

# Seed and regeneration ecology in dry Afromontane forests of Ethiopia: I. Seed production - population structures

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**Abstract:** A series of events occur in the process of regeneration, namely flowering, seed production and dispersal, incorporation of seeds into the soil, seed predation or germination, seedling establishment and growth and formation of seedling banks. Forests are subjected to both natural and anthropogenic disturbances, which disrupt the process of plant regeneration. In response to these disturbances, succession is triggered in which different plants use varying strategies to regenerate themselves. For instance, tropical forest plants regenerate from one or more pathways, namely seed rain, soil seed bank, seedling bank or advance regeneration and coppice. The objective of this paper is to present the first part of an overview of the available information on seed and regeneration ecology in dry Afromontane forests (DAF) of Ethiopia. The review focuses on: (i) seed production and dispersal; (ii) soil seed banks: incorporation of seeds into the soil, species richness and densities, spatial and temporal variation and depletion of seeds in the soil; (iii) seed dormancy and germination, requirements for seed germination: light, temperature, interaction between light and temperature, scarification, moisture and dry storage; and (iv) seedling banks, seedling survival, seedling growth and population structures of woody plants. Thematic areas for future research are recommended.

**Resumen:** Una serie de eventos tiene lugar durante el proceso de regeneración: floración, producción y dispersión de semillas, incorporación de semillas al suelo, depredación de semillas o germinación, establecimiento y crecimiento de plántulas y formación de bancos de plántulas. Los bosques están sujetos a disturbios tanto naturales como antropogénicos, los cuales afectan el proceso de regeneración de las plantas. En respuesta a estos disturbios, se dispara una sucesión en la que diferentes plantas usan diversas estrategias para regenerarse. Por ejemplo, las plantas de bosque tropical se regeneran a partir de una o más rutas, a saber: lluvia de semillas, banco de semillas del suelo, banco de plántulas, regeneración de avanzada o rebrote. El objetivo de este artículo es presentar la primera parte de una revisión de la información disponible sobre la ecología de las semillas y de la regeneración en bosques secos afromontanos (DAF) de Etiopía. La revisión se enfoca en: (i) producción y dispersión de semillas; (ii) bancos de semillas del suelo: incorporación de semillas al suelo, riqueza y densidades de especies, variación espacial y temporal y disminución de semillas en el suelo; (iii) latencia y germinación de las semillas, requerimientos para la germinación de las semillas: luz, temperatura, interacción entre luz y temperatura, escarificación, almacenamiento húmedo y seco; y (iv) bancos de plántulas, supervivencia de plántulas, crecimiento de plántulas y estructuras poblacionales de plantas leñosas. Se hacen recomendaciones sobre áreas temáticas para investigaciones futuras.

**Resumo:** No processo de regeneração ocorre uma série de eventos, principalmente a floração, a produção e a dispersão de sementes, incorporação de sementes no solo, predação de

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sementes e germinação, estabelecimento, crescimento e formação de bancos de plântulas. As florestas estão sujeitas, simultaneamente, a distúrbios naturais e antropogénicos, os quais interrompem o processo de regeneração das plantas. Em resposta a estes distúrbios, a sucessão inicia-se e na qual as diferentes plantas usam variadas estratégias para se regenerarem. As plantas florestais tropicais, por exemplo, regeneram-se de uma ou mais vias, nomeadamente por semente na época pluviosa, banco seminal no solo, banco de plântulas ou regeneração avançada ou talhadia. O objectivo deste trabalho é o de apresentar a primeira parte de uma revisão da informação disponível sobre a ecologia das sementes e regeneração nas florestas secas Afromontanas (DAF) da Etiópia. A revisão centra-se em: (i) produção de sementes e dispersão; (ii) bancos seminais no solo: incorporação de sementes no solo, riqueza específica e densidades, variação espacial, temporal e depleção de sementes no solo; (iii) dormência das sementes e a germinação, requisitos para a germinação das sementes: luz, temperatura interacção entre a luz e a temperatura, escarificação, humidade e armazenagem a seco; e (iv) bancos de plântulas, sobrevivência das plântulas, seu crescimento e estruturas de população das plantas lenhosas. As áreas temáticas para investigação futura são recomendadas.

**Key words:** Coppice, germination, population structure, seed dispersal, seed dormancy, seed production, soil seed bank, seedling bank.

## Introduction

The Ethiopian highlands cover more than 50% of the country's land area with Afromontane vegetation (Tamrat 1993, 1994; Yalden 1983), of which dry Afromontane forests form the largest part. Several names have been employed to refer to dry Afromontane forests in Ethiopia, e.g. tropical high montane conifer forest (Logan 1946), montane dry evergreen forest (Pichi-Sermolli 1957), highland *Juniperus-Podocarpus* forest (von Breitenbach 1961), dry montane forest (Coetzee 1978), upland dry evergreen forests (Friis 1986; Friis *et al.* 1982), upland dry evergreen forest and mixed upland evergreen forest (Friis & Mesfin 1990), coniferous forest (Anonymous 1988) and undifferentiated forest (Friis 1992). The dry Afromontane forests are either *Juniperus-Podocarpus* forests or predominantly *Podocarpus* forests, both with broad-leaved species. They occur in both the Northwest and Southeast Highlands, especially on the plateau of Shewa, Welo, Sidamo, Bale and Harerge at altitudes 1500-2700 m. The average annual temperature varies between 14 and 20°C and the annual rainfall between 700 and 1100 mm, with most of the rain recorded in July (Friis 1992). Detail description of the dry

Afromontane and other forest types in Ethiopia can be found in Friis (1992).

