

Seed and regeneration ecology in dry Afromontane forests of Ethiopia: II. Forest disturbances and succession

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Abstract: A series of events occur starting from the process of flowering up to the development of mature forest vegetation in the dry Afromontane forests of Ethiopia. Given time, the mature forest vegetation undergoes a series of changes, which are prompted by different types of disturbances. In response to these disturbances, succession is triggered in which different plants use varying strategies to regenerate themselves. The objective of this paper is to present the second part of an overview of the available information on seed and regeneration ecology in dry Afromontane forests (DAF) of Ethiopia. The review focuses on forest disturbances and succession, i.e. types of disturbances; species richness, densities, spatial distribution of soil seed banks and succession in cleared, cultivated and abandoned DAF; forest fire and response of plant communities to fire; and regeneration of native woody plants in tree plantations established after clearing DAF or after clearing DAF and planting of crops. Thematic areas for future research are recommended.

Resumen: Una serie de eventos tienen lugar a partir del proceso de la floración hasta el desarrollo de la vegetación de bosque maduro en la región seca afromontana de Etiopía. Con el tiempo, la vegetación de bosque maduro sufre una serie de cambios desencadenados por diferentes tipos de disturbios. En respuesta a ellos inicia una sucesión en la cual diferentes plantas usan estrategias variables para regenerarse. El objetivo de este artículo es presentar la segunda parte de una revisión de la información disponible sobre ecología de las semillas y la regeneración en bosques secos afromontanos (DAF) de Etiopía. La revisión se enfoca en los disturbios en el bosque y la sucesión, i.e. tipos de disturbios; riqueza de especies, densidades, distribución espacial de los bancos de semillas del suelo y sucesión en DAF aclarados, cultivados y abandonados; incendios forestales y respuestas de las plantas al fuego; y regeneración de plantas nativas leñosas en plantaciones forestales establecidas después de derribar el DAF o después del aclareo del DAF y la plantación de cultivos. Se hacen recomendaciones sobre áreas temáticas para investigaciones futuras.

Resumo: Uma série de eventos, a começar pelo processo de floração até ao desenvolvimento da vegetação da floresta madura, ocorreu na região seca Afromontana. Com o tempo, a vegetação florestal madura sofre uma série de mudanças, que são desencadeadas por diferentes tipos de distúrbios. Em resposta a estes distúrbios, a sucessão é desencadeada e na qual as diferentes plantas usam várias estratégias para regenerar-se. O objectivo deste trabalho é o de apresentar a segunda parte de uma revisão de conjunto quanto à informação disponível sobre a ecologia da semente e da regeneração nas florestas secas Afromontanas (DAF) da Etiópia. A revisão incide sobre os distúrbios e sucessão, i.e. sobre a tipologia dos distúrbios; riqueza específica, densidades, distribuição espacial dos bancos seminais no solo e sucessão em zonas de DAF abatidas, cultivadas e abandonadas; fogos florestais e resposta das

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comunidades vegetais ao fogo; regeneração das plantas lenhosas nativas em plantações florestais estabelecidas depois de corte raso e depois de corte e estabelecimento de culturas. São recomendadas as áreas temáticas para investigação futura.

Key words: Arable site, bark thickness, fire, forest disturbance, native woody species, tree plantations, soil seed banks, succession.

Introduction

In the first part of this paper, a synthesis of available information on the series of events that occur starting from the process of flowering up to the development of mature forest vegetation in the dry Afromontane region of Ethiopia was presented. Given time, the mature forest vegetation undergoes a series of changes, which are prompted by different types of disturbances.

The objective of the second part of the paper is, therefore, to provide a review of results from studies carried out in the dry Afromontane forests on forest disturbance and succession, impacts of clearing and permanent cultivation on the soil seed banks, soil seed bank and succession at an abandoned arable site, forest fire and its impact, response of plant communities to fire and regeneration of native woody species in tree plantations.

Plant nomenclature in this paper follows those of Cufodontis (1953-1972), Edwards *et al.* (1995), Edwards *et al.* (1997), Edwards *et al.* (2000), Friis (1992), Hedberg & Edwards (1989, 1995).

Forest disturbances and succession

Forest canopies are dynamic, changing continually as trees grow up and die and others replace them. Various disturbances initiate a forest growth cycle with three phases: gap, building and mature phases (Whitmore 1975, 1978, 1991). Gaps are the most important part of the cycle since what grows up in a canopy gap determines the composition of the forest for a long time, usually at least decades and sometimes centuries (Brokaw 1985; Denslow 1987; Hartshorn 1980; Whitmore 1975, 1991).

The size of gaps has been shown to determine the species composition of the next cycle. In small gaps climax species that became established in the

shade of the closed forest are released while pioneer species become more abundant in bigger gaps (Brokaw 1985; Denslow 1987; Hartshorn 1980; Whitmore 1991). This is believed to be correlated with the major shift in microclimate near and below the ground, such as light intensity, temperature and drought stress at the soil surface, as gap size increases. In contrast to the natural ones, shifting agriculture, especially with short periods of rotation and coupled with fire, tree felling and road construction are generally more severe disturbances, which hamper natural succession. In most tropical areas, forests are cleared and converted into permanent arable land. Under permanent cultivation, seeds of climax tree species become scarce for regeneration, and woody growth is eliminated by continuous burning and weeding.

Types of disturbances and succession

Evidences from palaeobotanical data indicate that major climatic and vegetation changes occurred in the highlands of Ethiopia during the quaternary and late tertiary period (Bonnefille & Hamilton 1986; Hamilton 1982; Kedamawit 1986). Pollen diagrams for the last 12,000 years in the Rift Valley and at higher altitude show arid vegetation during the late pleistocene and an increase in *Podocarpus falcatus* after 4000 B.P. (Bonnefille & Hamilton 1986). There are different opinions about the implications of increase in *Podocarpus* pollen. Lezine & Bonnefille (1982) interpreted the increase as a result of forest extension at lower altitudes indicating a wetter climate than today while Hamilton (1982) noted that coupled with other types of evidence, the pollen increase in *Podocarpus* indicates climatic aridity. The ice-age aridity, repeated at intervals during the last million years or so, is assumed to be the cause for the poverty of Ethiopian forests in

their species and endemics of forest trees (Bonnefille & Hamilton 1986). Based on evidences from palynological studies, Bonnefille & Hamilton (1986) suggested that in the Arsi Mountains of Ethiopia, the onset of major disturbance, including montane forest destruction, occurred around 1850 B.P., relatively earlier than further south in eastern Africa, e.g. Kenya.

Present day disturbances in dry Afromontane forests include wind throw, both natural and man-made fires, landslides, grazing, tree felling and clearing for cultivation. Among these, the major disturbance is the extensive clearing/burning of forests and converting them into permanent agricultural land. The impact of clearing dry Afromontane forests and converting them into permanently cultivated land on natural succession was assessed by investigating the composition and density of the soil seed bank in recently created gaps and arable land originally covered by forest (Demel 1996, 1997). The regeneration during three years after gap formation was also monitored. In addition, soil seed bank at an abandoned Afromontane arable land (Demel 1998a) and potential response of the soil seed bank on soil samples taken before and after experimental fire in an Afromontane forest and *Acacia* woodland sites (Ericksson *et al.* 2002) were studied.

Impact of clearing and permanent cultivation on soil seed banks

To investigate the impact of clearing and conversion of dry Afromontane forests into arable land on the composition and density of soil seed banks, a study was carried out at GA. In 1992, several gaps were created when the local people cleared portions of the forest for cultivation. Except for very few big trees, all the vegetation was cleared (Demel 1996, 1997). The farmers were stopped from cultivating the gaps since the forest is state owned and the clearings were illegally made. Two of the gaps, one with an area of 2550 m² (30 m x 85 m) and another with 3200 m² (40 m x 80 m), were selected to study the soil seed bank and regeneration. Large areas, which were covered by a similar forest during the study period, have been converted to arable land and kept under permanent cultivation for at least 45 years (Demel 1992). Soil samples were collected from the forest, gaps and arable land to analyze seed banks. The

forest and arable land were sampled only once while the gaps were sampled in two successive years, both in 1994 (gap-94) and 1995 (gap-95) (Demel 1997).

Species richness and density of the soil seed bank

The results revealed that there were 132 species representing 42 families of flowering plants from the litter and top three centimeters soil samples collected in the forest, gap-94, gap-95 and arable land. Of these, 70% were herbs, 14% were trees and shrubs, 11% were grasses and 5% were climbers. The forest had the highest total number of species and the highest proportion of woody species while the arable land had the second highest total number of species and the highest proportion of herbaceous species. The proportion of woody species in gaps and arable land was very low. Only 15 out of 132 species were common to the forest, gaps and arable land. All of these species were herbs including one grass and one sedge species. The forest and gap-95 had the highest number of common species compared with all other combinations. Sixty seven percent of the trees and shrubs and 11% of the herbs were recorded only from the forest soil samples. Similarly, 20% of the herbs were recovered only from the arable land samples (Demel 1997).

The total number of species from gap-94 and the forest (litter layer and soil samples down to nine centimeters) were 115. From the forest soil samples, a total of 92 species: 61 herbs, 18 trees and shrubs, 6 climbers and 7 grasses were recovered. A total of 65 species: 51 herbs, 5 trees and shrubs, 3 climbers and 6 grasses were recorded from gap-94. The forest and gap-94 had 34 herbs, 5 trees and shrubs, 2 climbers and 3 grasses in common. The proportion of woody species was much higher in the forest samples than in gap-94 while the proportion of herbs was higher in gap-94 than the forest (Demel 1997).

