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ECOLOGICAL STUDIES OF PLANTATIONS IN SOME PARTS OF ETHIOPIA,
WITH SPECIAL REGARD TO ECOLOGICAL EFFECTS OF THE USE OF
EUCALYPTUS spp.

by

Lisanework Nigatu

A thesis
presented to Addis Ababa University
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ABSTRACT

ADDIS ABABA UNIVERSITY
SCHOOL OF GRADUATE STUDIES

ECOLOGICAL STUDIES OF PLANTATIONS IN SOME PARTS OF ETHIOPIA, WITH
SPECIAL REGARD TO ECOLOGICAL EFFECTS OF THE USE OF EUCALYPTUS SPP.

by

Lisanework Nigatu
Department of Biology
Faculty of Science

Approved by the Examining Board:

Dr. Valemtsehay Mekonnen
Chairman, Department Graduate
Committee

Prof. Ib. Friis
Advisor

Dr. Tewolde Berhan Gebre Egziabher
Advisor

Dr. Ingvar Backeus
Examiner

Dr. P. Kuchar
Examiner

Dr. Ensermu Kelbessa
Examiner

ABSTRACT

Ethiopia has a long tradition of establishing plantation trees. *Eucalyptus* plantations, especially, have been developed in this country since the beginning of this century. This study presents information on the undergrowth vegetation characteristics, soil conditions and nutrient cycling in established plantations and natural forests in Ethiopia, combined with bioassays of germination, growth and nutrient uptake of plants.

Vegetation and environmental data were collected from ninety-two plantation and natural forest sites in west, north-east, south, and central regions of Ethiopia. Four permanent plots were established in three plantation and a natural montane forest stands for long term assessments of nutrient cycling and soil fertility. Soils collected from under plantations and a natural forest, and aqueous leaf extracts of the planted tree species were used as substrates in bioassays.

The study demonstrated that the floristic composition of the undergrowth vegetation was influenced by altitude and rainfall. These environmental gradients were associated with variations in soil physical and chemical properties and stand characteristics of the plantation tree species. Generally, the species richness, herbaceous biomass and coverage of plantations (except those of *Cupressus lusitanica*) were similar, or higher than that of the natural forests. Changes in soil chemical properties (decrease in pH, N, P, and Ca) were found in plantation soils. The relevance of litterfall and litter decomposition in relation to nutrient cycling is discussed. The data from the large number of plantation and natural forest sites, together with data from the detailed studies of nutrient use efficiency, plant performance and litter decomposition suggest that phosphorus was limiting plant growth and decomposition in the Ethiopian highland plantation forests.

Bioassay using aqueous leaf extracts of *C. lusitanica* and three *Eucalyptus spp.* significantly reduced seed germination, radicle and seedling growth of four crop plants: *Cicer arietinum*, *Eragrostis tef*, *Pisum sativum* and *Zea mays*. The destitute growth of plants under or adjacent to these plantation trees was related to allelopathy.

The significance of combining field studies with bioassays in surveys of the undergrowth species characteristics and the fertility of soils after plantation establishment is emphasized. The impact of plantation tree species selection and site management on soil fertility and herbaceous plant cover in the Ethiopian highland forests is discussed.

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CHAPTER I

GENERAL INTRODUCTION

1. Background of the study

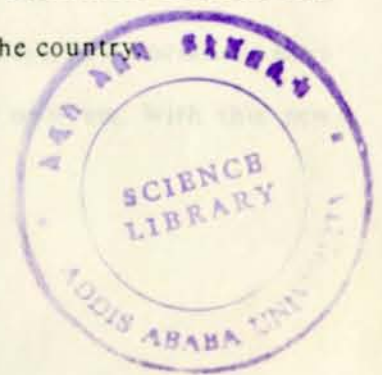
The environmental deterioration caused by combined effect of growing population and the pressure on the natural forests calls for the need to establish plantation forests in tropical regions. Ethiopia is one of the countries badly struck by widespread decline of environmental stability and productivity due to a rapidly increasing population and long lasting deforestation. In order to stop or slow down the deterioration, large sum of money and manpower have been invested to plant mainly fast growing exotic tree species, mostly in connection with the establishment of plantations for the production of fuelwood. One such exotic group is the *Eucalyptus*, whose popularity as plantation species is attributable to their being generally adaptable, fast growing and with a wide range of productive and a variety of uses.

Plantations are generally considered to be very beneficial to the environment, provided they are established with due background knowledge of their ecological effects. The large scale expansion, in Ethiopia, of plantation forests with exotic fast growing species notably conifers and eucalypts is likely to continue as long as there is a need to solve shortage of fuelwood and wood for industrial purposes. Yet, it is not known at this point what the impact of the established plantations with exotic tree species have on the environment. The planting of eucalypts is perceived in some countries to have undesirable environmental consequences. There is a well-publicised campaign against eucalypt plantations in India (Shiva & Bandyopadhyay, 1983) and in other countries. In Spain, an organization promoting the use of indigenous trees is called the 'Phoracantha Club' in praise of a bark beetle that kills the exotic eucalypt (Florence, 1986).