A good understanding of natural regeneration in any plant community requires information on the presence and absence of persistent soil seed banks or seedling banks, quantity and quality of seed rain, longevity of seeds in the soil, losses of seeds to predation and deterioration, triggers for germination of seeds in the soil and sources of regrowth after disturbances. Tropical forest plants regenerate from one or more pathways, i.e. (i) *seed rain*: recently dispersed seeds; (ii) *soil seed bank*: dormant seeds in the soil; (iii) *seedling bank* or *advance regeneration*: established, suppressed seedlings in the understorey; and (iv) *coppice*: root or shoot sprouts of damaged individuals (Garwood 1989).

Information on seed and regeneration ecology of the different forest types that occur in Ethiopia is scanty or, for most of the forest types, totally lacking. The relatively few studies undertaken in dry Afromontane forests, *Acacia* woodlands or woodlands restored by enclosures established at heavily degraded areas, focused on: seed production and dispersal (Demel 1996a; Friis 1992); composition, density, spatial distribution and depletion of soil seed banks (Abeje 2002; Demel 1996a, 1997a, 1998a; Demel & Granström 1995, 1997a; Emiru 2002; Feyera & Demel 2001,

2002a; Kebrom & Tesfaye 2000; Mekuria *et al.* 1999; Tefera 2001); requirements of seed germination (Demel 1994, 1996b, c, 1997b, c, 1998b, c, d, e, f, 2002; Demel & Granström 1997b; Demel & Mulualem 1996; Eshetu & Leinonen; 2002; Legesse 1992, 1993, 2002; Mekuria *et al.* 1999; Mulualem & Odén 2001); forest fire (Demel 2000), and response of plant communities to fire (Eriksson *et al.* 2002), composition, density and spatial distribution of seedling banks/populations (Demel 1996a, 1997d); survival and growth of seedlings (Demel 1996a, 1997d); regeneration profile of woody species (Abeje 2002; Alemnew 2001; Demel 1996a, 1997d; Demel & Tamrat 1995; Tadesse *et al.* 2000; Tamrat 1994; Tefera 2001); deforestation (Eshetu 1996, 2002); disturbance and succession (Demel 1996a); regeneration of native species under the canopies of plantation species (Eshetu 2001, 2002; Eshetu & Luukkanen 2001a, b; Feyera 1998; Feyera & Demel 2001, 2002b; Feyera *et al.* 2002; Yitebetu 1998); and mycorrhizal status of indigenous trees (Tefaye *et al.* 2003).

The objective of this paper, which is presented in two different parts, is to provide a review of results from most of these studies and recommend the areas that need immediate and future attention by researchers, development and conservation workers and policy makers. In this part of the paper, the review is divided into eight parts, namely introduction, seed production and dispersal, soil seed banks, seed dormancy and germination, seedling banks and population structure of woody plants followed by the second part, which focuses on forest disturbances and succession and regeneration of native woody species.

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).

### Seed production and dispersal

Although the time of flowering (Burger 1974), seed production, dispersal of forest species and seed rain, even of the most dominant and economically important trees is largely unknown in Ethiopia, and no specific investigations were carried out concerning seed production and dispersal, a few remarks can be forwarded from

casual observation made during field works and inspection of animal droppings (Demel 1996a). Seed production is irregular in most of the tree species, with the exception of a few species, e.g. *Calpurnia aurea* and *Juniperus procera*, which can be found in flower and fruit every year. Seeds of many species are dispersed by a variety of animals. For instance, seeds of *Allophylus* species, *Bersama abyssinica*, *Ekebergia capensis*, *Juniperus procera*, *Myrsine africana*, *Olea europaea* subsp. *cuspidata*, *Pittosporum viridiflorum*, *Schefflera abyssinica* are dispersed by birds. Fruits of *Cordia africana*, *Dovyalis abyssinica*, *Ficus* spp., *Pavetta* spp., *Podocarpus falcatus*, *Physalis peruviana*, *Rosa abyssinica*, *Rubus* spp., *Solanum* spp. and *Teclea nobilis* are eaten and their seeds dispersed by birds, baboons, colobus monkeys, apes and probably other animals. Clean seeds and heavily chewed epimatium of *Podocarpus falcatus* were found under big trees of different species at Gara Ades Afromontane forest, a sign of bat dispersal. Herbaceous species such as *Achyranthus aspera*, *Bidens pilosa*, *Dichrocephala chrysanthemifolia* and *D. integrifolia* possess seeds which stick tightly on animals and become dispersed to long distances. Seeds of many species in the Asteraceae family and small-seeded species of *Clematis*, *Lobelia* and *Hypericum*, *Erica arborea*, *Nuxia congesta*, *Polyscias fulva* and many herbaceous species are dispersed by wind.

In his study of the forest tree flora of Northeast Tropical Africa (Ethiopia, Djibouti and Somalia), Friis (1992) established the diaspore size and mode of dispersal of trees based on herbarium studies. He recognized five size classes (0-3 mm, 3-12 mm, 12-48 mm, 48-192 mm, 192-768 mm) and three modes of dispersal (wind dispersal, animal dispersal and unspecialized mode of dispersal). The percentage distribution of size-classes among the species were: 57% (3-12 mm), 28% (12-48 mm), 11% (0-3 mm), 3% (48-192 mm) and less than 1% (192-768 mm) while the corresponding proportions for the dispersal modes were 70% (animal = soft fruits or arilloid seeds), 21% (unspecialized) and 9% (wind). Friis (1992) also found that diaspore size decreases with increasing altitude and the mode of dispersal shows a continuous transition from dominance of diaspores with assumed animal dispersal at low altitudes (mangroves excepted) to dominance of unspecialized modes of dispersal at

the upper limit of the forest. Because of the steadily decreasing size of diaspores, the unspecialized diaspores at high altitudes, such as the tiny seeds of *Erica*, *Hypericum* and *Lobelia*, are assumed to be wind dispersed.

