 4 in 1995-96. Large seedlings dominated at sites 1 and 2 in 1995-96.

Table 1. Analysis of variance results for the effects of season, site, year and the interaction between these on recruitment rate (% yr^{-1}) in *Olea europaea* ssp. *cuspidata* populations in southern Wello, Ethiopia. Factorial GLM ANOVA with resampling (5000) was used. The recruitment rate was calculated following Hall & Bawa (1993).

Source of variation	F	df	p
Season	5.856	2	0.001
Site	3.853	3	0.012
Year	1.076	1	0.320
Season x Site	3.827	6	0.006
Season x Year	1.428	2	0.243
Site x Year	2.603	3	0.0551
Season x Site x Year	5.920	6	0.001

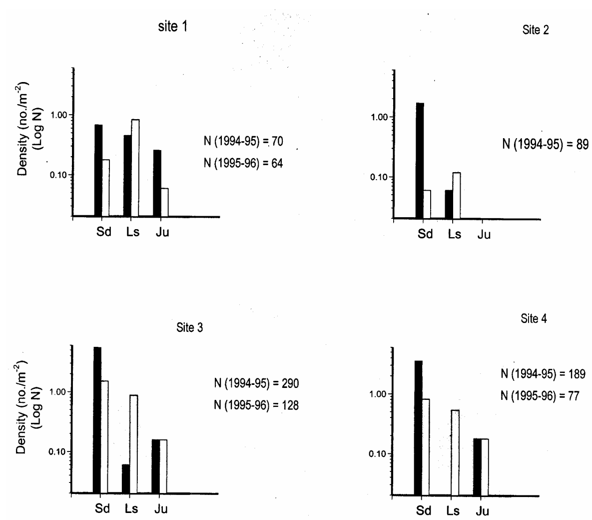

Fig. 4. Density (no./ m^{-2}) of small seedlings (Sd), large seedlings (Ls) and juveniles (Ju) of *Olea europaea* ssp. *cuspidata*). from site 1, site 2, site 3,and site 4 in southern Wello (Ethiopia). The Black (■) bars represent 1994-95 while the open bars (□) represent 1995-96.

Relative growth rate

The annual RGR ranged from - 84 % to 139 % during 1994-95 and from about - 117 % to 77 % in 1995-96. Seven percent (1994-95) and 23 % (1995-96) of the individuals decreased in height (n = 92); about 50 % of these were juveniles. The mean relative growth rate (mRGR) of the three size classes showed a marked decrease from 1994-95 to 1995-96 at all sites (Table 3). There were differences in the mRGR among the size categories with the highest growth rates consistently found for small seedlings (Table 3).

Table 2. Transition probabilities of remaining in the same stage (R), growing to the next stage (G), the stage specific mortality (M) and transition probability for reduction to the previous stage (Rd) of *Olea europaea* ssp. *cuspidata* in different size categories (the definition of the size categories are given in the text) at four sites in dry Afromontane forest in Southern Wello, Ethiopia. The transition periods are 1994-1995 and 1995-1996. The transition from juvenile to higher stage was not considered because higher categories were not used and is denoted by (-). Reduction to the previous stage occurred only in 1995-96.

Sites	Size category	1994-1995			1995-1996			
		R	G	M	R	G	M	Rd
1	Small seedlings	0.029	0.529	0.441	0.0	0.444	0.556	0.0
	Large seedlings	0.304	0.087	0.609	0.714	0.047	0.143	0.095
	Juvenile	0.846	-	0.154	1.000	-	0.0	0.0
2	Small seedlings	0.0	0.059	0.941	0.0	0.0	1.00	0.0
	Large seedlings	0.0	0.0	1.000	0.333	0.0	0.667	0.0
	Juvenile	0.0	-	0.0	0.0	-	0.00	0.0
3	Small seedlings	0.115	0.061	0.824	0.289	0.342	0.368	0.0
	Large seedlings	0.333	0.0	0.667	0.614	0.0	0.341	0.046
	Juvenile	0.889	-	0.111	1.000	-	0.0	0.0
4	Small seedlings	0.045	0.073	0.883	0.073	0.171	0.756	0.0
	Large seedlings	0.0	0.0	1.000	0.259	0.037	0.704	0.0
	Juvenile	1.000	-	0.0	1.000	-	0.0	0.0

Table 3. Mean relative growth rate (mRGR) (%) of *Olea europaea* ssp *cuspidata* for 1994-95 and 1995-96 for each size category (Total N = 92) in dry Afromontane forests in Southern Wello, Ethiopia. Definitions of the size categories are given in the text.