There are both positive and negative arguments for planting eucalypts. On the positive side it is recognized that eucalypts have many advantages for both small and large operations, particularly their fast growth rates, resistance to browsing and ability to coppice, supply of a range of wood products in high demand, and the significant contribution they can make to farm incomes (Poore & Fries, 1985). Alternatively, the planting of eucalypts has been criticised because it is claimed that the soil will be degraded through enhanced erosion, nutrient depletion and biological changes; that the established plantation affects the diversity of the underlying vegetation and the performance of cultivated crops adjacent to the plantation. Similarly, the view that eucalypts under certain conditions have a deteriorating effect on the environment is growing also in Ethiopia. As the issue of development and environmental conservation gains momentum, evaluation of the ecological impact of the established plantations should be very crucial for any future plant introduction or large-scale afforestation programmes. The purpose of the present study is to investigate the long-term ecological effects of established plantations, especially *Eucalyptus* plantations, which have a very long tradition in Ethiopia.

2. Plantation Forests in Ethiopia

In the past Ethiopia had rich forests. The forest area has, however, been rapidly reduced and the forests are at present less than three percent of the country's total area (Anonymous 1991). The clearing and burning of the natural forests has caused serious erosion problems and the availability of fuelwood and wood for industrial purposes has been steadily reduced in most parts of the country. As the destruction of the natural forest has gone, more attention is being given to establishment of tree plantations to meet the increasing demand for wood products and environmental protection. As part of the afforestation programmes, many plantations of exotic and few indigenous species have been established throughout the country.



The first species trial in the country were established about a century ago. Some years after the foundation of Addis Ababa, the town was extremely short of fuelwood. The use of *Eucalyptus* was suggested to Emperor Menlik II in 1895 by a French philologist, M. Mondon-Vidaillet (Horvath, 1968). Seed of 15 *Eucalyptus* species was imported into the country, and trial plantations were established. In the beginning of the 20th Century, some landowners planted small areas in the suburbs of Addis Ababa in order to sell small poles and fuelwood. Encouragement by the government, such as tax relief for land planted with *Eucalyptus* and free distribution of seed, increased planting. Around 1920 the streets and paths of Addis Ababa resembled clearings in an *Eucalyptus* forest. It was even suggested that the name of the city might appropriately be changed into Eucalyptopolis (Anonymous 1990).

The Italians were the first who surveyed the Addis Ababa *Eucalyptus* plantations during their occupation (1935-1940). The forest area was estimated to be not less than 4000 ha., and more likely over 5000 ha. (Horvath, 1968). In 1957 the plantation forest stands covered an area of 17,600 ha. and by 1964 the area had expanded to 24,600 ha. (Horvath, 1968). Prior to 1974, about 40,000 ha. plantations had been established on private land throughout the country, utilizing mainly *E. globulus* Labill ssp. *globulus* and, to a lesser extent, *E. camaldulensis* Dehnh (Anonymous, 1979; Pohjonen, 1989). They were established with the objective of supplying major population centres with fuelwood and construction poles. The plantation establishment rate was near to 500 ha per year (Horvath, 1968). By the mid-1970's, the plantation forests covered about 98,000 ha., and a further 20,000 ha. of new plantations were established during the years of 1984-1988 with the support of International Organizations (Pohjonen & Pukkala, 1990). The latter figure refers to the plantations established in the surroundings of Addis Ababa and some other highland towns: Debre Berhan, Dessie and Nazareth. Moreover, since the beginning of 1978, the Peasant Associations have been encouraged to establish village woodlots for their own use. With this new

programme it is estimated that about 20,000 ha. of fuelwood plantations have been established during the past few years. Currently the largest fuelwood plantations are growing around the capital of Addis Ababa.

Establishment of industrial plantations is a rather recent development in the country. The development of these plantation forests started in the 1950's in Assella and in the 1960's in Munesa-Shashemene. The activity was later expanded to other natural forest areas. The Munesa-Shashemene plantation, for example, comprises one of the largest planted site in this respect. Since 1968 considerable areas of trial plantations have been established particularly with *Eucalyptus* but also with *Cupressus* and *Pinus*. The Munesa-Shashemene plantation forests cover approximately 4,300 ha., of which conifers cover 3,100 ha. and *Eucalyptus* 1,200 ha. The conifers, especially *C. lusitanica* Mill, *Pinus patula* Schiede & Deppe ex Schlecht and *P. radiata* D. Don, have been established to substitute the vanishing timber resources of *Juniperus procera* Hochst. ex. Engl. and *Podocarpus falcatus* (Thunb.) Mirb. Other industrial plantation forests are being developed in the warm and humid highland regions of Illubabor, Keffa and Sidamo. The total size of plantation forests established within the National Forestry Priority Areas is estimated to be about 90,000 ha., at present (Anonymous, 1993).