### Soil seed banks

The soil seed bank refers to all viable seeds and fruits present on or in the soil and associated litter/humus. Soil seed banks can be either transient, with seeds that germinate within a year of initial dispersal, or persistent, with seeds that remain in the soil for more than one year (Leck *et al.* 1989; Simpson *et al.* 1989; Thompson & Grime 1979). They exhibit variations in space as well as time and display both horizontal and vertical dispersion, reflecting initial dispersal onto the soil and subsequent movement (Simpson *et al.* 1989). Soil seed banks reflect partly the history of the vegetation and can play an important role in its regeneration or restoration after disturbances. They have been exploited in two contexts: to manage the composition and structure of existing vegetation and to restore or establish native vegetation (van der Valk & Pederson 1989).

The pool of long-lived seeds in the soil accumulates over many decades and contributes as a source of propagules that ensure continual occupation of a site after disturbances while serving as a gene pool by buffering genetic changes in the population (Fenner 1985; Grime 1979; Harper 1977; Hill & Morris 1992; Silvertown 1982). Soil seed banks play a crucial role in the dynamics of plant populations. In forest management, natural seed banks play a vital role in regeneration after disturbances, for example, tree felling. The fact that many economically important trees are canopy species whose seeds have little dormancy makes it important to leave some individuals of the species to act as local seed sources. Knowledge of which species are not represented in the persistent soil seed bank can be just as important as knowing which species are represented. This is especially true in the management of vegetation for conservation. The dynamics of a soil seed bank include recruitment into the dormant seed bank population through seed rain, losses from the dormant seed bank through seed predation or death and transference

into the active seed bank to germinate and form a seedling bank, through a stimulus.

### *Incorporation of seeds into the soil*

Apart from information on the occurrence of viable seeds in the soil of dry Afromontane forests and arable land (Demel 1996a, 1997a, 1998a; Demel & Granström 1995), nothing is known about the mechanisms of incorporation of these seeds into the soil. In these areas, rooting by bush pigs, trampling by grazing animals, scatterhoarding rodents, ants, entrance of smaller seeds into cracks formed in the soil during the dry period and cultivation in arable land are among the factors responsible for the movement of seeds in the soil (own observation), although dung beetles (Estrada & Coates-Estrada 1986), entrance of seeds in tunnels created by burrowing animals and decomposing roots or uprooted trees (Hopkins & Graham 1983; Putz 1983; Young 1985), earthworms (McRill & Sagar 1973), termites (Lal 1987, cited in Garwood 1989) rain washing seeds into the soil (Hopkins & Graham 1983) and birds (Fenner 1995) have been shown to be important.

### *Species richness and density*

In a study carried out using soil samples collected from four dry Afromontane forests, namely Munessa-Shashemene (hereafter referred to as MS), Gara Ades (GA), Menagesha (ME) and Wof-Washa (WW) forests, the soil seed flora in 0-9 cm soil layers ranged between 58 species of flowering plants at MS and 92 at GA and the viable seeds ranged between 12300 m<sup>-2</sup> at ME and 24000 m<sup>-2</sup> at WW (Demel 1996a; Demel & Granström 1995). The seed bank was dominated by relatively few species in all the sites, and the most well represented family was Asteraceae. Although there were a few species with considerable persistent seeds in the soil, the contribution of woody plants to the total number of seeds in the soil was low. This suggests that dry Afromontane woody species do not depend on the soil seed bank for regeneration after disturbances. Instead, the seedling bank or coppice shoots from stumps are the sources of regrowth in these species (Demel 1996a, 1997d; Demel & Granström 1995).

### *Spatial and temporal variation*

The forest litter layer consisted of a relatively high number of seeds, although the density varies among samples and species (Demel 1996a; Demel & Granström 1995). The vertical distribution of the soil seed bank and number of species was consistent at all sites with the highest densities in the upper three centimeters of soil and then gradually decreasing densities with increasing depth. There was considerable variation among species in depth distribution. Some species, e.g. *Juniperus procera*, *Clematis hirsuta*, *Girardinia diversifolia* and *Pilea tetraphylla* were almost entirely confined to the litter layer. Some other species, e.g. *Laggera crispata*, *Lobelia giberroa*, *Crassula alsinoides*, *Veronica abyssinica* and *Poa leptoclada*, had almost uniform depth distribution. Another set of species, e.g. *Indigofera rothii*, *Solanum nigrum* and *Eragrostis schweinfurthii* had their seeds distributed in the deeper layers. In general, seeds of herbs, grasses and sedges were more deeply distributed in the soil than trees, shrubs and climbers. Herbs, grasses and sedges have small seeds compared with many woody species, and species with small seeds have a better chance of becoming buried in deeper layers of the soil (Thompson 1987). Considerable intra-site differences of horizontal distribution of seeds in the soil were also apparent among species. Some species such as *Crassula alsinoides* and *Dichrocephala integrifolia*, showed a relatively even distribution while most of the woody species and some herbaceous species had patchy or clumped distribution.

