Plant Population Dynamics of *Dodonaea angustifolia* and *Olea europaea* ssp. *cuspidata* in Dry Afromontane Forests of Ethiopia

BY

TESFAYE BEKELE
Human disturbance has led to excessive deforestation and to a very limited forest cover in the Afromontane zone of Ethiopia, which forms a large part of the country. Thus urgent conservation measures are required to ameliorate the situation. Understanding the natural regeneration processes and the dynamics of plant populations of tree and shrub species has a practical application in the restoration of these habitats.

The present study focuses on the population dynamics and regeneration of an early successional shrub *Dodonaea angustifolia* and a late successional tree *Olea europaea ssp. cuspidata* in southern Wello, Ethiopia. Population structure and dynamics, regeneration and seed banks in dry Afromontane habitats were considered.

For both species, three population structure patterns were identified: 1) high density, reversed J-shape structure with many seedlings and few large individuals, 2) lower density, unimodal structure with higher proportions of plants of intermediate size, 3) high density with higher proportions of large plants, in some cases bimodal with small and large individuals. Vegetation type and protection time were found to have a significant effect on the population structure of both species. *Dodonaea* can establish itself on degraded land, once the disturbance has ceased.

Projection matrix analysis on observations from permanent plots in *Dodonaea* populations in protected and unprotected sites resulted in one declining population, and one increasing in the protected site and declining populations at the unprotected site. The overall projected growth rate in *Dodonaea* calculated from a pooled matrix indicated positive population growth. The factors influencing the population growth, recruitment and survival are discussed.

The persistence of *Olea* populations seems to depend on the more stable environmental conditions in later successional stages of forest vegetation. There are possibilities of natural regeneration of *Olea* if regenerating individuals still occur in the area. Rainfall seasonality is a dominant factor in regulating establishment, recruitment, survival and growth, particularly during the seedling stage. Moreover, shade and herbivory are factors that need consideration. Since *Olea* grows better under shade than in the open sun, successful regeneration for this species relies on shade from other plants and on protection from grazing, at least during the seedling stage.

Most of the species that germinated from the seed banks were herbs and grasses with very few shrub and tree species. There was low correspondence between species composition of the seed banks and that of the standing vegetation.

Spatial and temporal variation in demographic parameters among populations of *Dodonaea* and *Olea* can be attributed to human and environmental influence. Under protection, both *Dodonaea* and *Olea* seem to have a possibility to regenerate naturally. Further research should consider factors mentioned in detailed investigations of other dominant Afromontane forest species.

**Key words**: Demography, *Dodonaea angustifolia*, Elasticity, Establishment, Germination, Natural regeneration, *Olea europaea ssp. cuspidata*, Population structure, Recruitment, Seed bank, Survival.

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To my parents,
brothers and sister
This thesis is based on the following four papers, which will be referred to in the summary by their Roman numerals (I – IV).


Paper II is reproduced with kind permission from the Journal

In paper I the co-author was involved in the planning and participated in the field work. Both of us shared responsibility for analysis and writing. Paper II both authors shared responsibilities. Paper III, co-authors were involved in planning, part of the field work, data analysis and writing.
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INTRODUCTION

The high-altitude forests of Ethiopia form part of the Afromontane forest zone (White 1983) which covers most of the highlands of Africa. More than half of the African highlands are found in Ethiopia (Grosjean & Mersserli 1990). The Ethiopian highlands constitute more than 45% of the total area of the country (Anon 1997), and since the climatic and ecological conditions are more suitable than in the lowlands, 88% of the human population and 60% of the livestock are concentrated in these highlands (Constable & Belshaw 1989).

In dry Afromontane forests, the succession after disturbance leads to various seral stages. Without the influence of anthropogenic factors the vegetation of pioneer species like Euclea racemosa and Dodonaea angustifolia leads to Juniperus-Olea forest vegetation (Kebrom et al. 1997) or other Afromontane forest types (Friis 1992). The regeneration of most of the dominant high forest species in the Afromontane zone is under shade of mature forest (Pohjonen 1989). The formation of a seedling-sapling bank under the forest canopy is the major regeneration route (Demel 1997). Therefore, studies of natural regeneration of the dominant species in dry Afromontane forests are relevant for rehabilitation and conservation purposes. Knowledge of factors influencing the dynamics in natural populations will lead to a better understanding of the regeneration processes of trees, and has practical applications in the management of forest tree species (Still 1996). Regeneration dynamics of tropical trees are still poorly known (Condit et al. 1996) especially in the case of species of tropical dry forest (Gerhardt & Hytteborn 1992).

Seasonal and inter-annual climatic influences

Seasonal variation in the distribution of rainfall is one of the most important and dominant ecological factors in tropical dry forests. Generally as few as two to three dry months period are sufficient to alter the composition and structure of the forest ecosystem (Murphy & Lugo 1986). Dry forests appear to show both spatial and seasonal variation of microsites (Gerhardt 1994). Topographic, climatic, and edaphic properties of a dry forest are important factors influencing the ecosystem degradation and rehabilitation process (Murphy & Lugo 1986, Daniel 1990, Gerhardt & Hytteborn 1992, Tamrat 1994). The influence of seasonal and inter-annual climatic variation in East Africa and in the highlands of Ethiopia is reported by several authors (e.g. Helldén & Eklundh 1988, Tewolde 1988, Eklundh 1996, 1998).
Anthropogenic influence on the Afromontane vegetation

Pichi-Sermolli (1957), stated that the montane evergreen shrublands of Northeast tropical Africa are the result of the removal of the original high forest vegetation. However, the degree of human influence and the extent to which the structure and composition of African forests has been modified since the pre-agricultural time is largely unknown (Hamilton 1992). Forest and woodland was said occupy up to 40 % of the land area in Ethiopia, but it is not certain if this area was fully covered with forest within historical times (Anon. 1997).

The human disturbance in the Afromontane zone in Ethiopia started around 5000 years BP with the inception of agriculture (Anon. 1997). The major forest destruction on Mount Badda in Arsi region (Ethiopia) for example occurred around 1850 BP suggesting extensive deforestation in the Afromontane forests. *Dodonaea* is found among the species with increasing pollen quantities, which is believed to be associated to human disturbances on the vegetation (Bonnefille & Hamilton 1986). Carbon dating of charcoal buried in the agricultural highlands in Wello dates back to 2450 BP (Hurni 1987). Besides deforestation for fuel and house construction, the inception of agricultural activities has very much influenced the natural vegetation of the Ethiopian highlands in general and that of Wello in particular for several thousands of years (eg. Hurni 1982, Tewolde 1988, Mesfin 1991, Demel 1996). At the end of the 17th century a change in land holding system in northern Ethiopia also resulted in a total lack of responsibility for uncultivated rural land (Tewolde 1989). Local people could herd their animals and collect firewood and other products from uncultivated rural lands without restrictions (Tewolde 1989, Anon 1997).