The programme for reforestation of degraded lands started in 1971 in Tigray, and later extended to cover more regions including Wollo, Hararghe and Gondar. With this programme about 24,430 ha. of land have been afforested upto the early 1980's. The areas planted under this programme are usually steep hill sides and marginal lands which have been exposed to soil erosion over a lengthy period. Hence the prime objective has been to establish a vegetation cover over degraded lands, so preventing further deterioration. These plantations are also expected to contribute to fuelwood supply for community needs without jeopardizing the main objective of their establishment.

At present it is estimated that Ethiopia has over 350,000 ha. of plantation forests, and most of them are established in the highlands, at altitudes over 1500 m, where the rainfall is favourable (700-2000 mm/a) (Pohjonen & Pukkala, 1990). The figure was based on statistics concerning planted seedlings and an average success (survival rate) in the plantations, which may have been over estimated. A proper inventory of the Ethiopian plantation forests has not yet been undertaken and documented.

The current focus in the afforestation programmes is on planting of mainly exotic tree species and the target plan for the years 1994-2014 indicates 282,000 ha. of land to be planted by the government (Anonymous, 1993). According to the proposed plan, 187,000 ha. of coniferous, mainly *C. lusitanica* and *P. patula*, and 95,000 ha. of eucalypts plantations will be established. Most of these reforestation would be for industrial and fuelwood purposes. Different exotic species of conifers, eucalypts and acacias have already been introduced in this large-scale plantation programme. The very few indigenous species, however, were established only on a trial scale; although the native *J. procera* seemed to be most commonly planted species in the highland regions of Ethiopia. The shift in priority from indigenous to exotic species to establish plantation forests appears to be due to the alleged absence of productive pioneer native tree species in the country and the availability of short-rotation exotic trees with superior growth. Most valuable indigenous tree species are suggested to be found in late-successional forests and productive pioneer tree species suitable for plantation establishment are said not to have been found in the Ethiopian flora (Pohjonen, 1989). These plantations with exotics are believed not only to provide a convenient wood supply, but also to divert cutting from remaining patches of indigenous forests which otherwise would have to supply the fuelwood and other wood product requirements.

The productivity of plantation tree species, especially *Eucalyptus*, introduced and established in Ethiopia have been studied in a number of research programmes

(Anonymous, 1986). Based on a per capita consumption of 1.23 m³/year, Anonymous (1990) indicated that a total of 5,175,000 ha. of plantations have to be established in order to meet the demand of fuelwood by the year 2000. This, at least, suggests a possible conversion of large areas of land for the establishment of fuelwood plantations; Eucalyptus being the obvious candidate. However, very little is known about the ecological effects of these plantation tree species on the sustainability of site productivity. A proper management of plantation forests can be only achieved on the basis of a thorough understanding of the structure and function of these ecosystems. The present study examines the pattern of the undergrowth vegetation, soil physical and chemical properties, nutrient cycling in the plantations and adjacent natural or secondary forests, combined with bioassays- using soils from under or leaf extracts of selected tree species.

Ethiopia is one of the NE African countries where the degradation of the natural forests compelling the unsustainable use of this valuable resource (Poulsen & Tadesse, 1990). Extensive plantations, mainly of *E. globulus* and *Acacia*, have been established in Ethiopia in the century with the primary intention of increasing the supplies of fuelwood and construction materials, and also to reduce the pressure on the remaining patches of the natural vegetation. Most of these *Eucalyptus* plantations are managed on coppice rotation, an intensive silvicultural method. Other common species include *C. dentata*, *A. galeata* and *A. radiata* they were all introduced from Europe to replace the timber resources disappearing from the high altitude forest (Poulsen & Tadesse, 1990). Plantation development schemes have been undertaken mainly after clear-felling of both undisturbed natural forests and forests in a stage of regrowth following total or partial clear-cutting (secondary forests). Land preparation is undertaken for plantation establishment involving manual labour only, in which the major part of the natural forest is clear-felled and burned or removed before planting.

CHAPTER II

UNDERGROWTH VEGETATION AND SOIL CHARACTERISTICS IN THE ETHIOPIAN TREE PLANTATIONS AND NATURAL FORESTS

1. Introduction

The environmental degradation of tropical forests underlines the urgency of tree planting. Fast growing exotics are often planted in order to compensate for the natural forest decline and meet the increasing demand for wood products (Parotta, 1992). Apart from the wood biomass produced a significant aim of such plantations should be to increase the diversity and abundance of the undergrowth vegetation in order to reduce soil erosion and improve the soil fertility.