The number of seeds in the litter and top three centimeters soil layers (including both germination trials and sieving) corresponded to a seed bank density of 9400 m⁻² in gap-94, 10750 m⁻² in the forest, 14790 m⁻² in gap-95 and 20740 m⁻² in the arable land. When soil samples collected down to 09 cm from gap-94 and the forest were compared, the seed bank densities were 15650 m⁻² and 20100 m⁻², respectively. In all cases, the seed bank was

dominated by a few species. For instance, the 10 species with the highest soil seed density accounted for 91% of the total estimated soil seed bank in gap-95, 89% in arable land, 87% in gap-94 and 68% in the forest. The contribution of a few individual species to the total soil seed bank was also high. For example, the agricultural weed, *Galinsoga parviflora*, alone contributed 61% of the total estimated soil seed bank in the arable land, *Helichrysum foetidum* contributed 31% in gap-95, *Veronica javanica* contributed 23% in gap-94 and 27% in gap-95 and *Crassula alsinoides* contributed 24% in the forest. Woody species contributed 15% of the total estimated soil seed bank in the forest but only less than 1% in the gaps and arable land while the rest is contributed by herbaceous species. Among the species recorded in both gap-94 and gap-95, 46% showed considerable increase, 10% showed more or less no change while 8% showed reduction in their soil seed densities (Demel 1997).

Seeds of several species were recovered by sieving the soil samples after the experiments were terminated and they were categorized as viable, eaten or dead based on visual examination and a cutting test. The total number of seeds recovered from the soil was 908 (representing more than 11 species) from the forest, 132 from gap-94 samples (more than 5 species), 51 from gap-95 samples (more than 4 species) and 16 from the arable land samples (more than one species). Most of the seeds sieved from the soil samples represented woody species, with *Juniperus procera* having the highest number of viable, eaten and dead seeds. From the arable land samples, no seeds of woody species were recovered except a few viable seeds of *Indigofera rothii*. In all cases, the proportion of viable seeds was small compared with the proportion of seeds, which was either eaten or dead (Demel 1997).

Spatial distribution of the soil seed bank

The number of species and density of seeds in the soil showed similar vertical distribution both in the forest and gap-94, with the highest densities in the upper three centimeters of soil and gradually decreasing densities with increasing depth. In all samples, the litter layers had lower number of species and seeds compared with the top three centimeters soil layers. Species differed in the distribution of their seeds in the soil. For instance 22% of the species recorded from the

forest were entirely confined to the litter and top three centimeters soil layers and 15% were confined entirely to the deeper soil layers (03 - 09 cm). Similarly, 32% of the species recorded from the gaps were entirely confined to the litter and top three centimeters soil layers while 19% were recovered only from the deeper layers. Seeds of the remaining species were distributed in at least three of the layers in both cases (Demel 1997).

Progress of succession

The ground in the gaps was completely covered with dense vegetation within a year, mainly with herbaceous species. In the following two years, few herbs conspicuously dominated the regrowth and sprouting shoots of woody species growing to heights of up to three meters. In the first gap the dominant species were, in decreasing order, *Solanum indicum*, *Vernonia* sp., *Laggera crispata* and *Carduus nyassanus* originating from seeds, and *Rhus glutinosa*, *Clusia abyssinica*, *Calpurnia aurea*, *Carissa edulis*, *Ekebergia capensis* and *Croton macrostachyus* sprouting from stumps. In the second gap, the dominating species were, in decreasing order, *Helichrysum foetidum* and *L. crispata* originating from seeds as well as *E. capensis* and *C. abyssinica* from sprouting shoots. Among the dominant colonizers, *H. foetidum*, *L. crispata*, *S. indicum* and *Vernonia* sp. produced a large seed crop in 1995 (Demel 1997).

The few trees left during the formation of the gaps were of the species *Allophylus abyssinicus*, *C. macrostachyus*, *Juniperus procera* and *Podocarpus falcatus*. In 1995, the gaps were colonized both by woody and herbaceous species. The woody regrowth originated mainly from shoots sprouting from stumps. Among the colonizing herbs, *S. indicum* reached more than two meters in height in 1995. Seedlings of *A. abyssinicus*, *Bersama abyssinica*, *E. capensis*, *Discopodium penninervium*, *Dovyalis abyssinica*, *Indigofera rothii*, *Maytenus arbutifolia*, *M. undata*, *Myrsine africana*, *Olea capensis* subsp. *hochstetteri*, *O. europaea* subsp. *cuspidata*, *Rosa abyssinica*, *Sidroxylon oxyacantha* and *Teclea nobilis* were found in the gaps. Herbaceous species, which were observed growing in the gaps but not recovered from the soil seed bank analyses included *Asparagus asiaticus*, *Cynoglossum* sp., *Rubia cordifolia*, *Rumex bequaertii* and *Salvia nilotica* (Demel 1997).

Most of the forests in Ethiopia have been cleared by either slashing or burning or both. The gaps created by slashing the forest vegetation are quickly colonized by plants recruited from the soil seed bank as well as seed rain originating from the surrounding vegetation, pre-existing seedlings and shoots sprouting from stumps of woody species. Most of the stumps of woody species produced abundant coppice shoots, in some cases reaching three meters within three years after cutting. However, since the gaps are cultivated soon after clearance, in most cases permanently, the regrowth is completely removed. Seedlings of woody pioneers germinating from seeds surviving in the soil as well as sprouting shoots from stumps are removed in the first and successive weeding. Stumps are split into pieces or dug out and used for fuelwood. These activities prevent the recovery of woody vegetation by exhausting the sources of woody regrowth while creating favorable conditions for the accumulation of more seeds of herbaceous species in the soil.

With continuous farming, the proportion of herbaceous forest species declines and the seeds of weedy species such as *Galinsoga* and *Guizotia*, which are favored by continuous cultivation, increase rapidly in the soil. As the cultivation progresses, the composition and density of the soil seed bank start to change gradually. The change is more pronounced in the woody component of the seed bank as evidenced from the lower number of woody species in the gaps and arable land than the forest. Seeds of many woody species are short-lived in the soil and dispersal of seeds from the closest forest is poor. Very few multipurpose trees are left on farms and these may or may not produce seeds depending on whether they are young, old, monoecious or dioecious. Since these trees are lopped from time to time, their reproductive capacity is greatly reduced. Even if they produce seeds, which eventually germinate, the seedlings are removed regularly. Consequently, herbs, including grasses, will dominate the soil seed bank since many herbs grow and reproduce quickly from seeds. At the study site and elsewhere in Ethiopia, weeding is done mainly by hand. Since hand weeding is not very effective, especially for some weeds such as grasses, species such as *Crassula alsinoides*, *Spilanthus mauritiana*, *Monopsis stellarioides*, *Veronica abyssinica* and many grasses regenerate from vegetative fragments left

behind during weeding. This contributes further to the building up of herbaceous soil seed bank.

The soil seed density of the gap in 1994, two years after its formation, was lower than in the forest, presumably because of rapid germination and death of seeds following the destruction of vegetation. However, the soil seed density increased substantially a year later and exceeded that of the forest. This could be associated with the input from the seed rain of herbaceous species such as *Digitaria velutina*, *Dicrocephala integrifolia*, *Halichrysum foetidum*, *Dicrocephala chrysanthemifolia* and *Solanum indicum*. The number of seeds of these species increased by 35, 12, 9, 4 and 3 folds in the soil, respectively, between 1994 and 1995. All are herbs with the capacity to grow and reproduce profusely in a relatively short period of time (Demel own observ.). They produce large numbers of small seeds with dormancy mechanisms, which help them to persist in the soil (Demel 1998b). The soil seed density in the top three centimeters soil layer of the arable land was almost two times higher than in the forest. However, the number of species recorded from the arable land was lower than in the forest, and a few species dominated the soil seed bank in the arable land compared with the forest.

Seeds of several woody species and a few herbaceous species were sieved from the soil when the experiments were terminated. A similar trend observed in the germinating seeds was evident from sieved seeds in that the number of species and seeds of woody species was much higher in the forest than in gaps and arable land. Except a few viable seeds of *I. rothii*, seeds of woody species were absent in the arable land soil samples suggesting complete depletion of seeds of woody species and disintegration of dead seeds as a result of continuous cultivation. Many seeds of the woody species sieved from soil samples collected from the forest and gaps, notably *J. procera*, were eaten, providing additional evidence to the importance of predation in reducing the seed population of woody species, especially with relatively large seeds, as already pointed out for dry Afromontane forests (Demel & Granström 1995) and other areas (Louda 1989 and references therein). The results from sieving the soil also provided evidence for mortality due to aging of a large proportion of the seeds of woody species deposited in the soil.

These results indicate that undisturbed gaps in dry Afromontane forests can regenerate quickly from plants recruited from the soil seed bank, sprouting shoots from stumps, pre-existing seedlings surviving the clearing and plants originating from newly dispersed seeds. However, if clearing of these forests is followed by permanent cultivation, almost all of the woody and part of the herbaceous components of the forest soil seed bank will diminish through time and become dominated or replaced by herbaceous, especially weedy species. In addition, regeneration of woody species through sprouting could be prevented by the complete removal of stumps from the arable land. This implies that natural regeneration of dry Afromontane forest areas converted into permanent arable land would be impossible if the adjacent patches of forests are completely removed. Therefore, efforts should increase to conserve the few remaining patches of dry Afromontane forests.

Soil seed bank and succession at an abandoned arable site

Studies on succession and changes in the floristic composition and density of seeds in the soil of Afromontane forest sites abandoned after cultivation are either scanty or completely lacking. However, results from such studies would provide knowledge about the soil flora and the vegetation that is likely to develop at the site in the future. The knowledge would be of practical importance in managing the landscape including the developing vegetation.

Species richness and density of the soil seed bank

A study was carried out on the species diversity, density and spatial distribution of the soil seed bank at a dry Afromontane site (GA) abandoned after clearing and cultivation (Demel 1998a) to determine whether the composition and density of the soil seed bank at the abandoned site was similar to those at the adjacent dry Afromontane forest or to those of the surrounding arable land. The results were also compared with those from soil seed bank studies undertaken earlier at the forest site (Demel & Granström

1995) and the arable land (Demel 1998a) using the same sampling and experimental procedures.