Sites	size category	mRGR % Year 1 (1994-1995)	mRGR % Year 2 (1995-1996)	N
1	Small seedlings	70.4±7.6	9.7 ±8.6	16
	Large seedlings	36.9±4.5	8.0±8.8	9
	Juveniles	2.8±8.6	-18.3±13.6	11
3	Small seedlings	56.2±4.7	19.0±3.8	35
	Large seedlings	-	-	-
	Juveniles	18.9±4.0	8.4±7.3	8
4	Small seedlings	95.2±9.6	21.2±6.7	4
	Large seedlings	-	-	-
	Juveniles	29.9±9.5	19.6±7.4	9

Age-specific seedling survivorship

The survivorship of seedling cohorts established during the long dry (n = 32), moderately wet (n = 177) and wet (n = 45) seasons differed significantly (LR = 3879.9, χ^2 df = 2, $p < 0.001$) with the moderately wet season showing the lowest survival (Fig. 5). Generally, the mortality decreased with age. This was particularly obvious for seedlings established during the long dry and moderately wet seasons (Fig. 5). Seedlings established during the moderately wet season had the highest mortality, losing 70 % of the individuals already during the first four months (Fig. 5).

Stage-specific survivorship

The seasonal survival varied markedly among small seedlings, large seedlings and juveniles, and also among sites as illustrated in Fig. 6. Small seedlings had lower survival than large seedlings and juveniles. Survival of all stages was high at site 1, while that of small and large seedlings was low at sites 2 and 4 (Fig. 6). The long dry season showed low survival, mainly for small and large seedlings, in most sites, but the wet season also had low survival for these stages in sites 2 and 4. The survival of juveniles was consistently high across all sites. Contrary to this, the small and large seedlings showed variation across seasons and sites (Fig. 6).

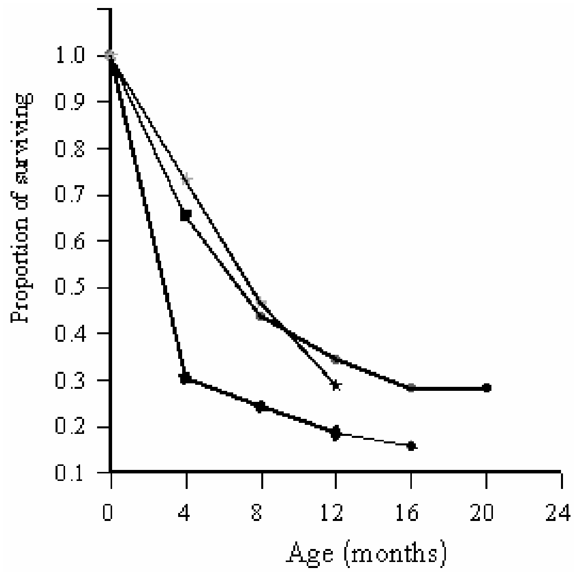

Fig. 5. Seedling survivorship for cohorts of *Olea europaea* ssp. *cuspidata* established during the dry (Oct1994 -Feb1995) (●), moderatly wet (Feb 1995-June 1995) (▲) and wet season (Jun 1995-Oct1995) (■). Age is given as the time since germination. There was significant difference in mortality among the three cohorts (LR = 3879.9, df = 2, p < 0.001). Log rank test was according to Pyke & Thompson (1986) and Hutchings *et al.* (1991).