Ethiopia is one of the NE African countries where the degradation of the natural forests endangers the sustainable use of this finite resource (Pohjonen & Pukkala, 1990). Extensive plantations, mainly of *E. globulus* ssp. *globulus*, have been established in Ethiopia in this century, with the primary objectives of increasing the supply of fuelwood and construction materials, and also to reduce the pressure on the remaining patches of the natural vegetation. Most of these *Eucalyptus* plantations are managed on coppice rotation, an intensive silvicultural method. Other common exotics include *C. lusitanica*, *P. patula* and *P. radiata*; they were all introduced into Ethiopia to replace the timber resources disappearing from the natural forest (Pohjonen & Pukkala, 1992). Plantation development with exotics have been undertaken mainly after clear felling of both undisturbed natural forests and forests in a stage of regrowth following total or partial clear cutting (secondary forests). Land preparation presumably for plantation establishment involves manual labour only, in which the major part of the natural forest is clear-felled and burned or removed before planting.

One constraint for the development of such large scale plantation forests is their possible effects on the environment. In particular, *Eucalyptus* species are alleged of depleting the soil of nutrient elements and water (Florence, 1986; Malik & Sharma 1990), and to suppress the undergrowth vegetation (Bhaskar & Dasappa, 1986; Lisanework & Michelsen 1993a), which exposes the topsoil to erosive forces. However, evidence is lacking whether these effects are due to the characteristics of the tree species, to the management practice, or to a combination of these (Madeira 1989).

A comparison of the soil fertility, litter turnover, nutrient utilization and biomass of forbs and graminoids in plantations and natural forest in the central highland of Ethiopia suggested that *E. globulus* plantation may reduce the soil fertility to a greater extent than *C. lusitanica* and *J. procera* plantations. But, at the same sites the species diversity and the above-ground biomass of the ground cover in *E. globulus* plantations was similar to, or higher than that of an adjacent natural forest, partly due to the higher light intensity in the coppiced *E. globulus* plantation (Lisanework & Michelsen, 1993b; Michelsen *et al.*, 1993). However, extrapolation of such results concerning the environmental effects of plantation establishment in Ethiopia as a whole is not without problems, and the necessity of more extensive studies then becomes obvious, especially studies in a range of different environments.

The aim of this study was to investigate the possible long-term effects of established plantations with respect to undergrowth vegetation and soil characteristics. To this end, the diversity, abundance, biomass and nutrient content of the forbs and graminoids in the plantation and natural forests, the fine root biomass as well as the physical and chemical properties of forest soil were investigated in ninety-two sites. It is considered that this large number of sites could, at least partly, compensate for the extensive variation in age, management, geology, climate and land use among forest sites in different parts of Ethiopia.