The results revealed that there were at least 89 species representing 29 families of flowering plants (Demel 1998a). Of these, 10 (11%) were woody species (trees/shrubs) while 79 (89%) were herbaceous species. The Asteraceae plant family had the highest number of species (16 species) followed by Poaceae (10 species) and Fabaceae (9 species). The number of viable seeds in the soil samples, from both germination trial and sieving of soil samples, corresponded to a mean seed density down to 9 cm in the soil of 11870 m⁻² (standard error = 3674 seeds m⁻²). The contribution of woody and herbaceous species to the total number of seeds was 07% and 93% respectively. A few herbaceous species dominated the soil seed bank quantitatively; for example, the five species with the highest number of seeds (*Veronica javanica*, *Crassula alsinoides*, *Veronica abyssinica*, *Oldenlandia corymbosa* and *Helichrysum foetidum*) contributed 65% of the total seed density. Out of the 89 species, 37 were represented by five or more seeds, 20 species by two to four seeds, and 30 species by only one seed.

A total of 223 seeds representing more than nine species were recovered from sieving the soil samples after the germination trial was terminated. Out of these, 90% were viable, 3% were eaten by seed predators and 7% were not viable. Only three of the species, namely *Acacia abyssinica*, *Dodonaea angustifolia* and *Indigofera rothii* contributed 71% of the total number of viable seeds sieved from the soil. A few eaten or dead seeds of *Croton macrostachyus*, *Juniperus procera*, *Olea europaea* subsp. *cuspidata*, *Podocarpus falcatus* and *Toddalia asiatica* were recovered during sieving, although they were represented neither by any seedling during the germination trial nor by any viable seed at the time of sieving.

These results indicate that the abandoned site possessed large quantities of buried viable seeds representing many plant species in the soil. The seeds in the soil reflect partly the composition of the standing vegetation at present and partly the vegetation cover that existed in the past at the site. They form part of the existing flora at the site with a great potential as sources of regrowth in the event of any disturbance in the future (Demel 1998a).

Spatial distribution of the seed bank

There was great variation in the spatial distribution of seeds of the species recorded (Demel 1998a). Out of the 89 species, 46 species were recorded from only one sample (frequency = 10%), 41 species from two to nine samples (frequency = 20% - 90%) and only two species from all the ten samples (frequency = 100%). There was a great variation in the number of seeds recovered from the ten samples as evidenced from the large standard error of the mean seed density (SE = 3674 seeds m⁻²) and the large range in seed density within the sample plots (2090 - 37070 seeds/m²). The mean density of seeds and number of species was highest at the top 3 cm soil layer, but declined both at the litter and deeper soil layers. The depth distribution of seeds of many species also showed a similar trend. When the average depth distribution of seeds of each species is considered, 6% of the species were confined to the litter layer (< 1 cm), 37% were found at the topsoil layer (1 - 3 cm) and 57% were distributed at the deeper layers (> 3 cm).

The spatial distribution of seeds of different species varied greatly, both vertically and horizontally (Demel 1998a). These variations may reflect differences of species in terms of seed longevity in the soil, mode of seed dispersal, seed predation and probably differences in local edaphic conditions where seeds land. About 39% of the species recorded in this study have been grouped as persistent soil seed bank species (Demel & Granström 1995), i.e. having more than five viable seeds and an average depth distribution of 1.5 cm or more. With the exception of *Acacia*, *Calpurnia*, and *Dodonaea*, the species, which have been shown in the present study to accumulate buried seeds in the soil have small seeds ranging between 0.03 and 4.0 mg (Demel unpublished). These species have the following characters related to their success in establishing after disturbance: production of numerous small seeds, means of long distance dispersal, formation of persistent soil seed banks and the capacity to remain viable in a dormant state for a long period of time (Thompson 1987; Whitmore 1991).

To determine the dormancy mechanisms in the seeds, germination tests have been performed for some of the species. For example, there were requirements of both light (light with relatively high red/far red ratio; no germination in darkness)

and alternating temperatures for germination in fresh seeds of *Acmella caulirhiza*, *Alchemilla cryptantha*, *Crassula alsinoides*, *Cyperus sesquiflorus* subsp. *appendiculatus*, *Digitaria velutina*, *Eragrostis tenuifolia*, and the three *Veronica* species, only light (light with relatively high red/far red ratio; no germination in darkness) for *Conyza abyssinica*, *C. steudelii*, *Dichrocephala chrysanthemifolia*, *D. integrifolia*, *Galinsoga parviflora*, *Helichrysum foetidum*, *Laggera crispata*, *Monopsis stellarioides* and *Poa leptoclada* and light with relatively high red/far red ratio (germination possible in darkness) and alternating temperatures for *Solanum luteum* and *S. nigrum* species (Demel 1998b; Demel & Granström 1997). Since seeds of most of these species are deeply buried, dormancy of the seeds can be broken only in connection with disturbances.

Progress of succession

The woody species recorded in this study are also favored by disturbances for their regeneration. *A. abyssinica*, *C. aurea*, *Discopodium penninervium*, *D. angustifolia*, *Myrsine africana* and *Polyscias fulva* were recorded neither from the forest samples (Demel & Granström 1995) nor from samples of the arable land (Demel 1997). The available literature on the ecology of these and the other woody species recovered from the soil seed bank (Fichtl & Admasu 1994; Friis 1989, 1992; Gilbert 1989; Hedberg 1989; Thulin 1989; Vollesen 1989) shows that they are successional species. *Acacia*, *Calpurnia*, *Dodonaea* and *Indigofera* possess seeds with hard seed coat that require high temperatures or strong acid for germination (Demel 1996; Demel & Granström 1997). Seeds of *Discopodium* need alternating temperatures and light with relatively high red/far red ratio simultaneously for germination (Demel 2002) while those of *Ficus sur* germinate only in light after dry storage (Demel unpublished). Fresh seeds of *Rhus glutinosa* and *Rubus apetalus* are also dormant and difficult to germinate in the laboratory, even after several treatments including sulphuric acid scarification (Demel unpublished). No germination test was carried out with seeds of *Polyscias*, but the ecology of the species (Fichtl & Admasu 1994) suggests that it is favored by disturbance. Exception among the woody species was *Myrsine africana*, which is known to germinate within a year after dispersal and

establish under forest canopy (Demel 1996; Demel & Granström 1997). Since the seeds of this species are dispersed by birds and possibly by mammals, the seeds can reach the abandoned fields easily.

In Ethiopia, forests are cleared and/or burned, ploughed during the dry season and planted with crops at the beginning of the rainy season. Then, the farming and weeding either continue permanently (Demel 1997) or, in very few cases, they are continued only for some years and the fields are abandoned, mainly due to the decline in fertility of the soil. When the forests or forest clearings are burnt, temperatures often exceed 100°C at and one centimeter below the surface (Ewel *et al.* 1981; Garwood 1989; Uhl *et al.* 1981), and soil surface temperatures become higher on bare soil than under unburned clearings after the burn (Hopkins & Graham 1984; Uhl *et al.* 1981). The high temperature kills seeds of many species lying on the surface or buried in the upper soil layers during the burn, and their seed density could be either eliminated or severely reduced. On the other hand, the high temperatures favor heat-resistant or heat stimulated species such as *Acacia*, *Calpurnia*, *Dodonaea*, *Indigofera* (Demel 1996; Demel & Granström 1997) and other hard-seeded species.

When the cleared sites are abandoned without being burnt, farmed or weeded, the vegetation would regenerate quickly from plants recruited from the soil seed bank, sprouting shoots from stumps, pre-existing seedlings surviving the clearing and plants originating from newly dispersed seeds (Demel 1997; Garwood 1989; Young *et al.* 1987). However, if the farming continues, which is a common practice in countries like Ethiopia (Demel 1997), soil seed bank density and dominance by weedy species rapidly increase while the soil seed bank of forest, especially woody species decline. Species germinating from the seeds surviving in the soil are removed in the first and subsequent weeding. Weedy species originate from the seed rain over long periods and many germinate after the first weeding and reproduce profusely before the second (Demel 1997; Garwood 1989; Kellman 1980; Uhl *et al.* 1981, 1982).

After abandonment, the rate at which the vegetation and soil seed banks return to pre-disturbance densities and composition depends on the severity of initial disturbance and frequency of subsequent disturbances, the duration of

agricultural activity, distance from seed sources of forest species and the regeneration strategy of the colonizing species (Garwood 1989). Because the abandoned site is adjacent to the forest and serves as a seed source, restoration of the vegetation and the build-up of woody pioneers in the seed bank is accelerated. In addition, the few trees of species such as *Juniperus procera* and *Podocarpus falcatus* that have been left intentionally at the cleared site by the farmers, and those of *Acacia* and *Dodonaea* that developed after the clearing are serving as roost for seed dispersers. Evidently, the areas under these trees are colonized by woody species (Demel pers. obser.), indicating dispersal from perches in the trees and the progress of succession at the site. At the time of sampling, the site was occupied by *D. angustifolia*, *A. abyssinica*, *Carissa edulis*, *Rosa abyssinica*, *Pterolobium stellatum*, *Maytenus arbutifolia*, *C. aurea*, *Osyris quadripartita*, *Clusia abyssinica*, *M. africana* and *Vernonia* species with scattered trees of *J. procera* and *P. falcatus*. It is interesting to note that *D. angustifolia* and *A. abyssinica* were found only at the northeastern side of the forest. However, the progress of succession at the site is being slowed down due to cutting of the developing shrubs and small trees for fuelwood or other purposes coupled with heavy pressure from grazing animals. The site may not return to its original composition and structure if these activities continue unabated.

These results show that the abandoned site contained a diversified soil seed bank dominated by herbaceous species and a few woody successional species. Results from Principal Component Analyses (PCA) of the data revealed that the soil seed bank at the abandoned site is more similar to that of the adjacent dry Afromontane forest than to the soil seed bank at the arable land in the surrounding. There is enough evidence at the site showing that regeneration of woody species is being accelerated by dispersal from nearby seed sources. Results from the study and casual observation also indicate that succession at the abandoned site is progressing towards the composition and structure of the nearby dry Afromontane forest vegetation. However, the regeneration of woody species is being slowed down or prevented by the local people who are continually removing wood from the site and by the pressure from grazing animals. Based on the results from this study and other indirect

evidences, it may be hypothesized that at dry Afromontane forest sites of Ethiopia abandoned after clearing and cultivation, succession proceeds from a woodland dominated by either one, several or all of the following species: *Acacia abyssinica*, *Calpurnia aurea*, *Discopodium penninervium*, *Dodonaea angustifolia*, *Ficus sur*, *Indigofera rothii*, species of *Rhus* and *Rubus* to *Juniperus procera*-*Podocarpus falcatus*-*Olea europaea* dominated forest, if human impact and grazing can be prevented. Further research is required to test the hypothesis.