In litter layer samples collected at the end of the dry season (March) and in the middle of the rainy period (July) within the same year at GA, there was a marginal difference in the quantity of seeds but a marked difference in species composition (Demel unpublished). This may be attributed to the differences in the timing of flowering, fruit maturation and dispersal of the species. Several climax species disperse their seeds on the onset of or during the long rainy period and germinate to form seedling banks on the forest floor (Demel 1997d; Demel & Granström 1997b) while many species disperse their seeds during the dry period (Burger 1974). For instance, *Ekebergia capensis* and *Schefflera abyssinica* were represented in the litter samples collected in July, but not in those collected in March, since many

trees were dispersing their seeds at the time of the sampling. Predators may also play an important role by either reducing or eliminating dispersed seeds, especially of large-seeded species, from the forest floor thereby creating variation in the soil seed bank composition (Demel 1996a, 1997a; Demel & Granström 1995). Forest gaps sampled at GA in 1994 (gap-94) and 1995 (gap-95) showed a large difference in the density of the soil seed bank but had almost similar number of species, although the composition differed (Demel 1996a, 1997a). There were 8 species (with > 5 seeds) that were recorded in Gap-94 but not in gap-95 and similarly eight species that were recorded in gap-95 but not in gap-94. Among the species recovered from 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. The species, which exhibited increased seed densities were tiny-seeded annual plants with high turnover coupled with much higher seed input than those recruited through germination. On the other hand, the species, which exhibited no change in their seed densities seem to have balanced input and recruitment while the reason for the reduction of seed densities in some of the other species was not clear.

### *Depletion of seeds in the soil*

An understanding of the functioning of the seed bank requires not just knowledge of the numbers present at one time but also knowledge of its dynamics: the rates of seed input and the rates at which seeds are lost (Fenner 1985; Thompson 1992; Whitmore 1983). The inherent properties of seeds such as germination, dormancy and viability, the environmental conditions where seeds land and subsequent changes as well as the presence of seed predators and pathogens determine the length of time which seeds can remain viable in the soil. Evidences of longevity in seeds comes from viability tests on specimens of known age, e.g. from archeological sites, dated herbarium sheets or experiments on shelf-stored seeds or seeds buried in the field. However, only viability tests of seeds, which have been subjected to the moisture, temperature and gaseous compositions of soil under field conditions provide results of ecological importance (Fenner 1985; Garwood 1989; Whitmore 1983).

The fate of seven tree species was followed for four years and one species for a year using a burial experiment in the soil of GA forest (Demel 1996a; Demel & Granström 1997a). Seeds of these species showed a large variation in their behaviour during the four years of storage in the soil. At one extreme were the seeds of *Acacia abyssinica* and *Croton macrostachyus* which maintained nearly full viability even after four years of burial while at the other extreme were the seeds of *Bersama abyssinica* and *Ekebergia capensis* which lost their viability within a year and *Podocarpus falcatus* with less than 25% viability after two years. Seeds of *Indigofera rothii*, *Juniperus procera* and *Olea europaea* subsp. *cuspidata* occupied intermediate position. Seeds of *Acacia* and *Croton* maintained their dormancy throughout the study period, and there was very low germination in the soil while in the other species seeds germinated in the soil, although to a varying degree. Almost all seeds of *Bersama* and *Ekebergia* were depleted within a year as a result of germination in the soil. Similarly, a large proportion of cleaned seeds of *Podocarpus* and *Indigofera* germinated during the four years of storage in the soil while only a few seeds germinated from the other species. In seeds of *Podocarpus*, dormancy release proceeded faster and germination in the soil became higher when the epimatium was removed from the drupes. Prolonged storage in the soil altered the dormancy gradually in most of the seeds of *Croton* and a small proportion of the seeds of *Olea* as evidenced from improved germination of seeds in the laboratory over the exhumation periods.

In general, loss of seeds in the soil can be attributed to germination and deterioration of seeds due to ageing and fungal attack. The magnitude of depletion of seeds as a result of germination in the soil differed among the species: *Bersama* > *Ekebergia* > *Podocarpus* (cleaned seeds) > *Indigofera* > *Podocarpus* (drupes) > *Olea* > *Juniperus* > *Croton* > *Acacia*. Similarly the importance of deterioration of seeds in the soil declined among species as follows: *Olea* (seeds collected in 1990) > *Podocarpus* (drupes) > *Juniperus* > *Olea* (seeds collected in 1991) > *Podocarpus* (cleaned seeds) > *Croton*.

The burial experiment excluded predation since the seeds were enclosed in cloth bags. However, indirect evidences showing the importance of predators in reducing the seeds of

large-seeded species, such as *Juniperus*, *Olea* and *Podocarpus*, in the soil have been found (Demel 1996a, 1997a; Demel & Granström 1995).

Dry Afromontane forests accumulate large quantities of persistent seeds of herbaceous species in the soil. The accumulation of seeds in the soil is favored by the dormancy of many of the seeds, which is caused by either the presence of embryo dormancy or impermeable seed coat or both. Dormancy is selected for in most of dry Afromontane species, which are characterized by long dry seasons and unreliable rainy periods. In non-dormant seeds, dormancy is induced if the seeds are dispersed under dense canopy or buried in the soil. Although there are a few exceptions, most of the woody component of the forest vegetation lacks reserves of long-lived seeds in the soil. Seeds of several woody species are large and contain high moisture, indicative of adaptations to immediate germination and seedling establishment and survival under the canopy of forests. The residence time of their seeds in the soil is relatively short compared with those of herbaceous species, which are capable of maintaining their viability for a long time. Those seeds, which do not germinate are consumed by predators or succumb to attack by microorganisms. By immediate germination and establishment, many trees and shrubs form large populations of seedlings in the forest. Many of them are also capable of re-sprouting from damaged stems or roots.

Therefore, the sources of regrowth of woody species are totally dependent on the presence of the whole or a portion of the forest vegetation with mature individuals, since the probability of long-distance dispersal of most woody species is very low due to the large size of their seeds. In the event of disturbance, herbaceous species can regenerate from both the soil seed bank or from recently dispersed seeds while the woody species from pre-existing seedlings, coppice shoots or from recently dispersed seeds. Due to the dominance of dormancy, the paucity of recalcitrant species, the ability of many woody species to produce both population of seedlings and coppice shoots from damaged stems and roots as well as their relative floristic simplicity and small stature, it is logical to predict that dry Afromontane forests have the potential to recover faster from both natural and anthropogenic disturbances than rain forests.