In recent times, there has been a dramatic decline of forest cover indicating rapidly vanishing forest resources in the country. Aklog (1990) for example noted that the high forest vegetation of Ethiopia covered about 3.4% of the country in the 1960s. The decline continued to around 2.4% by 1990 (Rodgers 1992).

The depletion of the natural vegetation in many parts of the country has led to the threatening, decline, and extinction of many plant species. Ensermu et al. (1992) listed 120 threatened endemic plant species from Ethiopia. Out of these, 35 species were from dry Afromontane forests and six of them were associated to *Juniperus-Olea* forests. The gene-pool of wild *Coffea arabica* is also at risk because of dwindling montane forests (Tewolde 1990).
In such circumstances where many endemic plant species are at risk, protected forest remnants (both state and community forests) are of very high importance for the conservation of biological diversity. They will not only contribute to the supply of construction material, fuelwood, medicines, the conservation of soil and water and the habitat for wild animals but will also serve as a genetic reserve.

To restore the degraded hillides in the country reforestation with mainly exotic trees such as species of *Eucalyptus*, *Cupressus* and *Pinus* have been practised for some decades. However, these are not without problems. A study on the role of exotic conifer plantations in rehabilitating degraded tropical forest in Uganda (Fimbel & Fimbel 1996) showed that regeneration beneath plantation stands was poor compared to that of the natural forests. Studies of plantations in some parts of Ethiopia by Lisanework & Michelsen (1994) and Michelsen et al. (1996) also showed the associated problems with plantations. Despite the problems of using these exotic plant species for reforestation, they can facilitate the establishment of native forest species and this practice is also found to play an important role in restoring and accelerating natural regeneration of native forest species (e.g. Lübke & Geldenhuys 1991, Parrota 1992, Geldenhuys 1997).

Pohjonen (1989) argued that the dry, hilly and badly eroded bare areas in the highlands of Ethiopia could be transformed into vegetated shrublands, provided that they are protected from human interference. This argument was further supported by field studies in southern Wello (Kebrom 1998). A succession from *Dodonaea-Acacia* dominated bush into *Juniperus-Olea* dominated high forest could be facilitated through intervention of enrichment planting (Pohjonen 1989).

**Plant population dynamics**

Demographic studies in plant populations provide useful information on population dynamics and can also be used to examine the biotic and abiotic factors affecting the plant population dynamics. The information obtained through demographic studies could thus be used in restoration of degraded lands. Many researchers emphasise the need for studying and understanding the population dynamics of rare, endangered or key stone species to find the best way of managing and preserving them within or out of their natural habitat.

The contribution of demographic studies in assessing the status of a population (e.g. Burgman et al. 1993, Shemske et al. 1994) and the role of plant population studies in examining demographic variation in relation to temporal and spatial environmental variation, succession and
nature management has provided important insights (e.g. Menges 1990, Bengtsson 1993, O'Connor 1993, 1994). Moreover, Silvertown & Franco (1993) mention the importance of succession and environmental factors (such as grazing and fire) in altering the relative sensitivity of population growth to changes in fecundity, survival and growth.

Matrix modelling is one of the recommendable methods for analysis of the demographic components of the population dynamics of plant species (Alvarez-Buylla & Garcia-Barrios 1993, Alvarez-Buylla et al. 1996). This gives the possibility of identifying the life history stages that have greatest impact on population growth rate and enables the investigation of the biological processes that most strongly affect the population and the designing of efficient recovery measures (Schemske et al. 1994, Caswell 2000, de Kroon et al. 2000). A demographic approach can also be used to study the regeneration of plant species and factors affecting the spatial and temporal patterns in population size structure.

**Objectives of the study**

The focus of this study is to examine the population ecology of *Dodonaea angustifolia* (hereafter *Dodonaea*), an early successional shrub, and *Olea europaea* ssp. *cuspidata* (hereafter *Olea*), a late successional tree. Both species are important in the Afromontane zone of the Ethiopian highlands. The study, which is part of a research project on natural regeneration of degraded areas of southern Wello, aims at:

1. Describing the patterns of population structure of *Dodonaea* and *Olea* in different habitats and their changes over time,
2. Assessing the possible role of soil seed banks for the ecological rehabilitation of degraded areas in Afromontane zone,
3. Studying the demography of *Dodonaea* in different populations and discussing the implications for conservation and management of the Afromontane forest area,
4. Investigating the regeneration characteristics of *Olea* in natural and experimental populations.

**MATERIALS AND METHODS**

**STUDY AREA**

**Topography and soil**

This study was carried out in southern Wello, Ethiopia, (11°00’- 11°30’ N and 39° 30’- 40°00’ E). The location of the study sites is shown in Fig. 1. The study area is generally characterised by rough topography with
mountains, deeply incised valleys, escarpments and plateaus. Southern Wello, which ranges from 1500 to 3500 m a.s.l. (MPED 1993), is in most parts covered by volcanic rocks, mainly basalts of Tertiary age (Anon.1988).

The major soil types in southern Wello are Cambisols, Arenosols, Lithosols and Vertisols (Anon. 1988, MPED 1993). Due to excessive erosion, large areas are covered by shallow soil. Almost 80% of the area
has a soil depth less than 20 cm leading to low soil productivity and low water holding capacity during periods of irregular rainfall (Henrickson et al. 1983, Barber 1984, Constable & Belshaw 1989, Hurni 1988).

**Climate**

The distribution of rainfall in southern Wello is characterised by wet seasons that mostly occur from July to September (big rainy season), locally known as "Kiremt", and February to May (small rainy season), locally known as "Belg". The small rainy season is erratic and highly variable. There is a long dry period from the end of September to February, and a short dry spell in June. Altitude has a decisive influence on temperature and rainfall. Rainfall generally increases and temperature decreases with altitude (Abebe 1977, Daniel 1990). The rainfall of the Dessie and Kombolcha stations during the study period is presented in (Fig. 2).

**Natural vegetation**

The natural vegetation of the study area is broadly classified as *Juniperus procera* forest or "dry single dominant Afromontane forest" with *J. procera* and/or *Olea* as dominant species (Friis 1992, Mesfin 1990). At higher elevations remnants of the original Afromontane forest occur as secondary forest with *Juniperus procera*, *Olea* and *Podocarpus falcatus* among the dominant trees. Kebrom et al. (1997) also described various types of seral communities These include shrublands with regenerating pioneer species such as *Dodonaea* and *Euclcea racemosa* and other species such as *Rhus natalensis*, *Dovyalis verrucosa* and *Acacia sieberiana* Grasslands also occur, which are grazed or cut for fodder. Very degraded sites have little cover of herbaceous species (*Arenaria leptoclados*, *Justicia* sp. and *Hypoestes forskalii*) and are characterised by shallow soils or stony outcrops (Kebrom et al. 1997).