Forest fire and its impacts

Fire is a disturbance factor in ecosystems worldwide and affects the reproduction of many plant species. For some species, it is just one of several disturbances that trigger seed germination and subsequent seedling recruitment, whereas in other 'fire-dependent' species, fire may be required for seedling recruitment. Fire may trigger seed regeneration directly, through the opening of serotinous fruits or cones or by inducing the germination of dormant soil seed banks. Fire may also indirectly initiate seedling recruitment by opening gaps in closed vegetation, thus providing conditions suitable for colonization. There is a multitude of mechanisms for capitalizing upon such disturbances and the particular mode is a function of fire regime, climate, growth form, phylogeny and biogeography (Keeley & Fotheringham 2000).

Both natural and anthropogenic fires could also lead to severe damage to forest resources. For instance, fire is reported to have been responsible for the disappearance of forests in northern Ethiopia (Kinfe 1993), and the culture of setting fire on forests has become a tradition, especially when additional land is required for crop cultivation (Demel 2000). Experience and causal observation show that the occurrence and behavior of fire vary in the various traditionally recognized ecological zones of Ethiopia (Anonymous 1988; Kinfe 1993), although we lack empirical data on the risk of fire hazard in these zones (Demel 2000).

The coldest highlands ("Wuurch" or "Kur")

This zone represents the highland areas above 3,300 m with temperatures between 0 and 10° C

and annual rainfall of 1000-2000 mm. It is a zone that is found above the upper tree line, with species such as *Erica arborea* at the lower reaches and alpine grasses. Sometimes, this zone may be covered with snow/ice. The very cold temperature makes permanent settlement of humans difficult. Therefore, due to the low temperature, occurrence of snow/ice and relatively low fuel load, the risk of fire hazard is very low or completely absent.

The cool highlands ("Dega")

This zone represents the highlands characterized by altitudinal range from 2,300 to 3,300 m, temperatures falling between 10-15° C, annual rainfall between 1000-2000 mm and strong wind. The trees commonly found in this zone include, among others, *Hagenia abyssinica*, *Juniperus procera*, *Prunus africana* and *Arundinaria alpina*. Other features of this zone include accumulation of forest fuel and sloppy terrain. Although the high elevation, which is associated with mild temperature conditions and a more or less even distribution of rainfall, reduces the risk of fire hazard in this zone, the distribution of fire becomes so rapid in the event of its outbreak. This can be attributed to the ample fuel accumulation and strong winds. Once fire is set, the wind carries it quickly to unburned areas, particularly uphill when the areas are mountainous and sloppy. Spot fire can also be carried to other adjacent areas. At times fire in this zone can be continuous and become out of control.

The warm highlands ("Woina Dega")

This zone is characterized by altitude ranges from 1,500 to 2,500 m, temperatures of 15 to 20° C and rainfall ranges between 800 and 2400 mm. It is also characterized by the occurrence of the only two conifers in the country, namely *Juniperus procera* and *Podocarpus falcatus*. The cold and dry parts of these highlands are dominated by *J. procera* while the moist and humid parts support *P. falcatus*, *Albizia* spp., *Ekebergia capensis*, *Hagenia abyssinica*, *Ocotea kenyensis*, *Olea europaea* subsp. *cuspidata*, *Schefflera* spp., *Syzigium guneense*, etc. In this zone two distinct nature of fire are recognized. In the cold dry parts of the mountain escarpments, where *J. procera* dominates, fire hazard may be high owing to

dryness of the area, discontinuous canopy that allows the growth of grasses and other plants as well as strong wind. Assisted by wind, that also dries the fuel and spreads fire, the grass and other biomass burn faster.

The other part of this zone, which is cold, moist and humid, exhibits low risk of fire ignition due to frequent cloud cover and rain. Even if fire outbreaks once in a while, the chance that it will be put out by the frequent rains is high. The high forests in this zone are, characteristically, found on areas of medium to high slopes making the risk of fire spread and hazard a big threat. Fire outbreak during dry seasons, associated with high temperature, low moisture and ample dry fuel, can be devastating in this zone.

Hot and relatively low lying lands ("Kolla")

This zone is characterized by altitude ranging from 400 to 1500 m, annual temperatures of 20 to 25° C and rainfall varying from 400 to 1600 mm. Two distinct sub-zones have been recognized in this zone, namely the moist and dry sub-zones. In the moist sub-zone, the characteristic trees include *Antiaris toxicaria*, *Celtis toka*, *Cordia africana*, *Milicia (Chlorophora) excelsa*, *Aningeria adolfi-friederici*, etc. The drier sub-zone is composed of different species of *Acacia*, *Combretum* and *Commiphora*, *Brucea antidysentrica*, *Tamarindus indica*, etc. Both sub-zones are prone to fire every year owing to high temperatures and evapotranspiration, accumulation of dry fuel and strong wind. However, the dry sub-zone experiences higher fire occurrence and spread compared with the moist sub-zone since the later receives more rainfall than the former. Since most of the areas in this zone are level or with gentle slopes, the role of topography in the spread of fire is significant. Nevertheless, in areas with sloppy terrain, the spread of fire could be very rapid, and at times difficult to control.

The hottest lowlands ("Harror" or "Berha")

This zone represents areas with altitudes less than 500 m, temperature of more than 25° C and annual rainfall less than 400 mm. It is dominated by different species of *Acacia*. As a result of high temperature, little or no moisture and strong wind, this zone experiences frequent fire outbreaks.

Causes and impacts of forest fire in Ethiopia

Owing to the lack of systematic studies on fire in the past, there are no fire statistical data permitting any analysis of causes, risk and extent of damage. However, general information has been accumulating over many years as a result of casual observation and experience that can be used to deduce, at least, the major causes of fire. Forest fires could be either human-induced or natural. People use fire to clear forests for crop cultivation, encourage new growth of grass for grazing animals, get rid off insects, pests and wild animals, fumigate traditional beehives placed on the branches of trees to collect honey and make charcoal. Fire escapes out of the control of people in the last two cases leading to severe damages to forest resources. Natural causes of fire include lightning and heat emanating from unusually very high temperatures (Demel 2000).

As stated above, impacts of fire could be either positive or negative. Although there are no specific studies made, fire favors the regeneration of some species, e.g. several species of *Acacia*, *Entada abyssinica*, *E. africana* and *Piliostigma thonningii* in the field. On the other hand, fire could also be a real hazard to plants, animals, micro-organisms and human beings, in general ecosystems. In 1984 alone, about 308,198 ha of vegetation resources have been burnt in Ethiopia, the largest impact being on high forests. The largest impact from these fires occurred in the year 2000, when about 150,000 ha of forests, 979 ha of natural coffee stands, 17 wild and 332 domestic animals, 2850 traditional beehives, 11 quintals of harvested coffee, 20 quintals of maize, 25 houses and 12 traditional grain storage facilities have been consumed by fire in the Bale and Borena zone of southeastern Ethiopia alone.

Response of plant communities to fire

To understand the role of fire as a disturbance factor in the dry Afromontane region of Ethiopia, fuel characteristics and fire behaviour were studied in two vegetation types: a dry Afromontane forest, an *Acacia* woodland and an ecotone between them in southern Ethiopia (Ericksson *et al.* 2002). Fire behaviour was analysed in experimental fires late in the dry season (February) and the potential response of the soil seed bank was studied using samples

taken before and after fire treatment. Bark thickness was measured, as an indication of fire resistance, on a suit of tree/shrub species representing the two vegetation types and the ecotone between them.

Fuel characteristics

In the dry Afromontane forest, leaf litter dominated the litter fraction, which was arranged in a thin layer of about five centimetres depth on the soil surface. In contrast, the dominant proportion of the fuels in the *Acacia* woodland was dry grasses and herbs, elevated above the ground surface. The average fuel depth in this community was estimated at about 100 cm, providing good conditions for fuel drying and spread of fire. The total fuel biomass in the two vegetation cover types did not differ significantly, but slightly greater values were observed in the *Acacia* woodland compared with the dry Afromontane forest. Biomass of the litter fuel (i.e. leaf litter, dry grasses and herbs), however, differed significantly and was two times greater in the *Acacia* woodland (673 g m^{-2}) than in the dry Afromontane forest (308 g m^{-2}). In contrast, the biomass of woody fine fuels was four times greater in the dry Afromontane forest (300 g m^{-2}) than in the *Acacia* woodland (76 g m^{-2}). The biomass of live fine fuels was also several times greater in the dry Afromontane forest (110 g m^{-2}) than in the *Acacia* woodland (15 g m^{-2}) (Ericksson *et al.* 2002).

The point of fuel moisture content below which the ignition and spread of fire is possible (Holdsworth & Uhl 1997) is around 12% (on a dry mass basis) depending on the fuel type. In the *Acacia* woodland, 40% of the fuel samples were under this threshold. The mean moisture content of fuel components differed significantly both in the *Acacia* woodland and dry Afromontane forest. Mean fuel moisture in the *Acacia* woodland was 17% in litter, 32% in woody fine fuels and 63% in live fine fuels. In the dry Afromontane forest only 10% of the fuel samples had moisture content below the threshold. At the time of ignition, mean fuel moisture contents under open canopy cover was 30% in litter, 32% in woody fine fuels, and 265% in live fine fuels. In areas with closed canopy cover, mean fuel moisture content was 21% in litter, 25% in woody fine fuels, and 356% in live fine fuels.