Although natural disturbances and human exploitation, such as careful selective cutting, may promote regeneration of the forest from seedlings, excessive exploitation of species or clearing and conversion of the forest areas into permanent cultivation, which is the most common practice in many tropical countries such as Ethiopia, will eliminate or reduce the seed reserve and seedling populations. When clearing of these forests is followed by permanent cultivation, almost all of the woody and a part of the herbaceous components of the forest soil seed bank diminish through time and become dominated or replaced by herbaceous, especially weedy, species. Regeneration of woody species by sprouting is also prevented by the complete removal of stumps from the arable land. The elimination of soil seed banks and seedlings, removal of mature trees as well as their stumps and roots coupled with poor long-distance dispersal will have severe consequences on the regeneration of the forest vegetation. This implies that the future existence of dry Afromontane forests depends on the protection and conservation of the remaining patches of forests.

### Seed dormancy and germination

Species differ in their seed dormancy and requirements for seed germination. The germination of seeds in a particular situation and season is determined by the interaction between the dormancy-releasing factors, such as temperature, light and moisture. The germination and dormancy mechanisms are of great adaptive importance to plants in ensuring that seedling emergence occurs at the most advantageous time and place (Bewley & Black 1994; Fenner 1985). Important studies of considerable ecological significance have been made about triggers for germination, mainly in tropical rain forest species (see reviews by Garwood 1989; Vazquez-Yanes & Orozco-Segovia 1984, 1993, 1994; Whitmore 1983).

Seeds of tropical species have been broadly categorized into 'recalcitrant' and 'orthodox' based on their features and germination characteristics (Roberts 1973; Swaine & Whitmore 1988). The term recalcitrant refers to seeds that cannot withstand desiccation or low temperatures and germinate immediately or within a few days after dispersal. Many climax and late secondary species, including most economically important timber and

fruit trees possess recalcitrant seeds. The term orthodox refers to seeds of pioneer species that can withstand desiccation and then become dormant with extended longevity at low temperatures. Extensive surveys of germination of fresh seeds sown under suitable conditions indicated that rapid germination is the most common response in tropical rain forests although delayed germination is fairly common (Garwood 1989; Vazquez-Yanes & Orozco-Segovia 1993). Seeds of pioneer species remain dormant when conditions are unfavorable for germination, for e.g. under closed vegetation, and may have extended viability in the soil.

The prevention of germination in such circumstances preserves the seeds for future occasion when conditions may be more favorable for establishment, e. g. canopy removal and soil disturbance alter the light, temperature, moisture content and chemical composition of the soil layers, which subsequently trigger the germination of seeds in the soil.

### Light

Light is one of the environmental factors used by seeds to detect the depth of burial in the soil and formation of gap in the canopy. The light transmitted through leaves is much reduced in the red spectrum so that the ratio of red to far-red radiation (R/FR), which is around 1.2 in sunlight, is markedly reduced to about 0.2 under forest canopy (Pons 1992). The germination of many seeds is inhibited by light with a low R/FR ratio because it transforms the phytochrome to an inactive form, which prevents germination (Fenner 1985, 1995; Pons 1992; Vazquez-Yanes & Orozco-Segovia 1994; Whitmore 1983). In a comparative study of seed germination involving 25 forest species in Ethiopia, Demel & Granström (1997b) found that germination was completely inhibited or suppressed significantly in darkness in 28% of the species while 36% of the species germinated almost equally well under light and dark conditions. Hard-seeded species had very low germination in both light and dark treatments, due to impermeable seed coats. Seeds of 10 out of 12 species incubated under leaf shade (R/FR ratio = 0.08) and in darkness had significantly lower germination than those incubated under direct sunlight (R/FR ratio = 1.12) and neutral shade (R/FR ratio = 0.92). Seeds of *Phytolacca dodecandra* did not germinate when re-exposed to

light after dark incubation, suggesting the induction of secondary dormancy.

Species, which showed light requirements for germination are characteristic of disturbed habitats and produce numerous small seeds, which are capable of persisting for a long time in the soil (Demel 1996a, 1997a, 1998a; Demel & Granström 1995). The requirement of light for germination had also been demonstrated for seeds of different species from Ethiopia, e.g. *Veronica anagallis-aquatica* and *Veronica javanica* (Demel 1998b), twenty herbaceous species (Demel 1998c), *Inula confertiflora*, *Hypericum quartianum* and *Lobelia rhynchopetalum* (Demel 1998d), five *Solanum* species (Demel 1998e) and *Discopodium penninervium* (Demel 2002). Inhibition of germination in darkness or under leaf shade would favor the formation of persistent soil seed bank by avoiding fatal seedling emergence from deeper soil and under closed vegetation where conditions are very inimical to seedling establishment because of intense competition for light, water and nutrients (Grime *et al.* 1981; Pons 1992; Vazquez-Yanes & Orozco-Segovia 1994).

#### *Temperature*

Another environmental factor, which stimulates germination of seeds in the soil is temperature. Temperature affects seed germination in several ways (Probert 1992; Roberts 1988). Three cardinal temperatures (Bewley & Black 1994) can be recognized for every species, namely the maximum and minimum temperatures beyond which germination is prevented and the optimum temperature, which allows maximum germination in the shortest time. In 68% of the species tested on a thermogradient, germination was higher either at 20 or 25°C, while it peaked at 30°C in 12% of the species. Germination was severely reduced, less than 20%, at either 10 or 30°C in 64% of the species tested. The response of hard-seeded species to different temperature regimes on the thermogradient was poor, although the scarification of seeds resulted in either an increasing trend of germination with increasing temperature or in germination over a wide range of temperatures (Demel 1996a; Demel & Granström 1997b). The speed of germination, measured as the time to reach 50% of final germination at the optimum temperature of each species, was faster (less than 20 days) in 91% of

the species while it was much slower in *Pittosporum* (34 days) and *Juniperus* (39 days). In general, germination was faster in smaller than bigger seeds. Faster germination coupled with high rate of seedling growth is an adaptation of small-seeded species to exploit temporarily favorable conditions (Grime *et al.* 1981).

