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Regeneration of indigenous woody species under the canopies of tree plantations in Central Ethiopia

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Abstract: The hypothesis that tree plantations may foster the regeneration of native woody species, was tested through studies of understory floristic composition, height-class distribution of naturally regenerated seedlings and saplings of indigenous woody species, and soil seed banks in the native and exotic tree plantations in Central Ethiopia. A total of 70 plots, having 10 x 10 m area each, were studied in six monoculture plantation stands of four exotic species, i.e. *Cupressus lusitanica* (2 stands of different age), *Eucalyptus globulus, Pinus patula, P. radiata* and *Juniperus procera*, an indigenous coniferous species. Ages of the plantations ranged between 14 and 42 years. Soil seed bank analysis was also undertaken from soil samples collected in each of the 70 plots to examine the similarity between the soil seed flora and aboveground vegetation. Vegetation diversity was assessed through analyses of floristic composition, species richness and abundance. A total of 37 naturally regenerated indigenous woody species were recorded beneath all plantation stands, with densities ranging between 1630 and 18270 individuals ha^{-1}. There was considerable variation among plantation stands/species with respect to the density of naturally regenerated native woody species. Generally, seedling populations were the most abundant components of the regeneration in most of the plantation stands, forming 85% of the total regeneration count. A total of 68 plant species represented by 53 herbs, eight woody species and seven grasses were recorded in the soil seed bank from all stands. Similarity between the soil seed banks and aboveground flora (both seedlings and larger plants) was very low implying that the role of soil seed banks in the regeneration is low and dispersal of seeds from the adjacent natural forest plays an important role in the process. These results support the concept that forest plantations can foster the regeneration of native woody species and increase biodiversity in the plantation stands, if seed sources are available in the vicinity of the plantations.

Resumen: Con el fin de probar la hipótesis de que las plantaciones de árboles pueden fomentar la regeneración de especies leñosas nativas, se estudió la composición florística del sotobosque, la distribución de clases de altura de plántulas y juveniles resultantes de la regeneración natural de especies leñosas nativas, y los bancos de semillas en el suelo de plantaciones de árboles nativos y exóticos en el centro de Etiopía. En total se estudiaron 70 parcelas de 10 × 10 m en rodales de plantaciones monoespecíficas de cuatro especies exóticas: *Cupressus lusitanica* (dos rodales de diferente edad), *Eucalyptus globulus, Pinus patula, P. radiata,* y de la conífera nativa *Juniperus procera*. Las edades de las plantaciones fluctuaron entre 14 y 42 años. El banco de semillas en el suelo fue analizado con base en muestras también recolectadas en cada una de las 70 parcelas con el fin de examinar la similitud entre la flora del banco de semillas y la vegetación establecida. La diversidad de la vegetación fue evaluada por medio de análisis de la composición florística, la riqueza de especies y la abundancia. Se registraron en total 37 especies nativas leñosas naturalmente regeneradas bajo todos los rodales de las

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plantaciones, cuyas densidades variaron entre 1630 y 18270 individuos/ha. Hubo una variación considerable entre los rodales de las plantaciones y entre las especies, con respecto a la densidad de las especies leñosas regeneradas de forma natural. En general, las poblaciones de plántulas fueron los componentes más abundantes de la regeneración en la mayoría de los rodales de las plantaciones, representando un 85% del total del conteo de la regeneración. Un total de 68 especies de plantas representadas por 53 hierbas, ocho especies leñosas y siete pastos fueron registrados en el banco de semillas del suelo en todos los rodales. La similitud entre los bancos de semillas en el suelo y la flora establecida (considerando tanto las plántulas como las plantas grandes) fue muy baja, lo que implica que el banco de semillas del suelo tiene poca importancia para la regeneración, pero que la dispersión de semillas provenientes de bosques naturales adyacentes juega un papel importante en el proceso. Estos resultados apoyan el concepto de que las plantaciones forestales pueden fomentar la regeneración de especies leñosas nativas e incrementar la biodiversidad en las plantaciones, siempre y cuando estén disponibles fuentes de semillas en el vecindario de las plantaciones.