Sustained combustion was not possible in the dry Afromontane forest, due to the packed arrangement of the leaf litter and its direct contact with the forest floor, which retards drying (Kauffman *et al.* 1988). Live fine fuels also retarded the spread of fire and increased the average moisture content within the fuel bed. Woody fine fuels, dry grasses and herbs burned readily, but as leaf litter formed a thin, relatively compact layer, the present fuels did not sustain a successful fire spread. When dry forests are not accidentally (in exceptionally dry years) or deliberately burned, fire may creep in and consume the thin leaf litter layer on the ground, without noticeable effect on the vegetation (Menaut *et al.* 1995). During the survey in the dry Afromontane forest, no evidences of past fires were found, although burning is frequent at higher altitudes dominated by grasslands (Ericksson pers. obser. in 1997 & 1999). On the forest floor, litter and woody fine fuels dominated fuel composition in an almost even distribution. The amount of woody fine fuels may have been unnaturally low in this study, as the local communities collect most fuel wood in the forest.

In the *Acacia* woodland, the typical fuel bed proved very favourable for fire spread (Ericksson *et al.* 2002). This site has been protected for more than 20 years from anthropogenic disturbances such as tree cutting, cattle grazing, and intentional burning, which has resulted in increasing biomass in the field layer and a large fuel load in the dry seasons. The dry microclimate coupled with abundant distribution of dry grasses and herbs increase its susceptibility to fires. In the natural condition, this environment should be associated with a high fire frequency, but as the surrounding landscape is heavily overgrazed, spread of fire from outside is prevented. Destructive grazing was observed adjacent to the protected study area and had, most likely, reduced the frequency of past fire events.

Fire behavior

The greater biomass in the field layer had accumulated combustible vegetation at the end of the dry season in the *Acacia* woodland. All ignitions were successful and the fires spread vigorously in the community, with significantly high mean rate of spread of 0.79 ± 0.22 (\pm SE) m min^{-1} and mean flame length of 108 ± 63 cm. The

experimental surface fires in the dry Afromontane forest did not propagate successfully. After ignition, the ground fuels alone could not sustain the spread of fire. When the ignition source ceased, the fire fronts only spread between 10-40 cm into the fuel beds. The mean rate of spread in this community ($n = 8$) was $0.11 \pm 0.09 \text{ m min}^{-1}$ and the mean flame length was $31 \pm 12 \text{ cm}$. Plots under open canopy cover had a mean rate of spread of $0.09 \pm 0.03 \text{ m min}^{-1}$ and a mean flame length of $35 \pm 13 \text{ cm}$. While plots with closed canopy cover had a mean rate of spread of $0.14 \pm 0.13 \text{ m min}^{-1}$ ($n = 4$) and a mean flame length of $28 \pm 13 \text{ cm}$. Highest fire intensities in the experiment were achieved when rates of spread and flame lengths were influenced by strong winds, resulting in a high rate of spread. In the *Acacia* woodland, fuel consumption was 100% for all burned plots (Ericksson *et al.* 2002).

Bark thickness

A total of 20 species of trees/shrubs were encountered during the investigation on bark thickness in all the three sites - 4 in the *Acacia* woodland, 9 in the ecotone and 13 in the dry Afromontane forest (Ericksson *et al.* 2002). Of these, *Acacia seyal* occurred in both the *Acacia* woodland and the ecotone while *Albizia gummifera*, *Calpurnia aurea*, *Celtis africana*, *Cordia africana*, *Croton macrostachyus* and *Ficus sur* were recorded both at the ecotone and the dry Afromontane forest. Dry Afromontane forest trees had in general thin barks, ranging from 2.5 mm for *Allophylus abyssinicus* to 9.2 mm for *Croton macrostachyus*. Most species from the dry Afromontane forest site showed a very small increase in bark thickness with increasing diameter. In this study only *Croton macrostachyus*, *Millettia ferruginea* and *Cordia africana* had a clear relation between bark thickness and diameter. Trees in the *Acacia* woodland had thick bark, ranging from *Acacia seyal* having 11.8 mm to *Balanites aegyptiaca* with 15.4 mm. Bark thickness varied greatly for samples taken at the same diameter for both *Acacia senegal* and *Acacia seyal* while *Acacia tortilis* and *Balanites aegyptiaca* had a smaller variation at the same diameter. In the ecotone, trees had medium bark thickness. Here, *Celtis africana* was the tree with the thinnest bark, 4.4 mm, and the thickest was *Acacia etbaica* with 13.4

mm. Most species showed a clear increase in bark thickness with increasing diameter, except *Celtis africana*, which did not generate any trend due to the low variation in tree diameters.

For the species that occurred in more than one habitat, there was a tendency for bark thickness to be greater in the more open habitats. *Acacia seyal* had 5% greater bark thickness in the *Acacia* woodland than in the ecotone. The same relation was found between the ecotone and the dry Afromontane forest, for the five species that occurred at both sites. The mean difference between the sites was greater than 38%, and ranged from *Celtis africana* with 24% greater bark thickness in the ecotone than in the dry Afromontane forest to *Cordia africana* with 57% greater bark thickness in the ecotone than in the dry Afromontane forest.

There was a considerable overlap in tree species composition between the three vegetation types. Several of the forest species and some of the woodland species were also present in the ecotone and these showed a site-related difference in bark thickness (Ericksson *et al.* 2002). Bark tissues protect cambial tissues from fire injury, and there is a strong relationship between bark thickness and peak cambial temperatures during fires (Pinard & Huffman 1997; Uhl & Kauffman 1990). All five species that occurred both in the dry Afromontane forest and the ecotone had greater bark thickness in the latter environment, and as expected, the tree species with the thickest bark were found in the *Acacia* woodland, where fire has been a natural ecological factor in the past. Although bark thickness is the most important variable for protection, cambial temperatures during forest fires are also influenced by external bark structure (Uhl & Kauffman 1990). The coarse-barked *Acacia* species and *Balanites aegyptiaca* have a bark structure that probably affects heat flow to their cambial tissues to reduce the impact of fire. Tree species in the dry Afromontane forest had relatively thin bark and may be vulnerable to low-intensity surface fires (Holdsworth & Uhl 1997).

Densities of soil seed banks

In the samples from the *Acacia* woodland, the number of viable seeds recorded from both sieving and germination trials amounted to a mean seed density of 3365 seeds m^{-2} ($n = 20$, depth = 9 cm).

When comparing the four plots sampled both before and after burning, the mean seed density before burning was 1100 seeds m⁻² and 2200 seeds m⁻² after burning (n = 4, depth = 9 cm). Most seeds belonged to non-woody species (either grasses or herbs). Only one tree species, *Acacia tortilis*, was represented in the soil seed bank. In the dry Afromontane forest, the mean seed density was 4755 seeds m⁻² (n = 20, depth = 9 cm). Plots with open canopy cover had a mean seed density of 6125 seeds m⁻² before burning and 4400 seeds m⁻² after burning (n = 4). Plots under the closed canopy cover had a mean seed density of 3425 seeds m⁻² before burning and 1325 seeds m⁻² after burning (n = 4). From trees, *Celtis africana* dominated the soil seed bank, followed by *Ficus sur*, *Albizia schimperiana*, *Croton macrostachyus*, *Cordia africana* and *Podocarpus falcatus* (Ericksson *et al.* 2002).

Spatial distribution of and effects of heat on seeds in the soil

Vertical distribution of seeds was highest at the top three centimeters soil layers but declined both at the litter and deeper soil layers in both sites. However, a notable decline of viable seeds both in the litter layer and the upper mineral soil layer was recorded after burning in the dry Afromontane forest. On the other hand, a small decline of viable seeds in the litter layer and an increase of viable seeds in the upper mineral soil layer were recorded after burning in the *Acacia* woodland (Ericksson *et al.* 2002).

Dry Afromontane (Demel 1997, 1998a; Demel & Granström 1995; Kebrom & Tesfaye 2000) and *Acacia* woodland (Mekuria *et al.* 1999; Skoglund 1992) ecosystems exhibit low densities of soil seed banks of woody species. The study of soil seed banks in the *Acacia* woodland also revealed that there were very few seeds from the tree strata. From all samples taken from the soil seed bank, only two seeds were from trees, indicating that very few tree seeds are added to the soil seed bank in this environment. Seed density in the dry Afromontane forest was slightly higher than in the woodland, but still low, compared with earlier studies (Demel 1997, 1998a; Demel & Granström 1995).

Wind speed, rates of fire spread, flame lengths and fuel consumption are subcomponents of fire intensity, which influence soil temperatures. With

the fine fuel loads of about 700-800 g m⁻² that burnt on the ground at both sites, soil temperatures exceeding 60 °C would reach a soil depth greater than 1 cm. The intensity of fire and soil temperatures (>60°C) during the experimental fires were sufficient to break seed dormancy in legume species (Bradstock & Auld 1995). The dominant part of the seeds was vertically distributed in the upper 0-3 cm of the soil. Heat from the experimental fire would either kill or stimulate germination of these buried seeds to a depth of more than 1 cm.

The results of this study suggest that the dry Afromontane forest has not developed with frequent fires and that species composition is likely to be substantially affected if fire enters into the forest. Fire could have great effects on biodiversity as well as the structure and composition of regenerating forest (Holdsworth & Uhl 1997). Dry forests are highly sensitive to clearing which results in the loss of atmospheric humidity and soil, and to burning, with the loss of the dominant non-fire-resistant species (Menaut *et al.* 1995). Under natural climatic conditions the dry Afromontane forest has a low potential for fire spread. Hence, it has a natural protection against the effects of fire, although the dry Afromontane forest contains many fire-sensitive tree species. A future scenario can, therefore, be a decline in canopy coverage from cutting and browsing, resulting in a dryer microclimate, and increased amounts of grasses and herbs in the litter fraction. This could foster a fire-spread potential that would alter the present species composition towards more fire tolerant forest or woodland tree species.

Regeneration of native woody species in tree plantations

Many recent studies have revealed that forest plantations can foster the regeneration of native woody species (NWS) under their canopies and catalyze the subsequent succession processes (Bone *et al.* 1997; Fang & Peng 1997; Fimbel & Fimbel 1996; Lugo 1992; Parrotta 1992, 1993, 1995; Parrotta *et al.* 1997; Tucker & Murphy 1997). In addition, tree plantations can improve degraded lands by stabilizing soils, improving soil nutrient status and increasing soil organic matter through enhancement of aboveground litter production (Lugo 1992; Lugo *et al.* 1993; Jordan &

Farnworth 1982; Michelsen *et al.* 1993; Parrotta 1995).