**Human population**

According to the 1994 census (CSA 1995), South Wello administrative region had 2.1 million inhabitants. The population increase from 1970 to 1994 is about 81% (CSO 1974, CSA 1995). This clearly shows the pressure on the natural vegetation, since 90% of the people live in rural areas and are engaged in rain fed crop production and animal husbandry. The seriousness of this situation in the highlands of Ethiopia was emphasised by Messerli et al. (1990).
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
STUDY SPECIES

*Dodonaea angustifolia* L. f. (Sapindaceae) a small tree or shrub, commonly up to 8 m high, widely distributed within and below the Afromontane zone and occurs throughout the tropics and subtropics (Leenhouts 1983, Friis 1992). It was earlier included in *Dodonaea viscosa*. It grows at the altitudes between 800 and 2650 m a.s.l. and in areas with a rainfall range of 500-1500 mm/year (Friis 1992). It grows in a variety of habitats and rapidly colonises open areas of recently cleared forests, invades overgrazed bushlands and fallow lands and is usually found in rocky and stony sites. It can withstand fires to an amazing degree (Beentje 1994, Hedberg & Edwards 1989). Succession of bushy vegetation of pioneer species like *Dodonaea* and *Acacia abyssinica* may lead to mature Afromontane forests (cf. Pohjonen 1989).

*Dodonaea* is an evergreen shrub and without thorns and buttresses. The diaspore is a winged nut about 1.5 cm in diameter. It produces large numbers of small seeds (about 100 seeds/g) and the seeds are dormant (Demel 1991, Azene 1993). It could be used to reclaim land, and is also good as hedge species and for sand binding (Azene et al. 1993, Beentje 1994). It is not much browsed except when there is a shortage of other palatable plants (Tesfaye B. pers. obs.). The wood is hard and, among other things, is used for firewood, as fencing material and also for making hut roofs in rural areas. In addition to its possible use for reforestation it is therefore a valuable addition for the supply of wood and other needs of the community. According to Jansen (1981), *Dodonaea* is known to have a medicinal value as wound dressing for skin disease in cattle, and in humans as a cure for sore throats and for lowering fever.

*Olea europaea* L. ssp. *cuspidata* (Wall. ex DC.) Ciffieri (synonym: *Olea africana* Mill.), the wild olive tree, is a species widely distributed in dry forest in Ethiopia. It is found in dry forests and forest margins between 1250 and 3100 m a.s.l. and is usually around 15 m high though it can reach in some places up to 25 m in height (Legesse 1993, Friis 1992). *Olea* is a long-lived tree. It shows strong xeromorphic characteristics and as an adult tree it can survive dry microclimatic conditions (Coetzee 1978). It is widely used for house construction, fences and for making household furniture. The bark, the wood, the leaves and the roots are burnt to produce a distinctive smoke used for fermenting and flavouring of traditional beverages "Tela" and "Irgo" (yoghurt) (Legesse 1995). *Olea* also has medicinal value. In southeastern Ethiopia, the processed wood sap is used for curing skin disease and mental problems, and its smoke is used as an insect repellent (Demel
1996). In Kenya the root or the bark decoction is used as a remedy for malaria (Beentje 1994). Detailed medicinal values of *Olea* is presented by Rizk & Gamal (1995). The diverse use of the species has led to its extensive exploitation in Ethiopia and other East African countries (Dale & Greenway 1961, Jones 1991, Legesse 1995).

**SAMPLING METHODS AND DATA ANALYSIS**

**Population structure** (Paper I)

A total of 38 plots (5 m x 20 m) distributed over 11 sites in southern Wello (Fig. 1) were surveyed for occurrence and population size structure of *Dodonaea* and *Olea*. The same sites were also included in an investigation of the soil seed bank (Kebrom & Tesfaye 2000) and for classification of the standing vegetation (Kebrom *et al*. 1997).

The vegetation of the study sites was classified into eight vegetation types by Kebrom *et al*. (1997). We grouped seven of these in three main categories: (1) Forest: *Juniperus-Olea* forest and *O. europaea* woodland on high altitudes (19 plots; types 3 and 4 in Kebrom *et al*. 1997). Mature *O. europaea* trees are present but grazing pressure and the degree of protection are varying. *Dodonaea* may occur but is seldom regenerating. (2) Shrubland: Open shrubland with *Euclea racemosa, Dodonaea, Pterolobium stellatum* and *Jasminium floribundum* on lower altitudes (12 plots; types 1, 2 and 5 in Kebrom *et al*. 1997). *Dodonaea* can be dominating but also sparse depending on grazing pressure. *Olea* may remain as re-sprouting stumps of cut trees. (3) Grassland: Protected or grazed grassland on lower altitudes (7 plots) (types 6 and 7 in Kebrom *et al*. 1997). These are degraded areas dominated by grass, some with *Acacia* spp. and some with high grazing pressure. *Dodonaea* and *Olea* are seldom found.

Most of the plots (34) were situated in areas that had been under governmental protection during time periods of varying lengths to prevent deforestation, and 11 plots were also initially fenced in between 1991 and 1994 and guarded by locally engaged field assistants.

*Dodonaea* and *Olea* plants were censused in 1993 and in 1998. Plant height, flowering, fruiting and the number of cut or browsed individuals were recorded. Based on height, the size structure in each population of the two species was defined in four classes. The reason for choosing height was that most of the individuals were small with stem diameters below 5 cm. For *Dodonaea* the height classes were: (1) <10 cm (2) 10-30 cm, (3) 30-75 cm, (4) >75 cm. For *Olea* the classes were: (1) <10 cm, (2) 10-50 cm, (3) 50-150 cm, (4) >150 cm. Altitude, slope, degree of erosion
and information on duration of protection were measured and collected for each plot.

The population size structures per species, year and plot, treated as independent samples, were grouped into three categories with the average-linkage clustering method using squared Euclidean Distance measure (MINITAB 1997). To avoid effects of density the number of individuals in the different height classes was calculated as proportions of the total number of individuals within each plot.

Changes in population size (unstructured) between years were tested with Wilcoxon's signed rank test for matched samples. The effects of time between censuses of 1993 to 1998, vegetation types, duration of protection and fencing on population size structures in *Dodonaea* and *Olea* were tested with G-tests on different subsets of the overall data.

**Seed banks (Paper II)**

For a soil seed bank study, ten soil samples from each of 49 plots (20 m x 20 m) were studied using the seedling emergence method (Kropác 1966, Roberts 1981). The samples were collected at 5 cm depth and 2 m intervals along a 20 m line. Roots and pebbles were removed from the soil samples. All samples were spread in pots with a surface area of 134 cm² at a depth of 2 cm on top of sterilised sand. Identified seedlings were removed from the pots while the others were either left to grow in the original pots or transplanted to bigger ones until they could be identified.