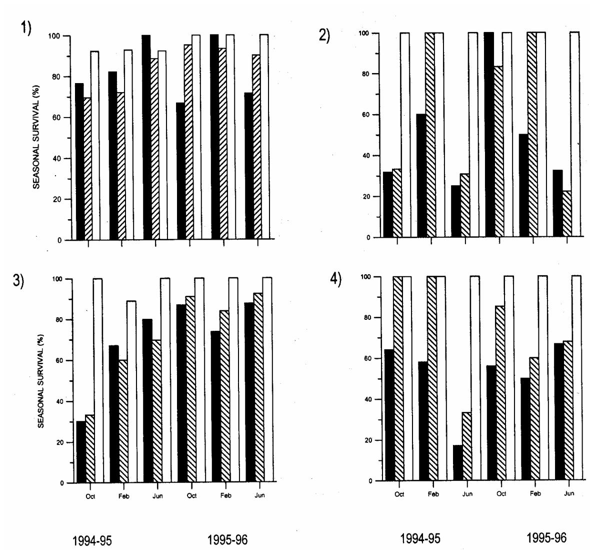

Fig. 6. Survival of *Olea europaea* ssp. *cuspidata* at four sites (1, 2, 3 and 4) in southern Wello, Ethiopia. The black bars represent small seedlings, hatched bars large seedlings and blank bars juveniles, during the the long dry (Ld), moderatly wet (Mw) and wet (W) seasons from October 1994 to October 1996.

Field germination experiment

Seedling establishment

In the field experiment, seed germination was high during the rainy seasons, i.e. during June-October and February-June (Fig. 7) for both intact and mechanically scarified seeds. This suggests that *Olea* seeds can remain in the soil for a relatively long time until adequate moisture is available for germination. Though the difference in cumulative germination between the seed treatments was not statistically significant (Table 4), the proportion of scarified seeds germinating in the open was twice as high as for untreated seeds (Fig. 8a). The same pattern was found in the plots under shade where the proportion of scarified seeds that germinated was 34 % higher than for intact seeds (p = 0.075) (Fig. 8a). Seeds sown in June had very poor germination (4 %).

Survival of the seedlings in both cohorts (Fig. 8 c & d) was not significantly different between the light and seed treatments. Seedlings in the shade grew higher than in the open. This effect was significant (p = 0.05) for the February cohort, but not for the October cohort (Table 4; Fig. 9 a & b). Seedlings under shade also showed a higher number of leaves than unshaded seedlings (Fig. 9 c, d), this difference being significant in February

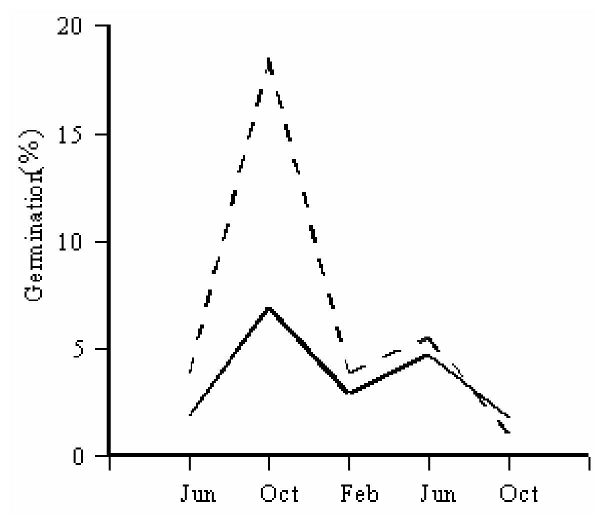

Fig. 7. Percentage germination of *Olea europaea* ssp *cuspidata* in a field experiment in southern Wello, Ethiopia from February 1995 to October 1996. Germination of intact seeds is represented by the continuous line and of mechanically scarified seeds by the discontinuous line.

Table 4. Results of ANOVA (Split - plot design) of cumulative germination, height and number of leaves of *Olea europaea* ssp *cuspidata* seedlings in a field germination experiment in southern Wello (Ethiopia). Light (open and shade) was the whole - plot treatment.

Cohort	Response	Effect	df	F	P
February	Germination (cum.)	Light	1	11.85	0.075
		Seed treatment	1	13.44	0.067
		Plots (Light)	2	0.01	0.921
		Seed treatment x Light	1	5.68	0.150
	Height	Light	1	18.36	0.050
		Seed treatment	1	0.41	0.588
		Plots (Light)	2	0.82	0.461
		Seed treatment x Light	1	0.77	0.565
	Number of leaves	Light	1	50.80	0.019
		Seed treatment	1	0.02	0.891
		Plots (Light)	2	0.69	0.494
		Seed treatment x Light	1	0.25	0.802
October	Germination (cum.)	Light	1	0.14	0.748
		Seed treatment	1	5.19	0.150
		Plots (Light)	2	0.01	0.948
		Seed treatment x Light	1	6.51	0.133
	Height	Light	1	8.95	0.096
		Seed treatment	1	0.52	0.546
		Plots (Light)	2	1.11	0.402
		Seed treatment x Light	1	0.03	0.971
	Number of leaves	Light	1	1.29	0.374
		Seed treatment	1	0.34	0.621
		Plots (Light)	2	1.75	0.317
		Seed treatment x Light	1	0.56	0.640

($p < 0.019$; Table 4).