Resumo: As hipóteses das plantações arbóreas poderem favorecer a regeneração de espécies lenhosas nativas foram testadas com recurso ao estudo da composição florística do sub-coberto, da distribuição das classes de altura das plântulas naturalmente regeneradas, da rebentação das espécies lenhosas nativas e dos bancos seminais no solo, quer nas plantações de espécies nativas, quer nas de exóticas na Etiópia Central. Foram analisadas um total de 70 parcelas de 10x10m em talhões plantados com seis plantações monoculturais de quatro espécies exóticas, i.e. *Cupressus lusitanica* (2 talhões de idades diferentes), *Eucalyptus globulus*, *Pinus patula*, *P. radiata* e *Juniperus procera*, e espécies coníferas nativas. As idades das plantações variavam entre os 14 e os 42 anos. A análise dos bancos seminais no solo, para examinar a semelhança entre a flora seminal no solo e a aérea, foi efectuada a partir de amostras de solo colectadas em cada uma das 70 parcelas. A diversidade vegetacional foi avaliada mediante a análise da composição florística, a riqueza específica e a abundância. Um total de 37 espécies lenhosas indígenas, naturalmente regeneradas, foram registadas sub-coberto de todas as parcelas plantadas com densidades oscilando entre os 1630 e os 18270 exemplares/ha. Verificou-se uma variação considerável entre as parcelas de plantação/espécies em relação à densidade das espécies lenhosas naturalmente regeneradas. Geralmente, as populações de plântulas eram as componentes mais abundantes da regeneração na maior parte dos talhões plantados, formando 85% da regeneração total contada. Num total de 68 espécies de plantas, representando 53 ervas, oito espécies lenhosas e sete gramíneas foram registadas nos bancos de sementes no solo em todos os talhões. Quanto à semelhança entre os bancos de sementes no solo e a flora aérea (quer plântulas quer plantas maiores), verificou-se que ela era bastante pequena, implicando que o papel dos bancos de sementes no solo na regeneração é pequeno e que a dispersão de sementes das matas naturais adjacentes desempenham um papel importante no processo. Estes resultados suportam o conceito de que as plantações florestais podem favorecer a regeneração das espécies lenhosas nativas e aumentar a biodiversidade nos talhões plantados se se dispuser de fontes de sementes na proximidade das plantações.

Key words: *Cupressus, Eucalyptus,* floristic composition, *Juniperus, Pinus,* soil seed banks.

Introduction

Recently many studies have indicated that forest plantations can foster the regeneration of native woody species under their canopy and catalyze the subsequent succession processes (Bone *et al.* 1997; Fang & Peng 1997; Feyera 1998; Feyera *et al.* 2001; Fimbel & Fimbel 1996;

Lugo 1992; Parrotta 1992, 1993, 1995; Parrotta *et al.* 1997; Tucker & Murphy 1997; Yitebitu 1998). Moreover, forest plantations can also improve degraded lands by stabilizing soils, improving soil nutrient status and increasing soil organic matter through enhancement of aboveground litter production (Jordan & Farnworth 1982; Lugo 1992; Lugo *et al.* 1993; Michelsen *et al.* 1996; Parrotta 1995).

While the catalytic role of plantations in enhancing native woody regeneration as well as improving degraded lands has been quite widely observed in many countries, understanding of the mechanisms and processes involved is quite limited. For instance, knowledge on the relationships among the catalyzing effect of tree plantations on succession of forests, the role of dispersal mode, origin of seeds (whether seed bank or seed rain), and the effect of management and types of species, is scanty. Therefore, monitoring composition, densities and the role of seed rain, soil seed banks and advance regeneration in the recolonization of indigenous woody species following plantation establishment is of great importance. In addition, changes in the biotic and physical components of the plantation site, both temporally and spatially, are gaps that need investigation in the future. Improved understanding of the processes that may allow us to develop plantation management for provision of urgently required goods and services, coupled with enhancement and maintenance of biodiversity, are very essential.