To examine the seed bank characteristics of different vegetation types, the study plots were grouped into four classes, namely forests, shrublands, grasslands and degraded lands. Seedling density for the identified species, and for their life-forms were examined. The similarity between the species composition in the seed bank and that of the standing vegetation was calculated using Sørensen’s similarity index (Sørensen 1948). The correlation between number of species in the seed bank and that of the standing vegetation was calculated using Spearman’s rank correlation coefficient. To examine the differences in seedling density among vegetation classes, the Kruskal-Wallis test was used. ANOVA was used for differences in species richness and diversity (Zar 1984). Species diversity in the different vegetation classes was calculated using the Shannon-Wiener index (Magurran 1991).

Species in the seed bank were grouped according to their geographical origin. Accordingly, three groups were formed: a) native species that have been in the region for a long time, b) exotic species that have arrived recently and c) uncertain species that could not be easily categorised into native or exotic. The soil seed bank flora was compared
with the flora of the standing vegetation acquired from Kebrom et al. (1997).

**Demography (Papers III & IV)**

A demographic approach was used to analyse the dynamics and regeneration of both study species. The sampling methods and the analyses are given for both species except where mentioned for specific species.

Demographic data were collected from seven permanent plots of 6 m x 15 m area. The plots were subdivided into nine subplots of 2 m x 5 m each. Five of these subplots (corners and centre of the plot) were censused on seven occasions from October 1994 to October 1996. In one of the permanent plots, both species were monitored.

Table 1. Description of the sites of the permanent demographic plots for *Dodonaea angustifolia* and *Olea europaea* ssp. *cuspidata* in southern Wello, Ethiopia. The location of these permanent plots are indicated in Fig. 1.

<table>
<thead>
<tr>
<th>Species</th>
<th>Plot</th>
<th>Altitude</th>
<th>Site conditions</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Olea</em></td>
<td>1</td>
<td>2590</td>
<td>Dense forest with old trees dominated by <em>Juniperus</em> and <em>Olea</em>. It is protected by the government.</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>2230</td>
<td><em>Juniperus</em>–<em>Olea</em> forest. Isolated small patch protected by the government.</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>2300</td>
<td>Dense secondary regrowth of <em>Juniperus</em> and <em>Olea</em>; previously degraded land and regenerated after the protection with some conservation measures. It is under protection of the government.</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>2520</td>
<td><em>Juniperus</em> and <em>Olea</em> forest with scattered old trees. Protected by the government.</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>2110</td>
<td>With scattered <em>Acacia</em>. The site is devoid of mature trees of <em>Juniperus</em> and <em>Olea</em>. Established within a fenced blocks of an area of 30x30 m^2 for field germination experiment.</td>
</tr>
<tr>
<td><em>Dodonaea</em></td>
<td>1</td>
<td>2300</td>
<td>Near <em>Olea</em> plot 3 above. But, is an open part of the forest with few large trees, and shrubs dominating. Hereafter named as &quot;protected-open&quot;.</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>2300</td>
<td>The same as <em>Olea</em> plot 3. Since it is with closed canopy hereafter named as &quot;protected-closed&quot;.</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>1860</td>
<td>The area was protected for 14 years until 1991 and the natural vegetation was recovering. After 1991 the area started to be converted to farmland and grazing fields. This plot is located on steep slope hillside, and hereafter named as &quot;disturbed-slope&quot;.</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>1780</td>
<td>The area is dominated by <em>Carissa edulis</em>, <em>Euclea racemosa</em> and <em>Dodonaea</em>. It was also protected for 14 years until 1991. Hereafter named as &quot;disturbed-rocky&quot;.</td>
</tr>
</tbody>
</table>

These permanent plots were selected based on the population structure survey of both species (see paper I). Descriptions of the sites are given in Table 1.
The first census took place in October after the big rainy season, the second in February after the long dry period and the third in June after the short rainy season in each year, representing periods of high, low and moderate moisture availability within a year. The corners of the plots and subplots were marked to define each subplot. Each individual plant was given a unique number and its position was marked on a scaled map, so that they could be relocated. Surviving, dead and new plants in each consecutive census were identified and recorded. Height of each individual plant was measured to the nearest centimetre; size categories defined for *Dodonaea* and *Olea* are presented in Table 2.

Table 2. Size classes defined for the demographic study of *Dodonaea angustifolia* and regeneration study of *Olea europaea ssp. Cuspidata*.

<table>
<thead>
<tr>
<th>Size class</th>
<th>Definition for the class</th>
<th>Size class</th>
<th>Definition for the class</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stage 1</td>
<td>Seedlings and individuals from the first census attaining a maximum of 10 cm height</td>
<td>Small seedlings</td>
<td>Bearing cotyledon leaves or ( \leq 5 ) cm of height</td>
</tr>
<tr>
<td>Stage 2</td>
<td>Individuals between 10 and 25 cm height</td>
<td>Large seedlings</td>
<td>Height from 5 to 15 cm</td>
</tr>
<tr>
<td>Stage 3</td>
<td>Non-reproductive and reproductive individuals between 25 and 75 cm height</td>
<td>Juveniles</td>
<td>Height from 15 to 200 cm</td>
</tr>
<tr>
<td>Stage 4</td>
<td>Reproductive and non-reproductive Individuals plants above 75 cm</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

**Survivorship and recruitment rates** (Papers III & IV)

Mortality rates for *Dodonaea* were calculated in each census interval according to Sheil & May (1996) and was examined by factorial analysis of variance (ANOVA), after transforming the data to approximate normality (Zar 1984). For *Olea* the stage specific mortality rate was calculated as \( (1 - \sum \text{survival probabilities}) \) for each size category (Bierzychudek 1982).

Differences in age specific survivorship of seedlings among cohorts established in October-February (long dry), February-June (moderately wet) and June-October (wet season) were analysed. For both *Dodonaea* and *Olea* seedling cohorts were pooled from all plots and were then
analysed for the differences among seasons. Survivorship curves were drawn and the differences between the curves were statistically tested with the log-rank test procedure according to Hutchings et al. (1991) and Pyke & Thompson (1986).

Recruitment rates for both species were calculated according to Hall & Bawa (1993) as

\[ r_i = 100 \left[ \ln \left( \frac{(N_0+a_i)}{N_0} \right) / t_i \right] \]

where \( N_0 \) is the number of initial individuals at the first census, \( a_i \) is the number of recruits added to the population at the time of the second census and \( t_i \) the census interval which is 1 year. The rate was tested for differences between plots, years and seasons and their interactions using factorial GLM (ANOVA) with resampling (Manly 1997) for Olea.

**Population projection matrices** (Paper III).

Lefkovitch matrices were used to analyse the demography of Dodonaea in different populations (Caswell 1989, Horvitz & Schemske 1995, Lefkovitch 1965). A total of five projection matrices were determined for pooled populations and for each population over the two-year period 1994-1996.