Germination of *Olea* seeds continued up to 35 months after sowing. Table 5 shows the percentage germination, growth and number of leaves of seedlings scored for the February and October cohorts after 35 and 27 months.

Discussion

The establishment, recruitment rates, survival and growth of seedlings and juveniles of *Olea* in the dry Afromontane forests in Wello have been shown to vary among seasons and between sites in natural populations. Shade and seed scarification were found to influence the germination and growth of seedlings in field experiments.

The long dry season, which extended from five to six months in the study area, clearly explains the low survival of the small *Olea* seedlings during this season, which also concurs with results from previous studies (Swaine *et al.* 1990). The smallest seedlings faced the highest mortality, which is in agreement with findings by other authors (Alvarez-Buylla & Martinez-Ramos 1992; Lieberman 1996). The consistently high survival of juveniles shows that individuals of *Olea* can probably survive adverse factors at this stage. The survival increased as the size increased, which was also found for *Olea europaea* subsp. *sylvestris* (Rey & Alcántara 2000). Seedling survival is affected by inter-annual fluctuation of rainfall in dry forests as reported by several authors (e.g. Garwood 1983; Lieberman & Li 1992). In the case of *Olea,* it can

Table 5. Survival, mean height and mean number of leaves of seedlings of *Olea europaea* ssp. *cuspidata* in a field germination experiment in southern Wello, Ethiopia. The germination (%) is only for the new seedlings scored in January 1998. Seeds sown in February and October 1995 and were scored in January 1998.

Cohort	Seed treatment	Light	Plot	Germination (%)	Survival proportion ± SE	Mean height (cm) ± SE	Mean number of leaves ± SE
February	Intact	Open	1	0.00	0.33 ± 0.33	10.0±0.00	16.0±0.0
	Intact	Open	2	1.52	1.00 ± 0.00	10.0±1.09	10.2±1.8
	Intact	Shade	3	3.03	0.93 ± 0.07	20.2±2.52	20.4±2.9
	Intact	Shade	4	1.52	1.00 ±0 .00	23.0±6.61	25.3±4.9
	Treated	Open	1	3.03	1.00 ± 0.00	8.6±1.38	10.3±2.2
	Treated	Open	2	0.00	0.90 ± 0.10	9.0±1.56	10.1±1.7
	Treated	Shade	3	1.52	1.00 ± 0.00	19.3±1.96	20.7±2.9
	Treated	Shade	4	0.00	1.00 ± 0.00	17.7±2.22	22.7±2.6
October	Intact	Open	1	3.03	0.20 ± 0.08	5.4±0.81	8.4±2.9
	Intact	Open	2	0.00	0.60 ± 0.25	7.0±0.65	7.7±0.7
	Intact	Shade	3	0.00	0.85 ± 0.08	11.7±1.03	14.8±1.7
	Intact	Shade	4	1.52	0.92 ± 0.07	9.3±0.83	9.9±0.9
	Treated	Open	1	0.00	0.56 ± 0.18	7.0±0.89	11.8±1.4
	Treated	Open	2	0.00	0.63 ± 0.18	5.8±0.66	8.8±0.6
	Treated	Shade	3	0.00	0.79 ± 0.09	11.1±1.18	13.8±1.9
	Treated	Shade	4	0.00	0.50 ± 0.05	15.0±0.00	17.5±0.5

be noted that the seedling density was lower during the second year in all sites. In sites 3 and 4 this reduction was observed in spite of fencing at the onset of the study. The existence of an irregular between-year variation in seedling establishment was further suggested by the non-existence of large seedlings at site 4 during the first year. In 1995-96 many of the small seedlings of 1994-95 had grown into large seedling size. The marked decrease in relative growth rate from the first to the second year could probably be due to the inter-annual fluctuation in rainfall.