Despite the fact that plantation forestry has a long history in Ethiopia, few investigations (Feyera 1998; Feyera *et al.* 2001; Michelsen *et al.* 1993; Michelsen *et al.* 1996; Yitebitu 1998) have been made on the ecology of plantations and their management. These studies indicated that forest plantations could foster the regeneration of secondary natural vegetation. Therefore, in the present study we have attempted to test the hypothesis that tree plantations can foster the regeneration of indigenous woody species provided that there are seed sources in their vicinity or buried seed reserves (seed banks) in the soil from the previous vegetation. The specific objectives of the study were to assess: the diversity, density and height class distribution of the naturally regenerated woody species and the role of soil seed banks in the regeneration process at Menagesha-Suba Forest.

Materials and methods

The study area

This study was carried out at Menagesha-Suba dry Afromontane forest, located 50-km southwest of Addis Ababa at 9^{O}00′ N and 38^{O} 35′ E, (Demel 1996; Friis 1992; Tamrat 1993) with altitude ranging between 2200 to 3000 m. The area consists of an isolated mountain surrounded by low lying plains. The soils at higher altitudes are shallow and light brown with rocky substrate. At lower altitudes, the soils are deep, reddish-brown and less gravelly (Tamrat 1993). The topography of the area is extremely dissected, with alternating ridges and valleys dominating the landscape. The annual rainfall in the area is estimated to be around 1225 mm and the mean monthly temperature ranges from 12 to 16^{O}C.

Originally the natural forest communities of Menagesha-Suba consisted of *Hypericum* belts, *Hagenia-Juniperus* forest, *Juniperus* forest, *Juniperus-Podocarpus* and *Podocarpus* forest in descending order of elevation (from 3500 m down to 2000 m). However, these forests had been under commercial exploitation as early as the beginning of the 20th century, when the first sawmill was established in the country (von Breitenbach & Koukol 1962). As a result, most of the forest was degraded or destroyed due to over-exploitation of timber from the forest. Additionally, the encroachment of agriculture to the forestland was observed.

Currently the forest covers an area of about 2500 ha of which 800 ha is man-made forest and the remaining is natural forest. The forest cover is concentrated on the northwestern and southwestern half of the mountain, while the eastern slope has been converted into farmland. Forest plantation establishment was initiated in the mid 20th century with some indigenous and exotic tree species, among which *Juniperus procera* Endl., *Eucalyptus globulus* subsp. g*lobulus* Labill, *Pinus radiata* D. Don, *Pinus patula* Schlechtendal & Chamisso, and *Cupressus lusitanica* Miller, were included. Plantations were established on areas already deforested for cultivation or affected by unsustainable commercial exploitation.

The Menagesha-Suba Forest is the habitat of numerous wild animals, including baboons, colobus monkeys, bushbucks, bush pigs, ghenet, caracal, spotted hyena, wildcat and a variety of

bird species (Forest Rangers, personal communication).

Plantation species

Six plantation stands comprising *C. lusitanica* (2 stands of different age), *E. globulus, P, radiata, P. patula* and *J. procera* and the adjacent natural forest were used for the study. The first four species are exotic evergreen tree species while the last one is an indigenous coniferous species. Except *E. globulus* and *C. lusitanica* (14-year old) stands, the other 4 plantation stands are adjacent to one another. The species were chosen because of their popularity among the plantation projects, their canopy structure/form and expected variation in floor characteristics. Descriptions and other relevant information about these species can be found in the works of Fichtl & Admasu (1994), Friis (1995) and von Breitenbach (1961).