With the objective of satisfying the increased demand of wood, relieving the pressure from natural forests and rehabilitating degraded lands, tree plantations have been initiated in Ethiopia, mainly with introduced species of *Eucalyptus*, *Cupressus*, *Acacia* and *Pinus*, since the turn of the 20th century (Amare *et al.* 1990). Through this attempt, about 270,000 ha of forest plantations have been established up to the early 1990s in Ethiopia (Pandey 1996). These species can be grouped into: (1) broadleaved evergreen trees, e.g. *Eucalyptus* spp.; (2) Broad-leaved deciduous trees, e.g. *Acacia saligna* and *A. decurrens*; and (3) Coniferous trees, e.g. *Cupressus lusitanica*, *Pinus patula* and *Pinus radiata*.

Species of *Eucalyptus* have been largely planted in Ethiopia for wood production (i.e. fuelwood, construction wood, poles and posts) both by the rural communities and different enterprises. Management of these plantations has focused on short-rotation-coppicing system of about five to seven years interval. The continued management operations of repeated harvesting in certain intervals could significantly affect the soil and light environment under the plantation during and after harvesting, which may be conducive for germination of propagules and subsequent establishment of seedlings of indigenous woody species. The *Acacia* species have been planted mainly for reclamation of degraded areas, and as sources of wood for energy. Usually less management practices are employed other than planting. The coniferous species have been planted mostly for industrial wood production. They have been managed under long-term rotation system with different thinning and pruning practices during the lifetime of the plantations.

Recent assessments of different tree plantations in the country (Eshetu 2001, 2002; Eshetu & Luukkanen 2001, 2003; Feyera 1998; Feyera & Demel 2001, 2002; Feyera *et al.* 2002; Michelsen *et al.* 1996; Yitebetu 1998) have shown that secondary succession involving the natural regeneration of native woody species is progressing under canopies of these plantations. This is contrary to the growing concern of people against tree plantations of exotic species for their "negative" effects on the environment, including biodiversity.

To test the hypothesis that tree plantations can foster the regeneration of native woody species, provided that there are seed sources in their vicinity, two similar but independent studies were undertaken in different plantation stands at Menagesha-Suba (central Ethiopia) and Munessa-Shashemene (southern Ethiopia) and the adjacent natural dry Afromontane forests (for comparison) (Table 1). Detailed reports of these studies have been published elsewhere (Feyera 1998; Feyera & Demel 2001, 2002; Feyera *et al.* 2002). Only syntheses of results from these studies are presented below.

Species richness of naturally regenerated NWS in the plantations

Munessa-Shashemene site

A total of 55 woody species, representing 12 species of upperstorey trees, 40 species of shrubs or small trees and three woody climbers were recorded in the plantation stands. At the same time, 27 woody species were recorded in the adjacent natural forest. Of the 55 woody species identified in the plantations seven were found in all stands. The highest number of species per plot was found under a nine-year old *Cupressus lusitanica* stand and 27-year old *Eucalyptus saligna* stand. The most common tree species found in the plantation stands were *Celtis africana*, *Croton macrostachyus*, *Podocarpus falcatus* and *Prunus africana*. The number of naturally regenerated woody species in the coppiced stands of *E. saligna* and *E. globulus* were significantly higher in most of the plots and almost comparable to the adjacent natural forest.

There were large variations in understorey stem densities among the various plantation stands and species (Table 1). The highest density of understorey woody plants (18650 plants ha⁻¹) was recorded in the coppice stand of *E. saligna* (27-year-old) and the lowest (2325 plants ha⁻¹) in a stand of *Pinus patula* (10-year-old) (Table 1). The density of naturally regenerated woody species in the adjacent natural forest was 9658 plants ha⁻¹. The relationship between plantation age and density of naturally regenerated woody species was observed more in *E. saligna* stands than in the other plantation species.

There was a significant variation in recolonization potential or understorey density

Table 1. Species richness and density of naturally regenerated native woody species in different exotic tree plantations at Munessa-Shashemene forest and the adjacent natural forest.

Plantation stand/species	Age	Distance from natural forest	Number of species	Density (stem ha ⁻¹)	Remark
<i>C. lusitanica</i>	9	200	30	7325	Seedling stand
<i>C. lusitanica</i>	17	250	22	7375	Seedling stand
<i>C. lusitanica</i>	25	300	16	5950	Seedling stand
<i>E. globulus</i>	13	100	16	6550	Seedling stand
<i>E. globulus</i>	16	200	13	2300	Seedling stand
<i>E. globulus</i>	22	350	17	13400	2 nd coppice
<i>E. saligna</i>	11	250	18	3575	Seedling stand
<i>E. saligna</i>	22	350	23	10100	Seedling stand
<i>E. saligna</i>	27	1000	25	18650	3 rd coppice
<i>P. patula</i>	10	200	18	2325	Seedling stand
<i>P. patula</i>	21	500	16	3750	Seedling stand
<i>P. patula</i>	28	300	15	2525	Seedling stand
Natural forest			25	9658	

Source: Feyera *et al.* (2002)

among coniferous and *Eucalyptus* plantations. This may be attributed to the management systems employed in the different stands, e.g. conifers are managed for timber production on long rotation whereas *Eucalyptus* species are managed on short rotation system. In addition, nature of the crown and extent of litter accumulation were significantly different in the stands. The coniferous stands possessed thick crown and greater litter accumulation than *Eucalyptus* stands, which may reduce germination and growth of understorey beneath them. *C. lusitanica* and *P. patula* plantation stands had different capacity to promote regeneration, which supports the report by Fimbel & Fimbel (1996). The difference between *E. saligna* and *E. globulus* stands was not significant in terms of composition of the naturally regenerated native woody species and density. All plantation stands exhibited low similarity of woody species composition despite the uniform climatic conditions prevailing in the surrounding.

The frequency distribution of height and diameter classes of individuals of the NWS indicated that the seedling populations (< 1.5 m high) were the most abundant component of regeneration in most of the plantation stands. They form about 68% of the total regeneration count in all stands and greater than 50% in each

stand. Saplings (1.5 - 03 m high) constituted about 25% of the total regeneration count in all the stands. In contrast, the proportion of regeneration under the category of trees was only 7% indicating that the smallest height class populations dominated the understorey regeneration. Though the stands had varied ages, the populations of naturally regenerating native woody species were dominated by lower height classes in all the ages suggesting that the colonization is at an early stage of development.

Menagesha-Suba site

A total of 42 woody species were recorded under plantation stands and in the adjacent natural forest, of which three were found only in the adjacent natural forest. In the plantation stands, a total of 37 native woody species and two exotic tree species, representing over 28 families of plants, were recorded. In the adjacent natural forest, 26 native woody species were recorded (Table 2). Among the 37 native woody species recorded in the plantation stands, nine species were upperstorey trees in the adjacent natural forest, 27 species were shrubs or small trees and two species were woody climbers.

The different populations of naturally regenerated indigenous woody species were dominated by species known to be either shrubs or

Table 2. Species richness and density of naturally regenerated native woody species in different tree plantations at Menagesha-Suba site and the adjacent natural forest.

Plantation stand/species	Age	Distance from natural forest	Number of species	Density (stem ha ⁻¹)	Remark
<i>C. lusitanica</i>	14	2000	18	5770	Seedling stand
<i>C. lusitanica</i>	24	250	11	1630	Seedling stand
<i>E. globulus</i>	17	300	27	7730	2 nd coppice
<i>P. patula</i>	24	200	17	3940	Seedling stand
<i>P. radiata</i>	24	200	15	3130	Seedling stand
<i>J. procera</i>	42	300	27	18270	Seedling stand
Natural forest			26	11680	

Source: Feyera & Demel (2001)

small trees in their growth forms. The fact that of the 37 indigenous woody species recorded in the plantation stands, only nine were upperstorey trees in the adjacent natural forest may indicate the scarcity of seed-producing trees of the other upperstorey species in the vicinity of the plantations. It could also be attributed to the dispersal mode of the seeds or the nature of dispersal agents for each tree species. This result concurs with a previous investigation in the Munessa-Shashemene forest (Feyera 1998; Feyera *et al.* 2002). Only nine woody species were common in all the study plots, implying the presence and abundance of mature trees of these species in the adjacent forest (Table 2).

The highest numbers of naturally regenerated woody species (27 species) were recorded under the *E. globulus* and *Juniperus* stands (Table 2). In addition, the density of naturally regenerated woody species under the *E. globulus* stand was the highest following the stand of *Juniperus* and adjacent natural forest. These findings provide preliminary evidence against the assertion that *E. globulus* does not allow the regeneration of other plants under its canopy (Florence 1986; Lisanework & Michelsen 1993).

The density of naturally regenerated woody plants was variable among the various plantation stands and species (Table 2). The highest density (18270 plants ha⁻¹) was recorded in the *J. procera* stand (42-year-old) and the lowest (1630 plants ha⁻¹) in the *C. lusitanica* stand (24-year-old). The density of naturally regenerated woody species in the adjacent natural forest was 11680 plants ha⁻¹, which is higher than most plantation stands except the *Juniperus* stand. The number and

density of naturally regenerated woody species decreases with increasing age in the *C. lusitanica* stands.

On the other hand, in the *Pinus* and *Cupressus* stands, densities of regenerated woody plants were low. This may be due to the effect of litter accumulation, as the average litter depth of these stands was higher than for other stands. Higher litter depth may hinder either the germination of seeds or the establishment of seedlings even if seeds arrive in equal numbers in the different stands. Litter depth increases with increasing age, especially if the decomposition process is slow. This might explain why the number and densities of naturally regenerated species decreased with increasing age in the *Cupressus* stands. This concurs with the results reported earlier from *Pinus* and *Cupressus* stands (Feyera 1998; Feyera *et al.* 2002; Fimbel & Fimbel 1996).