Seedling establishment can also be influenced by herbivory (Harper 1977). Seedlings of *Olea* are very palatable to wild herbivores, e.g. cattle and goats. Though it was impossible to quantify different types of injury, the height loss/decrease in height was the result of damage on individuals in the population associated with browsing animals. The damage was high at site 2, which could explain the irregular recruitment pattern in this site.

Presence of "safe sites", favourable conditions for breaking seed dormancy and provision of resources necessary for germination (Harper 1977) could also influence the establishment, recruitment rates, survival and growth of *Olea* seedlings. Results from laboratory experiments have shown that the hard endocarp of *Olea* seeds is a major factor in controlling germination, and that various treatments can enhance germination of the seeds (Demel & Granström 1997a & b; Jones 1991; Legesse 1993). For example, Legesse (1993) found that under laboratory conditions, *Olea* seeds with removed endocarps had 92 % germination within 15 days while seeds with intact seed coat (endocarp) did not germinate within three months. In the present study, mechanical treatment of the endocarp with sandpaper tended to increase germination in the February cohort (Fig. 7). Germination of seeds with the endocarp fully removed in field conditions would need its own investigation, but this study shows that the effect of the endocarp on the germination of *Olea* seeds under field conditions is high. Other factors such

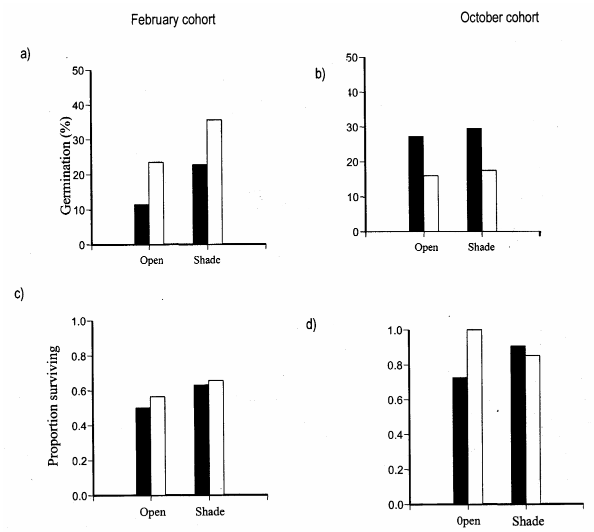

Fig. 8. Cumulative proportion of seeds germinated (a &b) and proportion of seedlings surviving (c & d) of *Olea europaea* ssp *cuspidata* in open and under shade in a field germination experiment in Southern Wello, Ethiopia. The cohorts of February and October were followed for 20 and 12 months respectivly. The black bar (■) represents the intact seeds while the open bar (□) represents seeds treated by rubbing with sand paper (mecanical scarification).

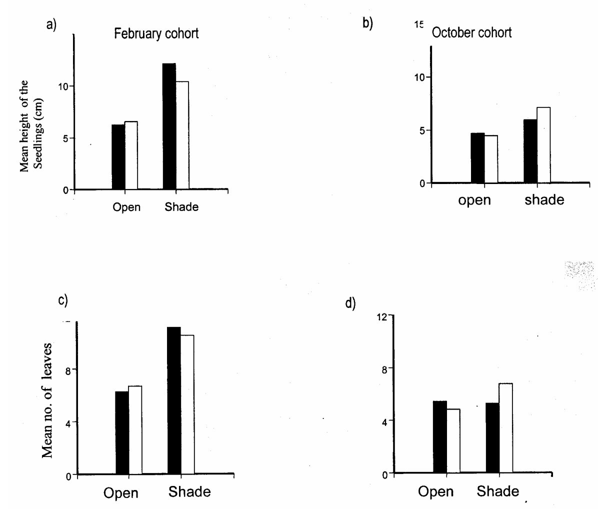

Fig. 9. Mean height (cm) (a & b) and mean number of leaves (c & d) of seedlings of *Olea europaea* ssp *cuspidata* in open and under shade in a field germination experiment in Southern Wello, Ethiopia. The cohorts of February and October were followed for 20 and 12 months respectivly. The black bar (■) represents seedlings of the intact seeds while the open bar (□) represents seedlings of the seeds treated by rubbing with sand paper (mecanical scarification).

as seed maturity, storage, parent plant characteristics and inter-annual weather variation may also influence germination of *Olea* seeds (Jones 1991; Legesse 1993).