The basic projection matrix model used in this study is:

\[ n(t+1) = An(t) \]

where \( n(t) \) is a vector of all individuals in the population at time \( t \), classified by stage categories, \( n(t+1) \) is the vector for the population at the next time interval, and \( A \) is the transition matrix that indicates how individuals in each stage category at one time may contribute to each stage one time unit later (Caswell 1989). The size categories are defined in Table 2.

Estimates of fecundity for the transition matrix were calculated using the proportion of reproductive individuals per stage (3 and 4). The projected population growth rate (\( \lambda \)), stable stage distribution, reproductive and elasticity values were calculated from each of the five matrices. The difference between the observed distribution and stable stage distribution was examined using the likelihood ratio, \( G \) (Sokal & Rohlf 1995). Matrices were analysed using PC-MATLAB (MathWorks 1997) to obtain the eigenvalues, eigenvectors, sensitivities and elasticities.
Field germination experiment (Paper IV)

A field experiment was conducted to examine the effects of light conditions and scarification on seed germination of Olea. Seeds were sown in four experimental plots of 1 m x 2.5 m on three occasions (February, June, and October of 1995; hereafter named as cohorts). Two plots were under shade (mesh with the size 5 mm x 5 mm) and two were in open (light). In each plot, there were two subplots with treated (mechanical scarification with sandpaper) and untreated seeds. The number of seeds sown in each subplot was 66.

Germination, survival, height and number of leaves produced by established seedlings were recorded in June, October and February from June 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 done in January 1998. Analysis of variance (split-plot design) was performed separately for each cohort to examine the effects of light, scarification and the interaction between these treatments on germination, survival, growth and number of leaves.

RESULTS AND DISCUSSION

SEED BANKS

Seedlings from 71 species (62 dicots and 9 monocots) and 30 families germinated in the glass house experiment from soil samples collected in the 49 plots. Asteraceae, Caryophyllaceae, Fabaceae and Poaceae accounted for 62 percent of the seedlings. Seedling density ranged from 391 seedlings/m² to 7807 seedlings/m². The mean seedling density in the vegetation classes ranged from 1309 to 2355 seedlings/m². Seedling density was higher in grasslands than in degraded areas ($K = 33.2$, $p < 0.003$) and higher in shrublands than in degraded sites ($K = 31.5$, $p < 0.005$).

Herbs comprised the majority of the seed bank species (75%), followed by grasses, climbers, shrubs and trees. Herbs were dominant in all the vegetation classes. Forest and shrubland soils had a very small number of seedlings belonging to those tree and shrub species growing on the sites. In the forest sites, dominated by Olea and Juniperus trees, only two seeds of woody species germinated, one from each of these two species.

From the identified seedlings, 58% of the total number of species were found to be native. All trees, climbers and shrubs were native species.
together with 57% of the grasses and 49% of the herbs. Of the 41 native species, the forests had the highest share (76%) compared to the shrublands, grasslands and degraded sites.

Forty-two species, most of them herbs, occurred both in the seed bank and in the standing vegetation. These represented 59% of all species in the seed bank but only about 16% of the species in the standing vegetation (Table 3). Sørensen’s index gave an overall 26% floristic similarity between the standing vegetation and in the seed bank.

Dominant tree species in vegetation often do not have soil stored seed banks (Garwood 1989). Dodonaea and Olea seedlings were observed in the standing vegetation, but except for one seedling of Olea they were absent in the seed banks. Dodonaea was not found at all. All seeds in the soil are not likely to germinate, which could be related to various reasons (see paper II). Dodonaea and Olea are both known to have high seed dormancy and long persistence (Jones 1991, Legesse 1993, Demel 1991, 1996). Thus seed dormancy seems to be the most probable reason for the absence or very few appearances of these species in the seed bank in the study area.

Species composition, abundance of seeds in the seed bank (Welling et al. 1988), seed ecology of the species under investigation and floristic similarity between seed banks and standing vegetation are important clues to the possible contribution of the soil seed banks to regeneration processes. More than 30 tree species that were recorded in the standing vegetation did not occur in the seed bank of our study area. The absence of these tree species in the seed bank may, probably, be due to short
viability and dormancy. The fact that trees usually have persistent seedling banks and large seeds which can not be easily dispersed over long distances (Demel & Granström 1995), reduces the possibilities of regeneration from seed bank if the present forests are destroyed. So even if the number of tree seedlings in the seed banks study were few, there is a chance of regeneration if the mature individuals are conserved.

*Dodonaea angustifolia*

**Population structure**

The overall size class distribution for pooled *Dodonaea* populations in 1993 included a high number of small plants (<10 cm) and c. 50% lower numbers in each of the three higher size classes (Fig. 3a). In 1998 the overall structure was slightly bimodal (U-shape) with still a high number of small plants but with the highest proportion of plants in class 4 i.e. taller than 75 cm (Fig. 3a).

*Dodonaea* occurred at least once in 22 plots, with densities ranging from 1 to 247 plants per plot (100 m²). The highest densities were found in plots with longer protection time. The maximum height observed for *Dodonaea* was 4.5 m and the maximum stem diameter was 7 cm. Chopped and browsed individuals accounted for 7% of the total number of plants of both species in 1993 and 1.5% in 1998, but was found to be up to 50% in some sites.

From the result of the cluster analysis three different patterns of population size structure were distinguished (Fig. 4.). The first pattern, type 1, showed a positively skewed population structure with seedlings and small plants dominating while larger sized individuals were few (reverse J-shape, see Fig. 4a). The second pattern, type 2, had higher proportions of individuals in the intermediate size class 3 (not illustrated) and smaller numbers in classes 1 and 4 (bell-shape or sometimes flat, see Fig. 4b). In the third pattern, type 3, the relative frequencies were highest for class 4 (J-shape, see Fig. 4c). The three distribution patterns, in particular type 2, also showed variation among plots within stages (Fig. 4a-c).

Vegetation type had a significant influence on population structure of *Dodonaea* comparing two sites with the same protection regime (Table 4). Duration of protection also had a significant effect on the size structure in plots within the same vegetation type on higher altitude (Table 4).

*Dodonaea* presents a shift over the census period of 52 months from an overall population structure dominated by small plants and seedlings
Fig. 3. Population structure of *Dodonaea angustifolia* and *Olea europaea* ssp. *cuspidata* in Afromontane forest, Ethiopia. The total number of individuals in four different height classes are shown for 1993 (filled bars) and 1998 (white bars). *D. angustifolia* height classes: (1) <10 cm, (2) 10-30 cm, (3) 30-75 cm, (4) >75 cm, *O. europaea* height classes: (1) <10 cm, (2) 10-50 cm, (3) 50-150 cm, (4) >150 cm.
Figure 4. Three types of population structure in *Dodonaea angustifolia* and *Olea europaea* ssp. *cuspidata* in Afromontane forest in Ethiopia. Data were collected in 100m² plots at two occasions, in 1993 and in 1998. The proportion of individuals in four different size stages are shown as averages calculated from the plots in each structure type. Error bars show standard deviation. Size stages, based on height are: 1 = <10 cm, 2 = 10-30 cm, 3 = 30-75 cm, 4 = >75 cm.
(reverse J-shape) to a more U-shaped pattern with numerous plants also in the largest size class. Since most study sites were continuously protected between the two censuses the changes in overall structures can be interpreted partly as effects of protection.