Similar to the Munessa-Shashemene site, seedling populations were the most abundant components (about 85% of the total regeneration) of the naturally regenerated individuals in most of the plantation stands. Saplings constituted about 11% of the total regeneration and the proportion of regeneration under the category of trees was only 4%, indicating that the smallest height class populations dominated the understory regeneration. This implies that the colonization is at an early stage of development in all plantation stands.

Tree plantations allow the regeneration of indigenous woody species, possibly enabling forest succession to occur over time. Results from the two studies, and other similar studies, conducted in Ethiopia (Eshetu 2001; Yitebetu 1998)

demonstrate that tree plantations can be useful to foster natural regeneration of native woody species, provided that there are seed sources in the vicinity of these plantations. As a result, tree plantations have the potential to enhance or restore plant diversity on degraded or deforested areas. From causal observation and indirect evidences at the study sites, it was noted that birds and mammals are involved in the transport of propagules of most of the woody species to the plantation stands thereby accelerating the natural regeneration of native woody species in the stands. This is an important reason to keep enough natural forest for the animal habitat and to maintain seed source in the vicinity of forest plantations.

Canopy characteristics and type of plantation species

In another recent study that dealt with the effects of canopy cover and understory environment of tree plantations on species richness, density and size of naturally regenerating NWS at Munessa-Shashemene site (Mulugeta *et al.* 2004), it was found that the canopy characteristics of plantation species, namely canopy closure percentage and leaf area index, greatly influence species richness, density and sizes (height and diameter) of naturally regenerating NWS by affecting the amount, duration and quality of radiation reaching the forest floor. The radiation reaching the forest floor affects the understory environmental factors such as soil moisture and temperature, air temperature and temperature fluctuations, which, in turn, influence the germination of seeds, establishment and growth of seedlings of NWS. As such, stands of plantation species with open canopies could enhance regeneration of more NWS than stands of plantation species with dense canopies. Both indigenous and exotic species could be equally used to foster regeneration of NWS as long as the plantation species provide reasonably open canopies that allow penetration of enough radiation to the forest floor (Mulugeta *et al.* 2004).

Given the wide coverage of seed and regeneration ecology, what has been reviewed and presented in this paper is far from being exhaustive or complete. Thematic research topics that require future attention include natural and anthropogenic disturbances and sources of

regrowth of plants after such disturbances and strategies used to detect gap formation or gap-phase dynamics. Further research should be carried out to have a better understanding of seed dispersal and agents involved in the seed dispersal, eco-physiological and successional processes within tree plantations such as the relationship between canopy architecture, microclimatic conditions and regeneration of indigenous species, seed germination in the field, seed predation, seedling establishment and growth. There is also a need to investigate how the plantation stands and established native woody species can be manipulated to facilitate the development of secondary forests over time.

References

- Anonymous. 1988. *National Atlas of Ethiopia*. Ethiopian Mapping Agency, Addis Abeba.
- Amare Getahun, Feyisa Abate & Belay Gebre. 1990. *A Brief History of Forestry Research Center (FRC) and Forestry Research in Ethiopia*. FRC, Addis Ababa.
- Bone, L., M. Lawrence & Z. Magombo. 1997. The effect of an *Eucalyptus camaldulensis* (Dehn) plantation on native woodland recovery on Ulumba Mountains, Southern Malawi. *Forest Ecology and Management* **99**: 83-99.
- Bonnefille, R. & A. Hamilton. 1986. Quaternary and late tertiary history of Ethiopian vegetation. *Acta Universitatis Upsaliensis Symbolae Botanicae Upsaliensis* **26**: 48-63.
- Bradstock, R.A. & T.D. Auld. 1995. Soil temperatures during experimental bushfires in relation to fire intensity: consequences for legume germination and fire management in south-eastern Australia. *Journal of Applied Ecology* **32**: 76-84.
- Brokaw, N.V.L. 1985. Treefalls, regrowth, and community structure in tropical forests. pp. 53-69. In: T. A. Pickett. & P. S. White (eds.) *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, New York.
- Cufodontis, G. 1953-1972. *Enumeratio Plantarum Aethiopiae Spermatophyte*. Vol. 1 & 2. Jardin Botanique National De Belgique, Meise.
- Demel Teketay. 1992. Human impact on a natural montane forest in southeastern Ethiopia. *Mountain Research and Development* **16**: 393-400.
- Demel Teketay. 1996. *Seed Ecology and Regeneration in Dry Afromontane Forests of Ethiopia*. Ph.D. Thesis, Swedish University of Agricultural Sciences, Umeå.

- Demel Teketay. 1997. The impact of clearing and converting dry Afromontane forests into permanent arable land on the composition and density of soil seed banks. *Acta Oecologica* **18**: 557-573.
- Demel Teketay. 1998a. Soil seed bank at an abandoned Afromontane arable site. *Feddes Repertorium* **109**: 161-174.
- Demel Teketay. 1998b. The role of light and temperature in the germination of twenty herbaceous species from the highlands of Ethiopia. *Flora* **193**: 411-425.
- Demel Teketay. 2000. Vegetation types and forest fire management in Ethiopia. pp. 1-35. In: MOA & GTZ (eds.) *Proceedings of the Round Table Conference on Integrated Forest Fire Management in Ethiopia*. Ministry of Agriculture (MOA) & Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), Addis Abeba.
- Demel Teketay. 2002. Germination responses of *Discopodium penninervium* to temperature and light. *Flora* **197**: 76-80.
- Demel Teketay & A. Granström. 1995. Soil seed banks in dry Afromontane forests of Ethiopia. *Journal of Vegetation Science* **6**: 777-786.
- Demel Teketay & A. Granström. 1997. Germination ecology of forest species from the highlands of Ethiopia. *Journal of Tropical Ecology* **14**: 793-803.
- Denslow, J.S. 1987. Tropical rain forest gaps and tree species diversity. *Annual Review of Ecology and Systematics* **18**: 431-451.
- Edwards, S., Mesfin Tadesse & I. Hedberg (eds.). 1995. *Flora of Ethiopia and Eritrea*. Vol. 2, Part 2. The National Herbarium, Addis Abeba University, Addis Abeba & Department of Systematic Botany, Uppsala University, Uppsala.
- Edwards, S., Mesfin Tadesse, Sebsebe Demissew & I. Hedberg (eds.). 2000. *Flora of Ethiopia and Eritrea*. Vol. 2, Part 1. The National Herbarium, Addis Abeba University, Addis Abeba & Department of Systematic Botany, Uppsala University, Uppsala.
- Edwards, S., Sebsebe Demissew & I. Hedberg (eds.). 1997. *Flora of Ethiopia and Eritrea*. Vol. 6. The National Herbarium, Addis Abeba University, Addis Abeba & Department of Systematic Botany, Uppsala University, Uppsala.
- Ericksson, I., Demel Teketay & A. Granström. 2002. Response of plant communities to fire in an *Acacia* woodland and a dry Afromontane forest, southern Ethiopia. *Forest Ecology and Management* **177**: 39-50.
- Eshetu Yirdaw. 2001. Diversity of naturally-regenerated native woody species in forest plantations in the Ethiopian highlands. *New Forests* **22**: 159-177.
- Eshetu Yirdaw. 2002. *Restoration of the Native Woody Species Diversity, Using Plantation Species as Foster Trees, in the Degraded Highlands of Ethiopia*. Ph.D. Thesis, University of Helsinki, Helsinki.
- Eshetu Yirdaw & O. Luukkanen 2001. Light transmittance of forest plantation canopies and the influence of gaps on native tree seedling growth in Ethiopian highlands. *Forest Ecology and Management* **168**: 53-61.
- Eshetu Yirdaw & O. Luukkanen 2003. Indigenous woody species diversity in *Eucalyptus globulus* Labill. subsp. *globulus* plantations in the Ethiopian highlands. *Biodiversity and Conservation* **12**: 567-582
- Ewel, J., C. Berish, B. Brown, N. Price & J. Raich. 1981. Slash and burn impacts on a Costa Rican wet forest site. *Ecology* **62**: 816-829.
- Fang, W. & S. L. Peng. 1997. Development of species diversity in the restoration process of establishing a tropical man-made forest ecosystem in China. *Forest Ecology and Management* **99**: 1-12.
- Feyera Senbeta. 1998. *Native Woody Species Regeneration Under the Canopies of Tree Plantations at Munessa-Shashemene Forest Project Area, Southern Oromia, Ethiopia*. M.Sc. Thesis, Swedish University of Agricultural Sciences, Skinnskatterberg.
- Feyera Senbeta & Demel Teketay. 2001. Regeneration of indigenous woody species in the canopies of tree plantations in central Ethiopia. *Tropical Ecology* **42**: 175-185.
- Feyera Senbeta & Demel Teketay. 2002. The role of tree plantations to foster regeneration of indigenous woody species in degraded lands of Ethiopia. pp. 51-58. In: Demel Teketay & Yonas Yemshaw (eds.) *Proceedings of the Fourth Annual Conference of Forestry Society of Ethiopia*. Forestry Society of Ethiopia, Addis Abeba.
- Feyera Senbeta, Demel Teketay & B-Å.Näslund. 2002. Native woody species regeneration in exotic tree plantations in Munessa-Shashemene Forest, Ethiopia. *New Forests* **24**: 131-145.
- Fichtl, R. & Admasu Adi 1994. *Honeybee Flora of Ethiopia*. Margraf Verlag, Weikersheim.
- Fimbel, R. A. & C.C. Fimbel. 1996. The role of exotic conifer plantations in rehabilitating degraded tropical forestlands: a case study from the Kibale Forest in Uganda. *Forest Ecology and Management* **81**: 215-226.
- Florence, R.G. 1986. Cultural problems of *Eucalyptus* as exotics. *Commonwealth Forestry Review* **65**: 141-163.