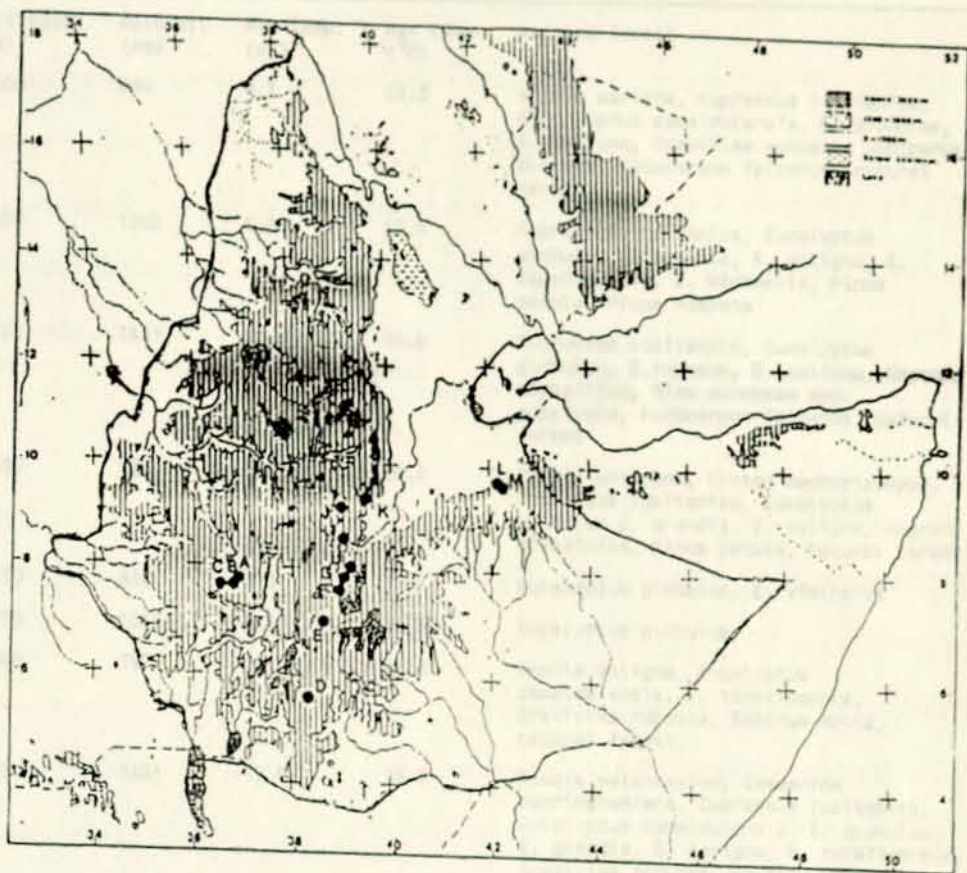


Fig. 1. Geographical position of the areas of study in Ethiopia. The letters refer to areas of study: A + B: Jimma; C: Belete; D: Magada; E: Wondo Genet; F: Degaga; G: Ardu; H: Nazareth; I: Menagesha; J: Entoto; K: Debre Brehan; L + M: Alemaya

Table 1. Climatic data of areas of study, and the sampled forest types.

Area	Altitude (m)	Rainfall (mm)	Min temp. (°C)	Max temp. (°C)	Sampled forest
Alemaya	2000	894	9.1	23.2	<i>Acacia saligna</i> , <i>Cupressus lusitanica</i> , <i>Eucalyptus camaldulensis</i> , <i>E. globulus</i> , <i>E. saligna</i> , <i>Grevillea robusta</i> , <i>Juniperus procera</i> , <i>Podocarpus falcatus</i> , natural forest
Ardu	2400	1262	8.0	20.5	<i>Cupressus lusitanica</i> , <i>Eucalyptus globulus</i> , <i>E. grandis</i> , <i>E. saligna</i> , <i>E. tereticornis</i> , <i>E. viminalis</i> , <i>Pinus patula</i> , <i>Pinus radiata</i>
Beleta	2150	1431	12.9	26.6	<i>Cupressus lusitanica</i> , <i>Eucalyptus globulus</i> , <i>E. regnans</i> , <i>E. saligna</i> , <i>Hagenia abyssinica</i> , <i>Olea europaea</i> spp. <i>cuspidata</i> , <i>Podocarpus falcatus</i> , natural forest
Degaga	2300	1299	5.8	19.6	<i>Cordia africana</i> , <i>Croton macrostachyus</i> , <i>Cupressus lusitanica</i> , <i>Eucalyptus globulus</i> , <i>E. grandis</i> , <i>E. saligna</i> , <i>Hagenia abyssinica</i> , <i>Pinus patula</i> , natural forest
Debre ¹	3130	808	3.8	19.6	<i>Eucalyptus globulus</i> , <i>E. viminalis</i>
Entoto	2950	1050	8.6	23.3	<i>Eucalyptus globulus</i>
Nazareth	1900	797	13.8	27.8	<i>Acacia saligna</i> , <i>Eucalyptus camaldulensis</i> , <i>E. tereticornis</i> , <i>Grevillea robusta</i> , <i>Schinus molle</i> , natural forest
Jimma	1850	1431	12.9	26.6	<i>Acacia melanoxylon</i> , <i>Casuarina cunninghamiana</i> , <i>Cupressus lusitanica</i> , <i>Eucalyptus camaldulensis</i> , <i>E. globulus</i> , <i>E. grandis</i> , <i>E. saligna</i> , <i>E. tereticornis</i> , <i>Grevillea robusta</i> , <i>Hagenia abyssinica</i> , <i>Lophostema conferta</i> , <i>Olea europaea</i> spp. <i>cuspidata</i> , <i>Pinus patula</i> , <i>P. radiata</i> , <i>Podocarpus falcatus</i> , natural forest
Magada	2000	864	12.5	24.9	<i>Cupressus lusitanica</i> , <i>Eucalyptus saligna</i> , natural forest
Menagesha	2360	1019	2.0	24.0	<i>Cupressus lusitanica</i> , <i>Eucalyptus globulus</i> , <i>Juniperus procera</i> , Natural forest
Wondo ²	1850	1011	11.6	26.1	<i>Acacia saligna</i> , <i>Cupressus lusitanica</i> , <i>Eucalyptus camaldulensis</i> , <i>E. citriodora</i> , <i>E. globulus</i> , <i>E. grandis</i> , <i>E. saligna</i> , <i>Grevillea robusta</i> , <i>Hagenia abyssinica</i> , <i>Juniperus procera</i> , <i>Pinus patula</i> , mixed planted <i>Cordia africana</i> - <i>Croton macrostachyus</i> , natural woodland

¹Debre Brehan ²Wondo Genet

2. Study areas

In 1990, ninety-two sites of natural and plantation forests were studied in Ethiopia. The sites were between latitudes $6^{\circ}15'$ and $10^{\circ}00'$ N and longitudes $36^{\circ}15'$ and 40° E; their geographical location are indicated on Fig. 1. An account of the geology and climate of Ethiopia is given in Mohr (1971) and Daniel (1977), respectively, and the natural vegetation in the areas investigated are described in Friis (1986, 1992).