Vegetation sampling

Vegetation assessment within the stands was conducted using a line transect survey. A total of 70 square plots of 0.01 ha (10 m x 10 m) were located at 100 m intervals along line transects which were 100 m apart. The starting point of any line transect was also located randomly in each stand. Ten plots were laid down in each stand and the first plot was located randomly. Then, the plots were laid at every 100 m distance on each line transect. All sample plots were located at least 50 m from plantation edge/road to avoid edge effect.

In each plot, all of the naturally regenerated woody species were identified and counted. When identification proved difficult in the field, specimens were collected for identification. The plants were categorized as seedling (height ≤ 1.0 m), sapling (height between 1 and 3 m) and tree (height > 3 m). The height (m) and collar diameter (diameter at the ground level) of seedlings and saplings within the plot were measured using a meter-marked stick and a caliper, respectively. Height, diameter at breast height (1.3 m) and percentage of crown cover of planted overstorey trees were measured. Hypsometer and caliper were used to measure height and diameter, respectively. Additionally, aspect, altitude and litter depths were recorded on each plot. For litter depth, 20 points per plot were measured. Nomenchlature follows Cufodontis (1953, 1972), Edwards *et al.* (1995) Friis (1992) and Hedberg & Edwards (1989).

Soil sampling

To examine similarity of aboveground and soil seed bank flora, a total of 280 soil samples (i.e. 40 soil samples in each of the seven stands, including the natural forest) were collected from six plantation stands and adjacent natural forest. The soil samples were collected from the plots used for vegetation sampling. At the center of each plot, a small plot of 10 cm x 10 cm (100 cm^2) was marked and four separate soil layers consisting of litter layer, and three successively deeper mineral soil layers, each 3 cm thick (to investigate depth distribution of seeds in the soil), were removed using a sharp knife. The soil samples were put into plastic bags separately and transported for analysis. In cases of dissimilarity between soil and aboveground flora, soil depth was used to speculate the seed sources (whether recently dispersed seed or from soil seed bank).

All soil samples were sieved using a mesh size of 0.50 mm to recover seeds of woody species before the soil samples were incubated to stimulate germination of seeds. The seeds recovered by sieving were collected into paper bags and identified using local reference material. The viability of seeds was determined by dissecting/cutting seeds; seeds were considered viable when their contents were firm and white (Demel 1996). The soil samples were incubated in a glasshouse for seven months. The emerging seedlings were identified, recorded and discarded once or twice every two weeks. Those seedlings difficult to identify were transplanted and grown to a larger stage to make identification easier and accurate.

Data analysis

The Shannon-Wiener diversity index (H′) and Shannon evenness index (Krebs 1989) were used to measure diversity of naturally regenerated indigenous woody species in the different plantations and adjacent natural forests. Similarity index of understory regenerated native woody species in the different stands was calculated using Jaccard's Coefficient of Similarity (JCS) (Krebs 1989). Similarity of the soil seed bank flora and the aboveground flora was compared using JCS between average paired sample plots in which both seed banks and aboveground species data were available. Variations in understory density of naturally regenerated indigenous woody species among the different plantation stands were compared by cal-

culating standard deviation. To evaluate the population structure of naturally regenerated indigenous woody plants, height class histograms were used.

Results

Stand structure

The characteristics of the plantation stands investigated in the present study varied among the stands and species (Table 1). The mean height ranged between 11 and 25 m, mean diameter at breast height between 9 and 26 cm, mean basal area between 5 and 45 m^2 ha^{-1}, and stem density between 710 and 980 stems ha^{-1}. The variation is most pronounced in the *E. globulus* stand.