Germination of seeds of *Phytolacca dodecandra*, *Urera hypselodendron*, *Solanum*, and *Veronica* was much higher at fluctuating temperatures of 20/12°C (12 hrs each) than at constant temperature of 20°C (Demel 1996a; Demel & Granström 1997b). These species are characteristic of disturbed habitats with small seeds that are abundant in the soil (Demel 1996a, 1997a, 1998a, 2002; Demel & Granström 1995). Temperature had also been shown to play an important role in germination of seeds of several species in Ethiopia (Demel 1998b-f). The requirement for fluctuating temperature is an adaptation to prevent germination when the seeds are buried in deeper soil layers. It also helps seeds to detect the formation of gaps in the canopy of vegetation since vegetation canopy acts as effective insulator of temperature changes (Grime *et al.* 1981; Thompson & Grime 1983; Thompson *et al.* 1977).

Chilling was found to enhance the germination of seeds of *Rosa abyssinica* collected at an altitude of 2850 m at Menagesha dry Afromontane forest in Ethiopia (Demel 1997c). The requirement of chilling would prevent seeds of *R. abyssinica* from germinating between October and February in the Ethiopian highlands, when the conditions for the emergence and establishment of seedlings are unfavorable. Although the phenomenon is not common in the tropics, the positive germination response of *R. abyssinica* following the extended period of seed storage at low temperature suggests that chilling could be an important factor to overcome seed dormancy of tropical species at higher altitudes.

#### *Interaction between light and temperature*

Laboratory experiments have demonstrated that germination of light-requiring seeds can be modulated by temperature conditions, especially diurnal temperature fluctuations (Vazquez-Yanes & Orozco-Segovia 1994). For instance, seeds of certain species requiring light for germination were shown to germinate in the dark under

diurnal fluctuations in temperature (Thompson & Grime 1983). In seeds of *Achyrospermum*, *Conyza*, *Laggera*, *Phytolacca* and *Urera*, germination in the dark was higher when incubated at a high amplitude of diurnal temperature fluctuations (28/13°C) than at either a lower amplitude (20/12°C) or at constant temperature (20°C) (Demel 1996a; Demel & Granström 1997b). The joint role of light and temperature had been demonstrated for the germination of seeds of several species from Ethiopia (Demel 1998b-e, 2002). The capacity of seeds of certain species to germinate in darkness in response to diurnal fluctuations in temperature is considered as a mechanism of depth-sensing and gap detection by buried seeds (Pons 1992; Probert 1992; Thompson & Grime 1983).

#### Scarification

Rupture of the seed coat is another mechanism, which triggers germination in many hard-seeded species with impermeable seed coats (Ballard 1973; Baskin & Baskin 1989; Bewley & Black 1994; Rolston 1978). This is brought about by several factors including exposure to high temperature (Dell 1980; Demel 1994, 1996a, b; Sabiiti & Wein 1987) and diurnal temperature fluctuation (Moreno-Casasola *et al.* 1994; Probert 1992), ingestion and, thus, acid scarification in the digestive tract of various animals (Gardner *et al.* 1993; Lamprey *et al.* 1974; Russi *et al.* 1992), action of soil acids (Bewley & Black 1994), scarification by being rubbed against rocks or other hard objects (Gutterman 1993) and attack by soil micro-organisms (Edmisten 1970).

Seeds of species with impermeable hard seed coats were rendered permeable when subjected to high temperatures either in hot water (at 100°C), or dry heat (60, 80 and 100°C) and germination was improved significantly (Demel 1996a; Demel & Granström 1997b). In *Calpurnia aurea* hot water treatment at 100°C, even for as little as one minute, proved to be lethal although seeds responded to hot water treatments at 60, 70 and 80°C. Of the four species, which responded to hot water treatments (at 100°C), the highest germination was obtained when the seeds were immersed in hot water for one minute in three of the species while seeds of *Acacia abyssinica* required five minutes. Seeds of *A. abyssinica* required the longest exposure time because the

seed coats were thicker than the other species. In the dry heat treatments, germination was highest when seeds were exposed to 60 or 80°C but it declined when seeds were exposed to 100°C in all the species tested. The exposure time which resulted in the highest germination varied from species to species: 80 minutes at 60°C in *C. aurea* and *Indigofera rothii*, 15 minutes at 80°C in *Abutilon longicupse* and *Dodonaea angustifolia* and 60 minutes at 80°C in *A. abyssinica*. Exposure to 100°C was lethal for all seeds except those of *D. angustifolia*, which showed considerable germination even after exposure for 60 minutes at 100°C. This indicates that *D. angustifolia* has greater heat tolerance while *C. aurea* was sensitive to higher temperatures as evidenced by the sharp decline in the germination of seeds after 60 minutes exposure at 60°C. The response of *C. aurea* seeds to high temperatures in the dry heat treatments confers with the low tolerance of the seeds in the hot water treatments (at 100°C). Several other species from Ethiopia had been shown to respond to hot water and/or dry heat treatments (Demel 1994, 1996b, c, 1997b, 1998f; Mulualem & Odén 2001).