The climate of the study areas is influenced by the Intertropical Convergence Zone, the distance from the equator and, not least, the topography. Meteorological and altitudinal data of the study areas are presented in table 1.

Geologically, Precambrian rocks overlain by sub-horizontal mesozoic marine strata and tertiary basalt traps. The bulk of the highland plateau consists of volcanic rocks. Sedimentary rocks, ranging from sandstone to limestone, appear in deep river valleys and in eastern lowlands. The soils in the highlands are, broadly, characterized as chromic vertisols to vertisols and are the outcome of the decomposition of the volcanic materials, whereas in the lowlands they range from calcareic fluvisols to calcareic regosols (Anonymous, 1988).

Floristically the broad vegetation types in the study areas include undifferentiated afro-montane forest, broad-leaved afro-montane rain forest, single-dominant afro-montane forest and semi-evergreen bushland thicket (Friis, 1992).

The study sites were selected to encompass the variation in topography and climate where plantations are established in Ethiopia. Other criteria of selection were their accessibility, and, furthermore, areas comprising a relatively high number of plantation tree species in adjacent, single-species plantation stands were preferred. Due to civil unrest no studies could be conducted in the north and north-western part of the country (the administrative regions of Gojam, Gondar, Wollo, and Tigray). Hence, 11 areas were studied in the southwest, northeast, south and central highlands

of Ethiopia, as well as in a few lowland areas in the central and northeast part of the country.

The field work took place in January and February and from mid-October to end of November, 1990. Within the areas of study adjacent plantation stands of known age were identified, and homogeneous sites considered representative of the stands were selected, with areas of 100 m² (10 m by 10 m). A spacing of 2 m by 2 m between plantation trees was the norm. Plantation stands in which no logging had taken place were selected, if present in the area. However, in most stands thinning and branch pruning had been performed, together with selective logging in some cases, but other management practices, e.g. fertilization, were rare. Most Ethiopian forests have by law been protected from human interference. Nevertheless, it is believed that illegal litter collection, tree felling and grazing by livestock have taken place in most of the sites, at least to some extent. Unfortunately, the exact magnitude of this influence is difficult to quantify. If nearby natural or secondary forests were present, they were studied as well, in 20 m by 20 m plots. In total, the investigation covered 84 plantation stands, and comparisons were made with 8 adjacent natural or secondary forest stands (Table 2).

3. Materials and Methods

3.1. Diversity and cover of woody and herbaceous plants

The cover (a perpendicular projection of the aboveground biomass) of the trees and shrubs was estimated visually, and the number of individuals of each species, as well as the spacing between trees were noted. The Braun-Blanquet (1964) cover-abundance scale, as modified by van der Maarel (1979) was used to obtain the quantitative data for herbaceous species. These are:

- 1: few species with small cover of the reference area (10 m x 10 m in plantation and 20 m x 20 m in natural forest sites)

Table 2. Extracts of stand and environmental data from plantations older than 9 yrs, and from adjacent natural forests.