Floristic composition and diversity

A total of 42 woody species were recorded growing under plantation stands and in the adjacent natural forest, of which three were only found in the adjacent natural forest (Table 2). In the plantation stands, a total of 37 native woody species and 2 exotic tree species, representing over 28 families of plants, were recorded. In the adjacent natural forest, 26 native woody species were recorded. Among the 37 native woody species recorded in the plantation stands, 8 species were upperstory tree in the adjacent natural forest, 27 species were shrubs or small trees and 2 species were woody climbers (Table 2). The highest number of species per plot was found in *J. procera* stand of 42 years of age and in the *E. globulus* stand of 17 years of age (second rotation). The most frequently (frequency = 100%) found species were *Bersama abyssinica, Burcea antidysentrica, Carissa edulis, Dovyalis abyssinica, D. verrucosa, Maytenus arbutifolia, Myrsine africana, Olea europaea* and *Spinilum oxyacantha* (Table 2) in both plantation stands and adjacent natural forest.

The Shannon-Wiener diversity index and index of evenness showed less variation among the various stands (Table 3). The number of understory woody species in the *Eucalyptus* and *Juniperus* stands as well as in the natural forest was higher than other plantation stands/plots.

Density and similarity of regeneration under plantation stands

The density of understory regenerated woody plants was variable among the various plantation stands and species (Table 3). The highest density of regenerated understorey woody plants (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 density of naturally regenerated woody species decreases with increasing age in the *C. lusitanica* stands (Table 3).

In terms of naturally regenerated woody species, the *C. lusitanica* (24 year old) and *P. radiata* (24 year old) stands exhibited the highest similarity (JCS = 0.73) while *C. lusitanica* (24 year old) and the *E. globulus* (17 year old) stands showed the least similarity (JCS = 0.31) (Table 4). The *Juniperus* (42 year old) stand and adjacent natural forest also exhibit high similarity (JCS = 0.66). The number of species shared by any two stands ranged between 9 and 21 (Table 4).

Table 1. Characteristics of the plantation stands sampled at Menagesha Suba forest.

Stands	Area (ha)	Distance to natural forest (m)	Range of altitude (m)	Age (yr)	Mean basal area (m^2 ha^{-1})	Mean dbh (cm)	Mean height (m)	Stems ha^{-1}	Average litter depth (cm)	Crown cover (%)
Cupressus lusitanica	18	2000	2660-2300	14	20	16	11	980	1	71
Eucalyptus globulus	25	250	2300-2410	17	5	9	12	790	1.1	25
Pinus patula	49	300	2470-2570	24	27	22	24	790	4.8	72
Pinus radiata	30	300	2460-2560	24	45	26	25	860	3.1	60
Cupressus lusitanica	32	200	2540-2630	24	31	22	20	820	3.8	76
Juniperus procera	8	200	2370-2400	42	22	20	21	710	1.7	65
Natural forest*	2500		2400-2440	500+	124	30	21	1760	2.7	80

*Only upperstorey trees ≥ 10 cm in diameter

Table 2. The most common naturally regenerated woody plants beneath different forest types at Menagesha Forest (DA = dispersal agent; B = birds; M = mammals; W = wind). (Figures in the table indicate density per 1000 m2). *The two letters used in the 2nd row are the first letters of genus and specific epithet while the numbers following the letters indicate age of the stands (in years).