Seeds were still found germinating 35 months after sowing (Table 5). This agrees with the results reported by Demel & Granström (1997a), who found the seeds of *Olea* to persist and remain viable after 4 years of experimental burial in forest soils. Germination over a long period of time may contribute to the recruitment observed over several different seasons in the natural populations. The sown seeds continued to germinate for a long time, but there was a tendency of decline in the germination rate over time (Fig. 7). The poor germination among the seeds sown in June could not be explained.

Olea seeds are dispersed by birds (Jones 1991), which may influence the spatial distribution of recruitment (Jordano 1987). Alcántara *et al.* (2000) showed that factors related to the microhabitat played a major role in shaping the seed fall pattern of bird-dispersed *Olea europaea* var. *sylvestris*, thereby influencing the spatial dynamics of recruitment. Chapman & Chapman (1999) emphasized the role of frugivore birds in facilitating seedling recruitment in moist evergreen forest. The observed regeneration of *Olea* in newly protected sites and fenced plots (Tesfaye & Bengtsson manuscript) in the absence of mature *Olea* trees indicate bird dispersal as one possible factor involved.

Natural regeneration of *Olea* is prolific suggesting that natural regeneration will not be difficult provided mature and reproducing individuals still occur in the area. Rainfall seasonality appears to be a dominant factor regulating establishment, recruitment, survival and growth, particularly during the seedling stage. Thus, if seeding is needed, it should take place during periods with adequate soil moisture. However, seeding should be needed only where no reproductive individuals occur in the vicinity. *Olea* seedlings grew better under shade than in the open sun and regeneration for this late successional species should be attempted only when the area is already vegetated. Germination is faster after scarification of the seed, which is, therefore, recommended.

Herbivory is also of greatest importance. Reforestation with *Olea* needs protection from grazing during the seedling stage. Restoration efforts in the Afromontane forests of the degraded highlands need to consider all the factors mentioned above, and more detailed investigations on factors affecting the natural regeneration process of the dominant Afromontane forest species are recommended.

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References

Abebe, A. 1977. *Rainfall Analysis in Mountainous Areas with Special Reference to Conditions in Ethiopia.* M.Sc. Thesis, Agricultural University of Wageningen, the Netherlands.

Alcántara, J.M., P.J. Rey, F. Valera & A.M. Sánches-Lafuente 2000. Factors shaping the seedfall pattern of a bird-dispersed plant. *Ecology* **81:** 1937-1950

Alvarez-Buylla, E.R. & M. Martinez-Ramos 1992. Demography and allometry of *Cecropia obtusifolia*, a neotropical pioneer tree - an evaluation of the climax-pioneer paradigm for tropical rain forests. *Journal of Ecology* **80:** 275-290.

Anonymous. 1988. *National Atlas of Ethiopia.* Ethiopian Mapping Authority, Addis Ababa.

Anonymous. 1997. *National Conservation Strategy of Ethiopia: The Resource Base, its Utilisation and Planning for Sustainability.* Environmental Protection Authority and Ministry of Economic Co-operation, Addis Ababa.

Bierzychudek, P. 1982. The demography of Juck-In-The-Pulpit, a forest perennial that changes sex. *Ecological Monographs* **52:** 335-351

Caswell, H. 1989. *Matrix Population Models*. Sinauer Associates Inc., Sunderland, Massachusetts.

Chapman, C.A. & L.J. Chapman 1999. Forest restoration in abandoned agricultural land: a case study from East Africa. *Conservation Biology* **13:** 1301-1311.

Coetzee, J. A. 1978. Phytogeographical aspects of the montane forests of the chain of mountains on eastern side of Africa. *Erdwiss. Forsch*. **11:** 482-494.

Dale, I.R. & P.J. Greenway 1961. K*enya Trees & Shrubs*. Buchanan's Kenya Est. Ltd., Nairobi.

Daniel, G. 1990. Some patterns of altitudinal variation of climatic elements in the mountainous regions of Ethiopia. pp. 65-78. *In*: B. Messerli & H. Hurni (eds.) *African Mountains and Highlands: Problems and Perspectives*, Walsworth Press Inc., Marceline.

Demel Teketay 1997. Seedling populations and regeneration of woody species in dry Afromontane forests of Ethiopia. *Forest Ecology and Management* **98:** 149-165.

Demel Teketay & A. Granström. 1997a. Seed viability of Afromontane tree species in forest soils. *Journal of Tropical Ecology* **13:** 81-95.