Species	Area	Age (Yrs)	Height (m)	Basal area (m ² /ha)	Light intensity (% of full)	Herb coverage (%)	pH	total N (%)	Avail P (ppm)
<i>C. lusitanica</i>	Magada	11	12.0	33.2	0.2	0	6.40	0.300	1.60
	Wondo	11	10.0	31.5	0.9	0	5.60	0.300	3.20
	Jimma	14	10.0	19.9	2.5	1	4.91	0.234	1.53
	Alemaya	20	15.0	39.7	5.2	0	6.80	0.130	1.60
	Beleta	20	22.0	66.8	1.3	2	6.10	0.350	1.80
	Degaga	21	30.0	71.6	0.6	0	4.90	0.110	0.60
	Ardu	22	20.0	77.5	11.2	6	6.22	0.280	0.96
	Menagesha	28	15.0	33.0	14.1	4	5.75	0.268	2.57
<i>E. globulus</i>	Wondo	10	19.7	36.0	16.2	93	6.20	0.340	7.60
	Degaga	11	20.1	27.9	55.7	100	5.60	0.300	1.80
	Jimma	13	20.0	40.1	22.9	90	5.40	0.229	0.53
	Beleta	15	25.0	46.0	.	100	5.60	0.500	3.00
	Ardu	25	27.5	171.4	12.0	15	5.47	0.253	0.73
	Alemaya	25	50.0	87.5	3.1	58	7.20	0.060	5.20
	Menagesha	40#	6.0	13.9	51.5	100	5.83	0.274	4.23
	Entoto	40#	4.3	6.1	44.7	2	4.35	0.188	3.53
	Entoto	40#	5.3	2.9	39.1	100	4.51	0.184	4.95
<i>E. grandis</i>	Jimma	13	25.9	39.6	5.9	100	4.94	0.381	1.51
	Ardu	18	25.0	47.9	33.7	54	5.64	0.134	0.56
	Wondo	18	25.0	42.9	14.7	30	6.00	0.380	4.00
	Degaga	21	35.0	66.0	17.7	70	6.40	0.320	3.20
<i>E. saligna</i>	Magada	11	11.0	28.6	24.6	89	5.80	0.220	24.00
	Wondo	11	12.0	18.2	50.5	90	5.30	0.180	4.20
	Jimma	20#	8.0	10.1	41.7	100	4.79	0.209	3.11
	Degaga	21	22.8	42.8	16.1	89	6.90	0.360	2.80
	Ardu	22	35.0	101.2	12.1	11	5.27	0.213	0.45
	Alemaya	30	45.0	97.5	14.8	60	7.40	0.180	18.40

2) abundant species, but with cover of up to 5%

3) abundant, with low cover 1-5%

4) abundant species, but with less than 2% cover

5) any number of species, with cover of 3-12%

Table 2. (cont.)

P. patula	Wondo	11	15.0	41.1	15.2	65	5.80	0.060	4.80
	Jimma	14	18.0	41.9	17.7	6	5.05	0.285	2.42
	Degaga	21	25.0	57.7	5.7	40	4.80	0.160	2.00
	Ardu	22	25.0	38.2	26.8	77	5.21	0.302	1.75
Natural forest	Beleta	.	40.0	.	1.0	25	5.75	0.447	56.22
	Menagesha	.	40.0	63.8	20.5	90	6.68	0.339	6.89
	Alemaya	.	6.5	0.9	39.3	29	6.90	0.130	7.00
	Magada	.	35.0	.	.	70	7.10	0.290	31.00
	Degaga	.	50.0	109.5	76.7	100	7.70	0.900	32.80

coppiced recently

2: scattered species, but with cover of upto 5%

3: abundant, with less than 5% cover

4: numerous species, but with less than 5% cover

5: any number of species with cover of 5-12%

6: any number of species with cover of 12.5-25%

7: any number of species with cover of 25-50 %

8: any number of species with cover of 50-75%

9: any number of species with cover of 75-100%

The species were identified and voucher specimens were kept at the National Herbarium, Addis Ababa University and the Botanical Museum, University of Copenhagen. A set of duplicates are at the herbarium of The Royal Botanical Gardens, Kew. The nomenclature followed the Flora of Ethiopia and the Flora of Tropical East Africa (e.g. Turrill *et al.*, 1952; Cufodontis, 1953-1972; Hedberg & Edwards, 1989).

3.2. Above- and below-ground biomass

A non-destructive method (Chapman, 1986) was used to estimate the biomass of the trees. In each site, stem diameter (DBH) and height of trees were measured for the estimation of the biomass of the trees. The diameter measurements were made at breast height (1.3 m) except for those trees with large buttresses or prop roots, occurring in the natural forests, which had their diameters measured 30 cm above these protrusions. Where trees had multiple stems, each stem was measured separately. A constant form factor (0.42) was assumed for all species, as in Pohjonen (1989).

The single harvest method (Chapman, 1986) was used to determine the herbaceous biomass. The aboveground biomass of herbs and grasses was collected in four randomly placed 1 m² quadrats in each site.

For the determination of fine root biomass, six replicate 0-10 cm and 50-60 cm depth

samples were randomly collected in each site after the removal of the litter within the 1 m² quadrats where the vegetation had been harvested for the estimation of above ground herbaceous biomass. A soil auger with an inner diameter of 5 cm was used for this purpose.

3.3. Environmental data

For each site altitude was recorded and the light intensity at the forest floor as compared to that in open was measured with a lightmeter. Meteorological data for each area were obtained from the Ethiopian Meteorological Services Agency.

In each site, a 1 m³ pit was dug for the collection of soil samples. Composite samples (consisting of 6 samples collected systematically) from depths of 0-40 cm (topsoil) and 50-100 cm (subsoil) were collected for soil physical and chemical analyses. Another set of samples were randomly collected at the same depths with a core sampler (inner diameter 5 cm) for determination of the soil bulk density.