Species	*C. lusitanica*		*P. patula*	*P. radiata*	*J. procera*	*E. globulus*	Natural Forest (NF500+)	DA
	CL14*	CL24	PP24	PR24	JP42	EG17		
Acacia abyssinica						1		M
Albizia schimperiana					4			M
Allophylus abyssinicus			3	5		1		B, M
Bersama abyssinica	7	6	62	62	15	1	3	B, W
Brucea antidysenterica	1	3	11	1	2	17	3	B
Calpurnia aurea				13	25		6	B, M
Carissa edulis	82	5	4	5	69	105	6	B, M
Clausena anisata	8		1			7	6	M
Croton macrostachyus			1	1		4		B, M
Cupressus lusitanica	302				4			M,W ?
Dodonaea angustifolia						13		B
Dovyalis abyssinica	1	11	41	33	55	7	16	B, M
Dovyalis verrucosa	5	75	44	147	242	1	85	B, M
Ekebergia capensis						4		B, M
Eucalyptus globulus						8		B
Euphorbia abyssinica							1	B
Fagaropsis angolensis					1		1	B
Ficus sur							7	B, M
Flacourtia indica					33		3	B, M
Hypericum revolutum						5		B
Juniperus procera	3				8	119	15	B
Maytenus arbutifolia	16	19	92	56	547	123	203	B, M
Maytenus undatus					99			B, M
Myrsine africana	37	5	4	10	15	54	401	B, M
Nuxia congesta							3	B, W
Olea capensis subsp. *hochestetteri*					14		2	B, M
Olea europaea	27	15	32	12	269	171	50	B, M
Olinia rochetiana			2		5	9	2	B
Osyris quadripartita	6				1	7		B, M
Pittosporum veridiflorum	1				1	2		B, M
Podocarpus falcatus				1	22	8	6	B, M
Prunus africana	2						2	B, M
Psydrax schimperiana	1				42	1	27	B
Rhamnus prinoides					2		3	B, M
Rhamnus staddo	30		1		3	24		B, M
Rhus glutinosa	9				1	4	2	B
Rosa abyssinica						4		M
Rubus apetalus						2		B, M
Scolopia theifolia		20	7	17	226		234	B, M
Spiniluma oxyacantha	39	3	6	28	119	41	78	B, M
Teclea nobilis		1	1	3	3		3	B
Vernonia sp.			1					W
Total	577	163	313	394	1827	773	1168	

Table 3. Average plot values of Shannon-Wiener diversity, Evenness and density of naturally regenerated woody species recorded in the different plantation stands and the adjacent natural forest. *Number of woody species; **Density of naturally regenerated woody species.

Stands	Age (yr)	Diversity (H′)	Evenness (H/lns)	Richness*	Density** (no. ha-1)	Standard deviation of density
C. lusitanica	14	1.67	0.576	18	5770	39
E. globulus	17	2.30	0.69	27	7730	68
C. lusitanica	24	1.79	0.74	11	1630	11
P. radiata	24	2.25	0.83	15	3130	12
P. patula	24	1.97	0.69	17	3940	17
J. procera	42	2.24	0.68	27	18270	60
Natural forest	500+	1.99	0.61	26	11680	109

Table 4. Jaccard's Coefficient of Similarity in species composition of naturally regenerated woody species between different stands investigated at Menagesha-Suba forest (abbreviations as in Table 2).

Stants	CL14	EG17	CL24	PP24	PR24	JE42	NF500
CL14	-	0.55	0.45	0.46	0.43	0.55	0.46
EG17		-	0.31	0.46	0.40	0.46	0.39
CL24			-	0.65	0.73	0.41	0.42
PP24				-	0.68	0.42	0.43
PR24					-	0.45	0.46
JP42						-	0.66
NF500							-

Structure of regeneration

Height class distribution of the naturally regenerated understory woody species showed similar trends in all stands (Fig. 1). The proportion of individuals showed a typical inversed J-shaped curve with many small individuals and few or no large individuals in most of the stands, indicating a high number of seedlings (85%), low proportion of saplings (15%) and relatively few mature trees (4%).

Floristic composition of soil seed banks

A total of 68 plant species (data from sieving and germination combined) were recovered from the litter and the top 9 cm soil samples collected beneath different plantation stands. Among the 53 identified species, herbs were represented by 43 species (81%), woody plants by 8 species (15%) and grasses by 2 species (4%). Among the 15 unidentified plant species, 10 were herbs and 5 were grasses. The species composition in different stands ranged from 20 to 32 species; the highest number of species was recovered in the *Juniperus* stand and the lowest in *Cupressus* stands.

The similarity between the aboveground and soil seed flora in each stand was negligible, with JCS ranging between zero and 0.02. Only 4 species (*C. lusitanica, Ficus sur, J. procera*, and *Rubus apetalus*) of the naturally regenerated woody species aboveground were represented in the soil seed bank. Most of the species encountered during soil sieving had very few viable seeds in the soil.