Demel Teketay & A. Granström. 1997b. Germination ecology of forest species from the highlands of Ethiopia. *Journal of Tropical Ecology* **14:** 793-803.

Friis, I. 1992. Forests & forest trees of northeast tropical Africa. *Kew Bull. Add. Ser.* **15:** 1-396.

Garwood, N. C. 1983. Seed germination in a seasonal tropical forest in Panama: a community study. *Ecological Monographs* **53:** 159-181.

Hall, P. & K. Bawa. 1993. Methods to assess the impact of extraction of non-timber tropical forest products on plant populations. *Econnomic Botany* **47:** 234-247.

Harper, J.L. 1977. *Population Biology of Plants*. Academic press, New York.

Helldén, U. & L. Eklundh. 1988. *National Drought Impact Monitoring. A NOAA NDVI and Precipitation Data Study of Ethiopia*. Lund studies in geography. Lund University press. No. 15.

Hutchings, M.J., K.D. Booth & S. Waite. 1991. Comparison of survivorship by the Logrank test: Criticisms and alternatives. *Ecology* **72:** 2290-2293.

Hurni, H. 1985. Erosion - productivity - conservation systems in Ethiopia. pp. 3-9. *Proceeding of 4th International Conference on Soil Conservation, Venezuela*, Jones, P. S. 1991. *Restoration of Juniperus procera and Olea europaea ssp. cuspidata woodlands in Eritrea.* Ph.D. Dissertation. University of Stirling, Scotland.

Jordano, P. 1987. Avian fruit removal: effects of fruit variation, crop size, and insect damage. *Ecology* **68:** 1711-1723.

Kebrom T., I. Backéus, J. Skoglund & Zerihun Woldu. 1997. Vegetation on hill slopes in Southern Wello, Ethiopia: Degradation and regeneration. *Nordic Journal of Botany* **17:** 483-493.

Legesse, N. 1993. Investigations on the germination behaviour of wild olive seeds and the nursery establishment of the germinates. SINET, *Ethiopian Journal of Sciences* **16:** 71-81.

Legesse, N. 1995. *Indigenous Trees of Ethiopia. Biology, Uses and Propagation Techniques*. SLU Reprocentralen Umeå, Sweden.

Lieberman, D. 1996. Demography of tropical tree seedlings: a review. pp. 131-138. *In*: M.D. Swaine (ed.) *The* Ecology *of Tropical Forest Tree Seedlings*. UNESCO, Paris

Lieberman, D. & M. Li. 1992. Seedling recruitment patterns in a tropical dry forest in Ghana. *Journal of Vegetation Science* **3:** 375-382.

Manly, B.F.J. 1997. *Randomization, Bootstrap, and Monte Carlo Methods in Biology.* Chapman & Hall, London.

Mesfin, W.M. 1991. *Suffering under the God's environment: A Vertical Study of the Predicament of Peasants in North-Central Ethiopia.* Walsworth, Marceline.

Pichi-Sermolli, R.E.G. 1957. Una carta geobotanica dell'Africa Orientale (Eritrea, Etiopia, Somalia). *Webbia* **13:** 15-132.

Pyke, D.A. & J.N. Thompson. 1986. Statistical analysis of survival and removal rate experiments. *Ecology* **67:** 240-245.

Rey, P. & J. Alcántara 2000. Recruitment dynamics of a fleshy-fruited plant (*Olea europaea*): connecting patterns of seed dispersal to seedling establishment. *Journal of Ecology* **88:** 622-633

Silver, W. L., S. Brown & A.E. Lugo. 1996. Effects of changes in biodiversity on ecosystem function in tropical forests. *Conservation Biology* **10:** 17-24.

Still, M. J. 1996. Rates of mortality and growth in three groups of Dipterocarp seedlings in Sabah, Malaysia. pp. 315-332. *In*: M.D. Swaine (ed.) *The Ecology of Tropical Forest Tree Seedlings,* UNESCO, Paris.

Swaine, M.D., D. Lieberman & J.B. Hall. 1990. Structure and dynamics of tropical dry forests in Ghana. *Vegetatio* **88:** 31-51.

Tewolde, B.G.E. 1989. The Environmental variables, which led to the ecological crisis in Ethiopia. *Coenoses* **4:** 61-67.