Table 4. Differences in population structure in *Dodonaea angustifolia* and *Olea europaea ssp. cuspidata* between different vegetation types, different duration of protection and fencing at sites in Afromontane forest, Ethiopia. Plots (5 m x 20 m) were censuses in October 1993 and February 1998. G-tests were carried for pooled plots within treatments. The number of plots was 6 for each factor, i.e. 3 for each treatment.

<table>
<thead>
<tr>
<th></th>
<th>G²</th>
<th>p</th>
<th>G²</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forest vs. shrubland</td>
<td>55.83</td>
<td>&lt;0.0001</td>
<td>43.13</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Site 11 – site 4</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>(Dodonaea)</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Long prot. vs. short prot.</td>
<td>37.57</td>
<td>&lt;0.0001</td>
<td>174.29</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Site 7 - 11</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>(Dodonaea)</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fenced vs. unfenced</td>
<td>-</td>
<td>-</td>
<td>3.73</td>
<td>0.29</td>
</tr>
<tr>
<td>Site 11, 7 and 10</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>(Olea)</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The three structure patterns described were, to some extent, associated with different vegetation types and duration of protection. In forest habitats the patterns were mainly of type 2 and 3 but some plots also showed type 1 structures. Protection had different effects on different populations, probably depending on vegetation type and status at the beginning of protection. Studies in tropical dry forest, west African moist forests and savannah ecosystems have also indicated that size class distribution may give an insight of past disturbances and successional trends (e.g. Murphy & Lugo 1986, Chapman & Chapman 1999, Swaine *et al.* 1987, Newbery & Gartlan 1996, Lykke 1998). However, the large variation found among plots shows that the demography of *Dodonaea* is influenced by habitat characteristics and management on a small geographical scale. The species seems to have a good capacity to regenerate naturally under protection. The observed low numbers of really large individuals do not seem to be a major problem at the sites where *Dodonaea* were present at all. It is, however necessary to prevent cutting of larger seed producing trees and also to regulate grazing and browsing, which most likely have a negative effect on seedling establishment and survival in this and other woody species in the Afromontane forest.
**Demography**

Survival and Recruitment rate

The annual mortality rates in *Dodonaea* among the four plots ranged from 10 to 53 % (Fig. 5). The mortality showed variation between the stages with Stage 1 differing significantly from stage 3 and stage 4 ($F = 5.62, P < 0.01$). Stage specific mortality had no significant difference among the plots and between the years.

The annual recruitment rates varied among plots (Fig. 5). The recruitment rate in the disturbed-rocky plots was very low in both years while in the protected-open plot recruitment rate was higher than the mortality rate (Fig. 5). In the protected-closed plot the recruitment and the mortality rates were more or less equal. In the disturbed-slope plot mortality was much higher than the recruitment and this was even more pronounced in the disturbed-rocky plot (Fig. 5).

Age specific survivorship for seedlings established during three
cohorts showed significant difference (Fig. 6) with the June-October cohort showing the lowest seedling survival. Seedlings established in October-February had 45% of their individuals surviving after 24 months. The February-June cohort had 37% surviving after 20 months. Generally, the mortality decreased with age for all cohorts.

Fig. 6. Stage specific mortality rates for *Dodonaea angustifolia* in four study sites in Afromontane habitats, Ethiopia. 1994-95 (black bars) and 1995-1996 (white bars) for protected-open (a), protected-closed (b), disturbed-slope (c) and disturbed-rocky plot. Size classes, based on height: 1 = < 10 cm, 2 = 10-25, 3 = 25-75 and 4 = >75 cm.

October-February had 45% of their individuals surviving after 24 months. The February-June cohort had 37% surviving after 20 months. Generally, the mortality decreased with age for all cohorts.
Pooled matrix

The demographic transition rates varied substantially among the plots. However, the general trend was that the probabilities of individuals surviving and remaining in the same stage were high compared to the probabilities of individuals growing to the next stage. The transition rates of the protected-closed plot were different from the rest of the plots. This plot contained a high number of seedlings, but very few in stage 3 and no plants in stage 4 (Table 5).

Table 5. Transition probability and elasticity matrices of population dynamics of *Dodonaea angustifolia* for pooled observations from all the plots from 1994-96. The population growth rate (λ) are shown in italics and fecundity values are shown in bold. Size classes, based on height: 1 = < 10 cm, 2 = 10-25, 3 = 25-75 and 4 = >75 cm.

<table>
<thead>
<tr>
<th>Transition probabilities</th>
<th>Elasticities</th>
</tr>
</thead>
<tbody>
<tr>
<td>1&lt;sub&gt;t+1&lt;/sub&gt;</td>
<td>0.0641</td>
</tr>
<tr>
<td>2&lt;sub&gt;t+1&lt;/sub&gt;</td>
<td>0.1539</td>
</tr>
<tr>
<td>3&lt;sub&gt;t+1&lt;/sub&gt;</td>
<td>0.0385</td>
</tr>
<tr>
<td>4&lt;sub&gt;t+1&lt;/sub&gt;</td>
<td>0.0265</td>
</tr>
</tbody>
</table>

The pooled matrix constructed from observations in four plots and two years shows the overall population dynamics and the life-cycle of *Dodonaea* (Table 5, Fig 7). The stage-specific survival, the stable-stage distribution, the reproductive values and the elasticity values varied across the stages (Fig. 7).

Plot matrices

The population growth rates (λ) varied between the plots from 0.2916 in the protected-closed plot to 1.1125 in the disturbed-slope plot. (Table 6). The λ values for the disturbed-slope plot and disturbed-rocky plot were both below 1 indicating declining populations (Table 6).

Mortality rates for *Dodonaea* decreased towards the higher size categories. Vulnerability of the small individuals and high survival of the later life-cycle stages is common to many perennial plants (Harper 1977) and it is the smallest seedlings that face the highest mortality.
(Lieberman 1996, Alvarez-Buylla & Martinez-Ramos 1992). The dry season, which extends from about five to six months in the study area (Fig. 2) is probably one of the reasons for the low survival of the seedlings. One other major factor is the disturbances observed, such as grazing or trampling by goats, sheep and cattle in the disturbed site. The low recruitment rate at the disturbed site is probably due to the cutting of

![Graphs showing stage-specific survival rates, stable stage distribution, stage-specific reproductive value, and elasticity value summed across each size class.](image)

Fig. 7. a) Stage specific survival rates  b) the stable stage distribution, c) the stage-specific reproductive value, and d) elasticity value summed across each size class, for *Dodonaea angustifolia* in four study plots in Afrotropical habitats, Ethiopia. The data are based on the observations of all plots from 1994 to 1996. Size classes, based on height: 1 = < 10 cm, 2 = 10-25, 3 = 25-75 and 4 = >75 cm.
the shrub for use by humans. The potential reproductive part of the population is constantly removed, which results in very few seed producing individuals.