In all the species treated with mechanical scarification, germination was improved significantly, although the magnitude differed from species to species (Demel 1996a-c, 1997b, 1998f; Demel & Granström 1997b; Mulualem & Odén 2001). In addition, except seeds of *Croton macrostachyus*, *Juniperus procera*, *Olea europaea* subsp. *cuspidata* and *Podocarpus falcatus*, treatment of seeds with concentrated sulphuric acid gave a similar result (Demel 1994, 1997b, 1998f; Demel 1996a-c; Demel & Granström 1997b; Demel & Mulualem 1996; Mulualem & Odén 2001). The exposure time, which resulted in the highest germination varied from species to species, probably depending on the thickness of the seed coat. Seeds of species of *Acacia* required the longest exposure times.

The response of seeds to the hot water, dry heat, mechanical scarification and sulphuric acid treatments suggests that the dormancy in these seeds is imposed by the hard seed coats which hamper imbibition of water and prevent germination. Seed coat impermeability is a valuable feature for survival of a species under conditions of climatic adversity. Impermeable seeds do not only remain viable in the soil seed

bank for a long time, but under natural conditions, also tend to vary when different portions of a seed population become permeable to water and germinate. Thus, seed germination under favorable conditions results in seedling production over many years, providing numerous opportunities for survival. In Ethiopia, most of the species with impermeable hard seed coats are characteristic of the dry and warm lowlands, which are subject to frequent fires that are caused by both lightning and people (Demel 1996a, 2000; Tewolde 1986, 1988; von Breitenbach 1963). Several of them are known to possess persistent soil seed banks (Demel 1997a, 1998a; Demel & Granström 1995) and to retain their viability for at least four years in the forest soil (Demel & Granström 1997a). They colonize forest margins, roadsides, overgrazed bushlands and areas cleared of forest vegetation, and in particular *Dodonaea* regenerates rapidly after fire (Fichtl & Admasu 1994). The release of seed coat imposed dormancy as a result of heat was also demonstrated for several indigenous leguminous species in Ethiopia. Therefore, it is logical to conclude that hard-seededness in species responding well to hot water and heat treatments is a fire-adaptation (Sabiiti & Wein 1987). However, wide temperature fluctuations which are characteristic features of these areas and wild and domestic animals, which browse on twigs, pods and seeds may stimulate germination in these species.

### Moisture

Water availability is one of the prerequisites for the germination of seeds. Seeds of species, which are non-dormant at the time of dispersal can germinate over a wide range of temperature provided enough water is available. In some habitats, e.g. deserts, seed germination occurs when there is enough water in the soil to sustain subsequent seedling emergence and growth (Karszen & Hilhorst 1992). Hence, seeds of many species avoid germination during light showers of rain and germinate only after heavy rainfall. A requirement of heavy rainfall for germination has been observed in intact drupes of *Myrsine africana*, which is a widespread shrub of the Afromontane flora (Demel 1996a; Demel & Granström 1997b). Intact drupes of *M. africana* were unable to germinate, while removal of the exocarp and endocarp (simulating bird dispersal)

as well as a 48 hours pre-soaking in water of intact drupes (simulating heavy rainfall) resulted in good germination. The cause of inhibition of germination in intact drupes may be due to the presence of a chemical in the exocarp, which has to be leached out of the drupes. Although nothing is known about the process of leaching from drupes lying on the forest floor, this mechanism might possibly restrict the time of germination somewhat to the rainy season when there is plenty of moisture (Burger 1974). Most of the drupes of *M. africana* buried in the top-soil of a dry Afromontane forest germinated within 11 months (Demel unpub. data), suggesting the possible role of heavy rainfall to leach out the inhibitory chemical, although the timing of germination in relation to the rainfall is unknown. This species possesses a large population of seedlings in the dry Afromontane forests (Demel 1997d).

### *Effect of dry storage on seed germination*

Drying is the final phase of maturation in orthodox seeds and, therefore, the seeds retain their viability in dry storage, i.e. at low moisture content. However, recalcitrant seeds must retain relatively high moisture content during storage in order to maintain maximum viability (Bewely & Black 1994; Murdoch & Ellis 1992; Roberts 1973). For instance, *Bersama abyssinica* seeds collected in a dry Afromontane forest in Ethiopia failed to germinate in the initial tests involving seeds, which were air-dried before they were transported to the laboratory. Apparently, the seeds lost their germinability as a result of desiccation. However, seeds that were sown within a few days after collection had higher germination than those stored under room temperature for different periods without air-drying (Demel 1996a; Demel & Granström 1997b). This characteristic was also apparent in other trees, e.g. *Clausena anisata*, *Galiniera saxifraga*, *Schefflera abyssinica* and *Teclea nobilis* (Demel 1996a). A similar but less pronounced decline of germinability was also observed in seeds of *Ekebergia capensis* with time of dry storage (Demel 1996a; Demel & Granström 1997b). These results suggest that the seeds of these species are recalcitrant. In contrast, germinability was not significantly altered with time of dry storage in seeds of *Juniperus procera*, *Allophylus abyssinica* and *Carissa edulis*.

## Seedling banks and population structures of woody species

Following the germination of seeds, the next phase in the process of regeneration by seeds is the development of seedlings. Vulnerability of seedlings to hazards from environmental and biotic factors is higher at the early stages of seedling establishment (Fenner 1987; Whitmore 1996). One of the most effective adaptations for ensuring successful seedling establishment is the possession of a large seed, which provides an ample reserve of nutrients during the period immediately after germination (Foster 1986). Climax species typically have bigger seeds, than pioneer species, which germinate immediately or within a few days after dispersal under forest canopy (Swaine & Whitmore 1988; Whitmore 1989, 1990). By immediate germination they escape seed-eaters and also degradation of their usually fatty storage tissues by micro-organisms and form a seedling bank on the forest floor in contrast to the soil seed bank of pioneers (Whitmore 1990). The large seed found in species of dense vegetation indicate adaptation to establish in shade. Since seedlings of climax forest species may spend years under poor light conditions before a suitable gap appears, ample food reserves, coupled with shade tolerance and a low rate of growth are necessary for survival (Fenner 1985; Swaine & Whitmore 1988; Whitmore 1996).