- Friis, I. 1989. Moraceae. pp. 271-301. *In*: I. Hedberg & S. Edwards (eds.) *Flora of Ethiopia*. Vol. 3. The National Herbarium, Addis Abeba University, Addis Abeba & Department of Systematic Botany, Uppsala University, Uppsala.
- Friis, I. 1992. Forests and forest trees of north east tropical Africa. *Kew Bull. Add. Ser.* **15**: 1-396.
- Garwood, N. C. 1989. Tropical soil seed banks: a review. pp. 149-209. *In*: M.A. Leck, V.T. Parker & R.L. Simpson (eds.) *Ecology of Soil Seed Banks*. Academic Press, San Diego & California.
- Gilbert, M. G. 1989. Anacardiaceae. pp. 513-532. *In*: I. Hedberg & S. Edwards (eds.) *Flora of Ethiopia*. Vol. 3. The National Herbarium, Addis Abeba University, Addis Abeba & Department of Systematic Botany, Uppsala University, Uppsala.
- Hamilton, A. 1982. *Environmental History of East Africa. A Study of the Quaternary*. Academic Press, London.
- Hartshorn, G.S. 1980. Neotropical forest dynamics. *Biotropica* **12** (Suppl.): 23-30.
- Hedberg, I. & S. Edwards (eds.). 1989. *Flora of Ethiopia*. Vol. 3. The National Herbarium, Addis Abeba University, Addis Abeba & Department of Systematic Botany, Uppsala University, Uppsala.
- Hedberg, I. & S. Edwards (eds.). 1995. *Flora of Ethiopia and Eritrea*. Vol. 7. The National Herbarium, Addis Abeba University, Addis Abeba & Department of Systematic Botany, Uppsala University, Uppsala.
- Hedberg, O. 1989. Rosaceae. pp. 31-44. *In*: I. Hedberg & S. Edwards (eds.) *Flora of Ethiopia*. Vol. 3. The National Herbarium, Addis Abeba University, Addis Abeba & Department of Systematic Botany, Uppsala University, Uppsala.
- Holdsworth, A.R. & C. Uhl. 1997. Fire in Amazonian selectively logged rain forest and the potential for fire reduction. *Ecological Applications* **7**: 713-725.
- Hopkins, M.S. & A.W. Graham. 1984. Viable soil seed banks in disturbed lowland tropical rain forest sites in North Queensland, Australia. *Australian Journal of Ecology* **9**: 71-79.
- Jordan, C. F. & E. G. Farnworth. 1982. Natural vs. plantation forests: A case study of land reclamation strategies for the humid tropics. *Environmental Management* **6**: 485-492.
- Kauffman, J.B., C. Uhl & D.L. Cummings. 1988. Fire in the Venezuelan Amazon 1: Fuel biomass and fire chemistry in the evergreen rainforest of Venezuela. *Oikos* **53**: 167-175.
- Kebrom Tekle & Tesfaye Bekele. 2000. The role of soil seed banks in the rehabilitation of degraded hill-slopes in Southern Wollo. *Biotropica* **32**: 23-32.
- Kedamawit Yemane. 1986. A new palynoflora from an upper neogene lacustrine deposit on the northwestern Ethiopian Highlands, Chilga. *Acta Universitatis Upsaliensis Symbolae Botanicae Upsaliensis* **26**: 64-67.
- Keeley, J.E. & C.J. Fotheringham. 2000. Role of fire in regeneration from seed. pp. 311-330. *In*: M. Fenner (ed.) *Seeds: The Ecology of Regeneration in Plant Communities*. (2nd Edition). CABI Publishing, Wallingford.
- Kellman, M. 1980. Geographical patterning in tropical weed communities and early secondary successions. *Biotropica* **12** (Suppl.): 34-39.
- Kinfe Abebe. 1993. Forest fire: its causes and behaviour related to Ethiopian conditions. pp. 122-142. *In*: A.G. Berhanu (ed.) *Proceedings of the National Workshop on Setting Forestry Research Priorities in Ethiopia*. Forestry Research Center, Addis Abeba.
- Lisanework Negatu & A. Michelsen. 1993. Allelopathy in agroforestry systems: the effect of leaf extracts of *Cupressus lusitanica* and three *Eucalyptus* spp. on four Ethiopian crops. *Agroforestry Systems* **21**: 63-74.
- Lezine, A.M. & R. Bonnefille. 1982. Diagramme pollinique holocene d'un sondage du lac Abijata (Ethiopie, 7°42' nord). *Pollen et Spores* **24**: 463-480.
- Louda, S.M. 1989. Predation in the dynamics of seed regeneration. pp. 149-209. *In*: M.A. Leck, V.T. Parker & R.L. Simpson (eds.) *Ecology of Soil Seed Banks*. Academic Press, San Diego.
- Lugo, A.E. 1992. Comparison of tropical tree plantations with secondary forests of similar age. *Ecological Monographs* **62**: 1-41.
- Lugo, A.E., J.A. Parrotta & S. Brown. 1993. Loss in species caused by tropical deforestation and their recovery through management. *Ambio* **22**: 107-109.
- Mekuria Argaw, Demel Teketay & M. Olsson. 1999. Soil seed flora, germination and regeneration pattern of woody species in an *Acacia* woodland of the Rift Valley in Ethiopia. *Journal of Arid Environments* **43**: 411-435.
- Menaut, J.-C., M. Lepage, & L. Abbadie. 1995. Savannas, woodlands and dry forests in Africa. pp. 62-92. *In*: S.H. Bullock, H.A. Mooney & E. Medina (eds.) *Seasonally Dry Tropical Forests*. Cambridge University Press, Cambridge.
- Michelsen, A., Lisanework Nigatu & I. Friis. 1993. Impacts of tree plantations in the Ethiopian highland on soil fertility, shoot and root growth, nutrient utilization and mycorrhizal colonization. *Forest Ecology and Management* **61**: 299-324.

- Michelsen, A., Lisanework Nigatu, I. Friis & N. Holst. 1996. Comparison of understory vegetation and soil fertility in plantations and adjacent natural forests in the Ethiopian highlands. *Journal of Applied Ecology* **33**: 627- 642.
- Mulugeta Lemenih, Taye Gidyew & Demel Teketay. 2004. Effects of canopy cover and understory environment of tree plantations on species richness, density and size of colonizing woody species in southern Ethiopia. *Forest Ecology and Management* **194**: 1-10.
- Pandey, D. 1996. *Tropical Forest Plantation Resources. Assessment of Extent and Methods for Yield Estimation*. Ph.D. Thesis, Swedish University of Agricultural Sciences, Umeå.
- Parrotta, J.A. 1992. The role of plantation forests in rehabilitating degraded ecosystems. *Agriculture, Ecosystems and Environment* **41**: 115-133.
- Parrotta, J.A. 1993. Secondary forest regeneration on degraded tropical lands: the role of plantations as "foster ecosystems". pp. 63-73. *In*: H. Lieth & M. Lohman (ed.) *Restoration of Tropical Forest Ecosystems*. Kluwer, Dordrecht.
- Parrotta, J. A. 1995. Influence of overstorey composition on understory colonization by natives species in plantation on a degraded tropical site. *Journal of Vegetation Science* **6**: 627-636.
- Parrotta, J.A., J.W. Turnbull & N. Jones. 1997. Catalyzing native forest regeneration on degraded tropical lands. *Forest Ecology and Management* **99**: 1-7.
- Pinard, M.A. & J. Huffman. 1997. Fire resistance and bark properties of trees in a seasonally dry forest in eastern Bolivia. *Journal of Tropical Ecology* **13**: 727-740.
- Skoglund, J. 1992. The role of seed banks in vegetation dynamics and restoration of dry tropical ecosystems. *Journal of Vegetation Science* **3**: 357-360.
- Thompson, K. 1987. Seeds and seed banks. *New Phytologist* **106** (Suppl.): 23-34.
- Thulin, M. 1989. Fabaceae. pp. 49-251. *In*: I. Hedberg & S. Edwards (eds.) *Flora of Ethiopia*. Vol. 3. The National Herbarium, Addis Abeba University, Addis Abeba & Department of Systematic Botany, Uppsala University, Uppsala.
- Tucker, N.I.J. & J.M. Murphy. 1997. The effects of ecological rehabilitation on vegetation recruitment: Some observations from the wet tropics of North Queensland. *Forest Ecology and Management* **99**:133-152.
- Uhl, C., K. Clark, H. Clark & P. Murphy. 1981. Early plant succession after cutting and burning in the upper Rio Negro region of the Amazon Basin. *Journal of Ecology* **69**: 631-649.
- Uhl, C., H. Clark, K. Clark & P. Marquirino. 1982. Successional patterns and processes associated with slash-and-burn agriculture in the upper Rio Negro region of the Amazon Basin. *Biotropica* **14**: 249-254.
- Uhl, C. & J.B. Kauffman. 1990. Deforestation, fire susceptibility, and potential tree responses to fire in the eastern Amazon. *Ecology* **71**: 437-449.
- Vollesen, K. 1989. Sapindaceae. pp. 490-510. *In*: I. Hedberg & S. Edwards (eds.) *Flora of Ethiopia*. Vol. 3. The National Herbarium, Addis Abeba University, Addis Abeba & Department of Systematic Botany, Uppsala University, Uppsala.
- Whitmore, T.C. 1975. *Tropical Rain Forests of the Far East*. Clarendon Press, Oxford.
- Whitmore, T.C. 1978. Gaps in the forest canopy. pp. 639-655. *In*: P.B. Tomlinson & M.H. Zimmermann (eds.) *Tropical Trees as Living Systems*. Cambridge University Press, London & New York.
- Whitmore, T.C. 1991. Tropical rain forest dynamics and its implications for management. pp. 67-89. *In*: A. Gomez-Pompa, T.C. Whitmore & M. Hadley (eds.) *Rain Forest Regeneration and Management*. UNESCO, Paris.
- Yitebitu Moges. 1998. *The Role of Exotic Plantation Forests in Fostering the Regeneration of Native Trees in an Afromontane Forest Area in Ethiopia*. M.Sc. Thesis, Wageningen Agricultural University, Wageningen.
- Young, K.R. & J.J. Ewel & B.J. Brown, B. J. 1987. Seed dynamics during succession in Costa Rica. *Vegetatio* **71**: 157-173.