Discussion

Floristic composition and diversity

The different populations of naturally regenerated indigenous woody species were dominated by species known to be either shrubs or small trees in their life forms. Of the 37 indigenous woody species recorded in the plantation stands, only nine are upperstory trees in the adjacent natural forest. This may be attributed to the scarcity of seed-producing trees of the other upperstorey species in the vicinity of the plantations, 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 (Feyea 1998; Feyera *et al.* 2001). 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).

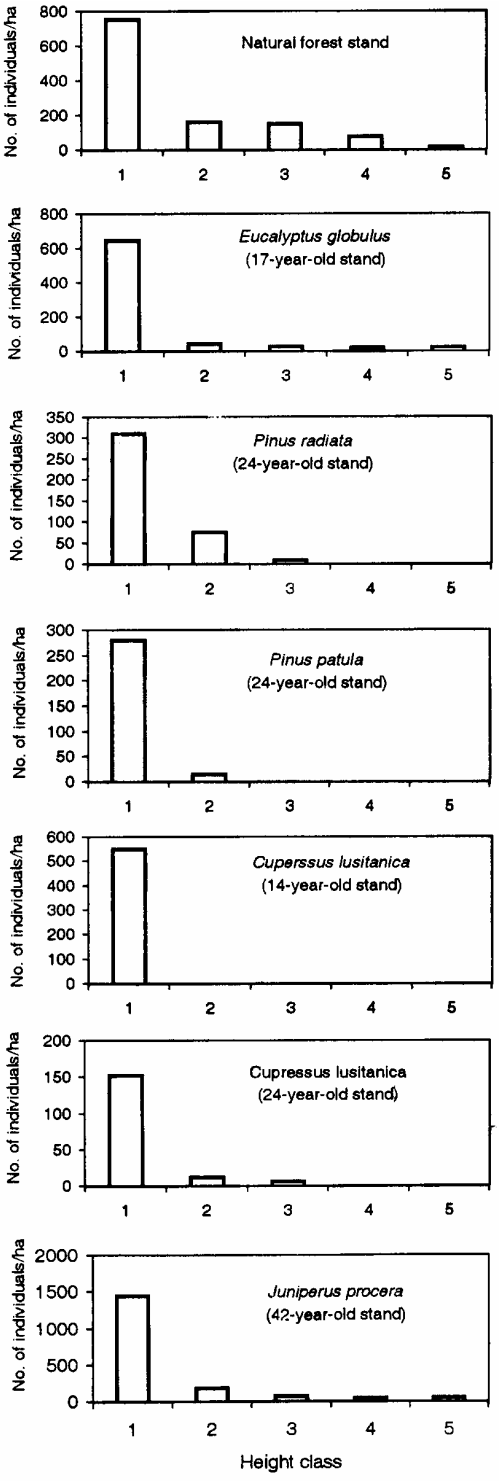

Fig. 1. Number of individuals of naturally regenerated woody species (in 1000 m2) in each height class category (height class category: 1 = ≤ 1 m; 2 = 1-2 m; 3 = 2-3 m; 4 = 3-4 m; 5 = >4 m).

It is very interesting to note that the highest number of naturally regenerated woody species (27 species) was recorded under the *E. globulus* and *Juniperus* stands (Tables 2 & 3). In addition, the density of naturally regenerated woody species under the *E. globulus* stand was the highest followed by the stand of *Juniperus* and the 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).

Density and similarity of naturally regenerated woody species

The density of naturally regenerated woody species was variable among the different plantation stands. The highest density of understory woody plants was observed in the *J. procera* (42 year old) stand and this may be attributed to the age of the stand. As the age of the stand increases, the number of newly arriving and germinating seeds increases. In addition, soil and light environment beneath the canopy could be modified to allow the arriving seeds to germinate and add new individuals to the established populations of naturally regenerating woody species. 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 (Table 1). Greater litter depth may hinder either the germination of seeds or the establishment of germinating seeds 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 densities of naturally regenerated plants 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.* 2001; Fimbel & Fimbel 1996). As expected, the density of naturally regenerating woody plants in the adjacent natural forest was higher than in most plantation stands except the *Juniperus* stand.