*Dodonaea* is mostly found at the edges or in open parts of the forest and not under closed canopy (Hedberg & Edwards 1989, Pohjonen 1989) as is common among pioneer species. In the protected-open plot the *Dodonaea* population is growing and recruitment rate exceeds mortality rate, which indicates good regeneration and population growth under protection. However, as the canopy of the forest closes, the population declines as has occurred in the protected-closed plot. The population

Table 6. Transition matrices of population dynamics for *Dodonaea angustifolia* for transition period from 1994-96 in southern Wello, Ethiopia. a) protected-open, b) protected-closed, c) disturbed-slope and d) disturbed-rocky plot. The population growth rates ($\lambda$) is shown in Italics and fecundity values are shown in bold. Size classes, based on height: 1 = < 10 cm, 2 = 10-25, 3 = 25-75 and 4 = >75 cm.

<table>
<thead>
<tr>
<th>Plot</th>
<th>Transition Probability</th>
<th>$\lambda$</th>
</tr>
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<tbody>
<tr>
<td>a)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1 t+1</td>
<td>0.2500</td>
<td>0.0227</td>
</tr>
<tr>
<td>2 t+1</td>
<td>0.2917</td>
<td>0.1818</td>
</tr>
<tr>
<td>3 t+1</td>
<td>0.0417</td>
<td>0.7500</td>
</tr>
<tr>
<td>4 t+1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>b)</td>
<td>0.0149</td>
<td>0.0702</td>
</tr>
<tr>
<td>2 t+1</td>
<td>0.1642</td>
<td>0.2456</td>
</tr>
<tr>
<td>3 t+1</td>
<td>0</td>
<td>0.0165</td>
</tr>
<tr>
<td>4 t+1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>c)</td>
<td>0.0333</td>
<td>0</td>
</tr>
<tr>
<td>2 t+1</td>
<td>0.1000</td>
<td>0.1429</td>
</tr>
<tr>
<td>3 t+1</td>
<td>0.0667</td>
<td>0.6071</td>
</tr>
<tr>
<td>4 t+1</td>
<td>0</td>
<td>0.0714</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>d)</td>
<td>0.2000</td>
<td>0</td>
</tr>
<tr>
<td>2 t+1</td>
<td>0</td>
<td>0.0455</td>
</tr>
<tr>
<td>3 t+1</td>
<td>0.2000</td>
<td>0.5455</td>
</tr>
<tr>
<td>4 t+1</td>
<td>0</td>
<td>0.0909</td>
</tr>
<tr>
<td></td>
<td></td>
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</tr>
</tbody>
</table>
growth in the protected site seems to be dependent on the existence of open patches containing reproductive individuals, which are sources of seeds for both the open and closed patches of the forest.

The decline in population size in the disturbed site resulted from a combination of lack of reproduction and mortality. In this site, after 14 years of protection the vegetation again suffered from cutting and heavy grazing. Since the main tree species, such as *Juniperus procera* and *Olea* have almost disappeared over time, shrubs such as *Dodonaea* are the targets for the daily needs of the rural people and are also supplying major urban centres with fuelwood where the demand for wood is high. Hence selective cutting of the larger, reproductive *Dodonaea* shrubs seems to have a negative effect on the population growth rate. Trampling of cattle might also have contributed to the high mortality observed.

In the disturbed-slope plot stages 3 and 4 dominated both in the observed and stable stage distributions. This pattern of distribution is mainly due to the disturbance caused by cattle. There may also be differences in local climatic conditions, since the site is at lower altitude and at the periphery of the lowlands and gets less rainfall.

It is clear that *Dodonaea* does not readily endure severe disturbance. Protection of degraded areas is therefore a necessary prerequisite for recovery. Once the disturbance has ceased, *Dodonaea* may grow on highly eroded, stony and rocky hillsides (Pohjonen 1989, Hedberg & Edwards 1989 and own observations). This ability to colonise barren areas suggests that it could be used at early stages of restoration of natural forest, before reintroduction of species such as *Juniperus* and *Olea*.

*Olea europaea* ssp. *cuspidata*

**Population structure**

The total *Olea* population had a skewed size distribution with higher numbers of individuals in class 1 than in the other stages (reverse J-shape) in both years, although the number of small plants was particularly high in 1998 (Fig. 3b). The maximum height for *Olea* was 15.5 m and the maximum d.b.h. was 47 cm. *Olea* also showed the three size structure patterns found for *Dodonaea* (Fig. 4). The number of *Olea* individuals increased in most plots over the period.

Vegetation type had a significant influence on population structure. Fencing had no significant effect on the population structure in *Olea* when comparing fenced plots with unfenced plots (Table 4) with at least 40 individuals. However, fencing and protection had a clear effect on
population density in *Olea* as the number of individuals increased from 1993 to 1998 in almost all plots.

The population structure for *Olea* in 1993 had slightly higher proportions of small plants than larger plants and in 1998 this reverse J-shaped pattern was very distinct. *Olea* maintained mainly the type 1 (reverse J-shape) structure between years, indicating continuous high regeneration and stable mortality rates. Since most study sites were continuously protected between the two censuses the changes in overall structures can be interpreted partly as effects of protection. New recruitment of *Olea* seedlings occurred, either through distant seed dispersal or from a persistent soil seed bank, during the census period in recently fenced plots. The seed regeneration within these plots shows the potential for recovery of the forest vegetation with the help from protection measures.

**Regeneration**

Establishment and Survival

Seedlings of *Olea* were established in all seasons during the two years in three of the four sites (Fig. 8) and showed marked variations among the sites and seasons. The establishment shows a tendency to be associated with the moderately wet and the wet seasons.

Age specific survivorship of the seedling cohorts of *Olea* established during the long dry, moderately wet and wet seasons differed significantly. The mortality rate decreased with age for all cohorts. This was particularly obvious for the seedlings established during the long dry and moderately wet season.