In seedling population surveys of woody plants made by following altitudinal and exposure gradients at Gara Ades (GA) and Menagesha (ME) dry Afromontane forests (Demel 1996a, 1997d), a total of 57 species were recorded from both sites, of which 67% were trees, 21% shrubs and 12% woody climbers. At GA, the seedlings represented 40 species while at ME the number of species was 41 and the two sites shared only 24 of the species in common. The density at GA and ME was 16,290 and 32,650 seedlings/ha, respectively. The number of species increased with increasing altitude up to 2450 m at GA and 2650 m at ME, but declined thereafter. The total number of seedlings peaked at 2400 m at GA and 2550 at ME but declined below and above these altitudes. However, species showed great variations in the distribution of their seedlings along the altitudinal gradient. At GA, the number of seedlings of more than 50% of the

species peaked at either 2350 m or 2400 m while about 83% of the species at ME peaked between 2500 and 2800 m. At GA, 57% of the quadrats and 75% of the total number of seedlings were found under shade while the corresponding figures at ME were 71% and 75%, respectively. The number of quadrats and seedlings recorded under shade increased with increasing altitude up to the middle of the altitude ranges at both sites, but declined thereafter.

### *Seedling survival and growth*

In a study made through monitoring the survival and growth of naturally regenerated seedlings of *Juniperus procera* and *Podocarpus falcatus* at Gara Ades dry Afromontane forest, the number of surviving naturally regenerated seedlings of both *J. procera* and *P. falcatus* declined progressively during the three years of investigation both under shade and in clearings (Demel 1996a, 1997d). In *J. procera*, seedling survival did not differ in the open and under shade while seedlings of *P. falcatus* survived better under shade.

In planted seedlings of *Bersama abyssinica* and *J. procera*, survival did not differ under shade and in the open. On the other hand, the number of surviving seedlings of *Ekebergia capensis* under shade was significantly higher than those in the open. A few of the naturally regenerated seedlings disappeared due to unknown causes. However, there were evidences of damaged seedlings showing the impact of grazing/trampling animals and probably people. On the other hand, several planted seedlings died as a result of drought during the long dry seasons. Insect defoliation and burial by siltation also contributed to the mortality of seedlings of *B. abyssinica* and *E. capensis* (Demel 1996a, 1997d).

Annual height increment was generally low (< 15 cm) in both naturally regenerated and planted seedlings of the species studied. During the three years of study, the mean annual height increment did not differ significantly in naturally regenerated and planted seedlings of *J. procera* growing under shade compared with those in the clearings. However, naturally regenerated seedlings of *P. falcatus* growing in the clearings had significantly higher mean annual height increment than those growing under shade. Comparison of the mean annual height increment in seedlings of both *B.*

*abyssinica* and *E. capensis* planted under shade and in clearings did not show significant differences. Seedlings of climax species in tropical rain forests have been shown to grow slowly under forest canopy but commence rapid height growth after canopy gap develops (Whitmore 1990, 1996). Although the study period was relatively short and only a few species were studied, results from the survival and growth study did not show rapid height growth of seedlings in gaps as was found for rain forest species, suggesting that gap-phase dynamics is less important in dry Afromontane forests. This may be attributed to the marked differences in climatic conditions prevalent in dry Afromontane forests compared to those in tropical rain forests. In dry Afromontane forests, the long dry season, in which moisture is the limiting factor, coupled with the unreliable rainy period affects seedling growth. In contrast, the stable climatic condition in rain forests is conducive for seedling growth throughout the year.

#### *Population structures of woody plants*

Analysis of population structures, using frequency distribution of the height and diameter classes of naturally regenerated woody species, can provide an insight into their regeneration status (Brokaw 1987; Burrows 1990; Silvertown 1982; Silvertown & Doust 1993). In a study made at Gara Ades (GA) and Menagesha (ME) dry Afromontane forests, three groups of woody species were recognized based on the frequency distribution of height classes of individuals of the species (regeneration profile) (Demel 1996a, 1997d). The first group of species exhibited a pattern with the highest proportion of individuals lower than 50 cm and with a gradual decrease towards the larger classes; seventeen species from GA and eighteen species from ME belong to this group. This pattern indicates good reproduction as well as good seedling and sapling development, although some species, e.g. *Juniperus procera*, *Olea europaea* subsp. *cuspidata* and *Podocarpus falcatus* suffered from selective cutting of bigger trees. The species categorized in the second group had a high proportion of individuals only in the lowest height classes but no individuals at the intermediate and higher height classes; four species from GA and seven species from ME belong to this group. This pattern shows good early recruitment and establishment of seedlings but

failure of further development. It also indicates the threat of local extinction of the species since the mature individuals will not be replaced. Species with one or more of the height classes missing were placed in the third group; some of these species do not possess seedlings in the lowest height class; others lack individuals in the intermediate height classes; a few species are represented by individuals in only the lowest and highest classes or in the highest height classes. To this group belong 14 species from GA and seven species from ME. The second and third patterns are the results of human disturbance through selective removal of individuals, especially in the intermediate and higher height classes thereby hampering regeneration of the species.

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 phenology and ecology of flowering and fruiting, seed production and dispersal ecology, pre- and post-dispersal seed predation, seed rain, fate of dispersed seeds, dynamics of soil seed banks, ecophysiology of field seed germination, seedling establishment and growth, longevity of seeds once they are incorporated into the soil, seed dormancy and cues for seed germination as well as rate and processes of recruitment of seedlings from the soil seed bank.

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