Most plantation stands exhibited low similarity in the composition of naturally regenerated indigenous woody species despite uniform climatic conditions. Hence, it seems likely that other factors such as the type of plantation species, edaphic

conditions of the stands, management practices, age, etc. may have contributed to the differences in the similarity of species composition among the plantation stands. Other authors (Feyera 1998; Feyera *et al.* 2001; Pande *et al.* 1988) have reported similar results, i.e., low similarity among plantations of different species.

Population structure of regeneration

Analysis of the pattern of height and diameter class distribution of naturally regenerating plant species can provide insight into their regeneration status. Apparently, the seedling populations were the most abundant components (about 85% of the total regeneration) of naturally regenerated individuals in most of the plantation stands (Fig. 1). Saplings constituted about 11% of the total regeneration count and the proportion of regeneration under the category of trees amounted to only 4%, indicating that the smallest height class populations dominate the understory regeneration. Though the stands were of different ages, the populations of understory native woody species were dominated by individuals of lower height classes, implying that succession is at an early stage of development in all plantation stands. The fact that no species with height classes above one meter were recorded under the *Cupressus* stands (Fig. 1) might suggest that growth of seedlings after establishment is hampered. The reason for this phenomenon requires further investigation.

The data indicated that seeds of most of the naturally regenerated woody species are being brought in continuously, but the overstorey planted trees seem to affect the patterns of population structure of naturally regenerating woody plants. Likewise, in the adjacent natural forest, the proportions of seedlings were 65%, saplings 27% and trees 8%. The low number of trees in the natural forest can be attributed mainly to human disturbances such as cutting of trees for different uses (Demel 1996, 1997 and Personal observation). As a result, the regeneration of indigenous woody plants in the adjacent plantation stands may have been affected, since the mature trees that would have contributed as seed sources had been removed.

Similarity between soil seed bank and aboveground flora

The similarity between the soil seed bank and aboveground flora was very low. Most of the soil seed banks under the different plantation stands were characterized by high proportions of herbs and grasses (almost 96%) while the aboveground flora recorded was dominated by woody plants. Several studies have supported the lack of similarity in species composition between the seed in the soil and the aboveground vegetation (Dessaint *et al.* 1997; Tucker & Murphy 1997; Whipple 1978). The conclusion from these studies was that the soil seed banks usually contain a high proportion of early successional species which rely on the persistent seed bank as a part of their opportunistic strategy. Therefore, their representation in the seedling bank or advance regeneration is usually low. On the other hand, seeds of the late successsional plant species may germinate soon after dispersal or may be affected by pathogens and predation agents (Demel 1997; Demle & Granström 1995, 1997), and as a result few such species were represented in the soil seed bank. Instead, they form persistent seedling banks.

Conclusion

Our results indicate that tree plantations can be useful to foster natural regeneration of native woody species, particularly on sites where soil seed banks of native forest species are lacking. They enhance the process of native forest succession over time by attracting seed dispersal agents and providing a nurse effect for the colonizing native species. As a result, tree plantations can enhance plant diversity of indigenous species. However, the need to have seed sources in the vicinity to facilitate the regeneration of native woody species under the canopies of tree plantations is a pre-requisite. It also appears that birds or mammals transport almost all woody species in the understorey. Therefore, it is very important to keep enough natural forest not only to maintain seed sources in the vicinity but also habitats for seed dispersing animals.

We recommend that more research should be carried out for better understanding of the succesSsional processes within tree plantations such as the dynamics of seeds, i.e. seed dispersal, germination in the field, seed predation as well as seedling establishment and growth. It is also necessary to investigate how the established native woody species can be manipulated to develop a secondary forest.

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