Stage specific survival varied markedly among small seedlings, large seedlings and juveniles and among sites. The small seedlings had the lowest survival probability while the juveniles had the highest. Juvenile survival was consistently high. Mortality was higher among small and large seedlings than among juveniles. Site 2 had the highest seedling mortality (94%) of all the plots in both years.
Fig. 8. Establishment of seedlings (no./m²) of *Olea europaea* ssp. *cuspidata* from plots of 50 m² each, in Southern Wello (Ethiopia). The establishment was during the long dry (October to February, 'Ld'), moderately 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.
Recruitment rates differed significantly among the seasons and among sites (p < 0.05 and p<0.001); (Table 7). There were also significant season x site and season x site x year interactions. The long dry season had the lowest recruitment and differed significantly from the moderately wet and wet seasons. Site 2 had the lowest recruitment rate while site 3 had the highest.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>F</th>
<th>df</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Season</td>
<td>5.856</td>
<td>2</td>
<td>0.001</td>
</tr>
<tr>
<td>Site</td>
<td>3.853</td>
<td>3</td>
<td>0.012</td>
</tr>
<tr>
<td>Year</td>
<td>1.076</td>
<td>1</td>
<td>0.320</td>
</tr>
<tr>
<td>Season x Site</td>
<td>3.827</td>
<td>6</td>
<td>0.006</td>
</tr>
<tr>
<td>Season x Year</td>
<td>1.428</td>
<td>2</td>
<td>0.243</td>
</tr>
<tr>
<td>Site x Year</td>
<td>2.603</td>
<td>3</td>
<td>0.0551</td>
</tr>
<tr>
<td>Season x Site x Year</td>
<td>5.920</td>
<td>6</td>
<td>0.001</td>
</tr>
</tbody>
</table>

Table 7. 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 and Bawa (1993).

Density

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. The density of *Olea* individuals in different size classes and in each of the four sites is illustrated in Fig. 9.
Field germination experiment (Paper III)

In the field experiment, *Olea* seed germination was high after the rainy seasons (Fig.10) for both intact and mechanically scarified seeds. Germination also continued until up to 35 months after sowing, confirming that *Olea* seeds can remain in the soil for a relatively long time until adequate moisture is available for germination.

![Graphs showing germination data](image)

Fig. 9. Density (no./m²) 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 grey bars represent 1995-96.

In both open and shade treatments the scarified seeds showed higher cumulative germination in the February cohort. Seedlings in shade attained higher height than in open and the effect of light on height was significant (p < 0.05) in the February cohort, but not in the October cohort (Table 8). Seedlings in shade also showed a higher number of leaves than in open (Table 8).
In the present study, the significant seasonal variation found in the recruitment of natural population of *Olea* indicates the influence of the rainy seasons on the recruitment rate. The percentage germination in field experiment of *Olea* was also high during the wet season (Fig. 10).

The formation of a seedling bank under the forest canopy is a major regeneration route especially for species of a mature forest (Demel 1997). Non-pioneer species may germinate and often be established in shade (Garwood 1996). As seen in the population structure *Olea* was found regenerating in protected sites in the absence of mature *Olea* trees which probably indicates bird dispersal (Tefsaye & Bengtsson manuscript). It was also seen that *Olea* prefers shade for a better establishment. The existence of the remaining forests is, therefore, very important for the maintenance of the seedling bank and as a seed source of *Olea* seeds from mature *Olea* trees. Direct seeding of *Olea* seeds in areas to be restored might be an alternative to planting. This could also be cheaper than the management of nurseries.

The hard endocarp of *Olea* seeds prevents rapid germination. As was mentioned earlier seeds were found germinating 35 months after sowing. Germination over a long period of time may contribute to the recruitment observed over several different seasons in a natural population. The germination also showed a tendency to decline over time. Laboratory

![Graph showing germination percentage](image-url)
experiments have shown that this is a major factor in controlling germination and that various treatments can enhance germination (Legesse 1993, Jones 1991). The treatment of the hard seed coat (endocarp) of *Olea* is still necessary, if fast germination is to be achieved even in a field condition.

Table 8. 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.

<table>
<thead>
<tr>
<th>Cohort</th>
<th>Response</th>
<th>Effect</th>
<th>df</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>February</td>
<td>Germination (cum.)</td>
<td>Light</td>
<td>1</td>
<td>11.85</td>
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<tr>
<td></td>
<td></td>
<td>Seed treatment</td>
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<td>13.44</td>
<td>0.067</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Plots (Light)</td>
<td>2</td>
<td>0.01</td>
<td>0.921</td>
</tr>
<tr>
<td></td>
<td></td>
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<tr>
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<td>Light</td>
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CONCLUSIONS

The environmental and anthropogenic factors responsible for the variation in Afromontane vegetation affect the dynamics of *Dodonaea* and *Olea*. *Dodonaea* thrives in newly protected open areas but disappears in later stages of succession. *Olea* grows better in shade and remains as a dominant tree later in the succession.

The study has given an insight into the different successional characters of the habitats and the possible implications for natural regeneration. Exotic trees have been used in Ethiopia as nurse crops for the establishment of native forest species, because seedlings of late-successional tree species planted in open areas in many cases die or develop poorly. Indigenous, early successional trees and shrubs could potentially play a similar role in forest rehabilitation with a goal to facilitate natural successional processes. *Dodonaea* is a promising species in this respect. Its ability to colonise barren areas suggests that it could be used at early stages of restoration of natural forest, before reintroduction of species such as *Juniperus procera* and *Olea europaea*. It can, however, not readily endure severe ongoing disturbance. Protection of degraded areas is therefore a necessary prerequisite.

*Olea* was found to regenerate vigorously, despite high seedling mortality, suggesting that natural regeneration will not be difficult provided regenerating individuals still occur in the area. Regeneration of *Olea* was seen also in early stages of protection, but such individuals are likely to become stunted, and *Olea* regeneration should therefore not be attempted until the area is vegetated.

Rainfall seasonality appears to be a dominant factor regulating establishment, recruitment, survival and growth, thus, if seeding is needed, it should take place during periods with adequate soil moisture.

A similar approach to the one used in this study on other species would provide important information for further silvicultural and ecological development. Studies are needed, e.g. on the early successional species *Acacia abyssinica* and the late successional species *Juniperus procera* and *Podocarpus falcatus*.

An assessment of the population structure and status of native plant species is a first step to obtain information on the natural populations and factors affecting them. However, long-term demographic studies are also needed to obtain more detailed knowledge of the species that have a potential use in restoration. Such studies may also give information on how to use these species in a sustainable way.
In a broader context, the natural regeneration and conservation in the fragmented Afrotropical forests in most mountain habitats of Ethiopia and the eventual rehabilitation of the degraded areas may be successful only if there are possibilities of arresting the degrading anthropogenic factors. In this connection hillside closures (making free from human and animal intervention), reduction of human influences such as clearing of vegetation, cattle grazing, and implementation of conservation measures (such as plantation of tree and shrub seedlings native as well as exotic) are important. However, as was also observed in most parts of the study area, such and other measures will not be successful without the participation of the local people. This, in turn, would be possible only if people get the possibility of finding their daily needs without using the areas that need to be restored.

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