3.4. Laboratory methods

Soil physical and chemical analyses were carried out at the Soil laboratory of the Ministry of Agriculture, Addis Ababa, Ethiopia, following standard procedures (Allen, 1989). Bulk density was determined by drying the sample volume at 105°C. The samples were air dried and passed through a 2 mm sieve. Soil texture was measured using Boyoucos hydrometer, pH in 1:2 (v/v) soil:water suspension, electric conductivity (EC) in 1:2 (v/v) soil:water suspension, organic matter (OM) by the Walkely-Black wet oxidation method, available P (phosphorus) by the Bray II method and total N (nitrogen) by the Kjeldahl method. Cation exchange capacity (CEC) and the exchangeable bases Ca (calcium), K (potassium), Na (sodium) and Mg (magnesium) were determined after extraction with 1 N ammonium acetate at pH 7. Ca and Mg were measured using an atomic absorption spectrometry (AAS), and Na and K by

flame photometry.

The aboveground herbaceous biomass was dried for 48 h at 70°C, and weighed. The content of nutrient elements was analyzed at the Department of Plant Ecology, Univ. of Copenhagen, Denmark, using ASS for Ca, K and Mg, a semi-micro Kjeldhal method for N and the molybdenum blue method for P after wet acid digestion.

The soil samples for fine root biomass estimation were air dried and kept at 2°C until analysis. The samples were wet sieved by employing a series of sieves and decantation, and roots less than 2 mm in diameter were carefully separated from the remaining soil and litter debris. No attempt was made to distinguish between live and dead roots; the roots sampled were comparable to those of Vogt *et al.* (1989). The roots were dried for 24 h at 70°C and weighed.

3.5. Data treatment and statistical analysis

Multivariate methods were used to analyze the vegetation and the environmental data. Principal components analysis (PCA) produced an overview of the main sources of variation in soil and climatic data. The major environmental gradients governing the species distribution among sites were identified by canonical correspondence analysis (CCA). Furthermore, CCA was used to test if the choice of plantation tree species had an effect on the ground flora. This was done after removing the variation between sites due to climate and topography; The CCA was then performed on the residual variation. Along the same line the residual variation was used to test whether the plantation tree species had an effect on the soil; for this redundancy analysis (RDA) was used. In the two latter tests data from natural forests and plantations of *C. lusitanica*, *E. globulus*, *E. grandis* W. Hill ex Maid, *E. saligna* Sm. and *P. patula* older than nine years were used exclusively. All multivariate analyses were performed using the

program CANOCO (ter Braak, 1992) and they are well described in Jongman *et al.* (1987). The few missing values were supplanted by the average of the variate (ter Braak 1992).

One-way analysis of variance (ANOVA) was performed with SAS Proc GLM (SAS Institute, 1988) in order to determine if the soil or plant variables were affected by the type of forest. The Student-Newman-Keuls (SNK) test was used to separate the means (Day & Quinn, 1989). The data, apart from temperature, rainfall, altitude and pH, were subject to $\log(n+1)$ transformation before all analyses (Sokal & Rohlf, 1981). For the multivariate analyses environmental variables were transformed to zero mean and unit variance.

4. Results

4.1. Exploration of environmental data of the forests

Extracts of the stand and the environmental data of the 36 sites in plantations of *C. lusitanica*, *E. globulus*, *E. grandis*, *E. saligna* and *P. patula* with age older than 9 years as well as the adjacent natural forests are presented in Table 2. Other 56 sites were sampled in plantations of the above mentioned species younger than 9 years, and in plantations with other, less common plantation trees.

Data from the 92 sites were used in a PCA to reveal the correlations between the 52 variables characterizing the sites (Fig. 2). The first (PCA1) and the second (PCA2) principal components accounted for 20% and 14%, respectively, of the variation among sites. The variables located most distant from the origin in the scattergram are those contributing most to the differences among sites. Of the three climatic and topographic variables, annual rainfall is dominant along PCA1, making this axis a dry-wet gradient. At the drier end of the gradient high sand contents in the soils and high pH are found, whereas at the moister end a high clay content predominates and trees

are endowed with large basal areas and increased heights. The comparisons are all with regards to the average of all sites; i.e. "high pH" means : higher than the average . The other two climatic and topographic variables : average temperature and altitude are negatively correlated between themselves, and together they make up a temperature-altitude gradient running diagonally in the PCA scattergram. Warm lowland soils are

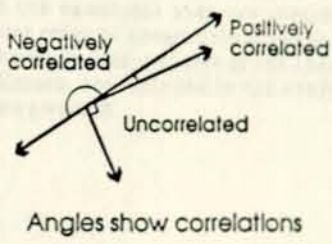
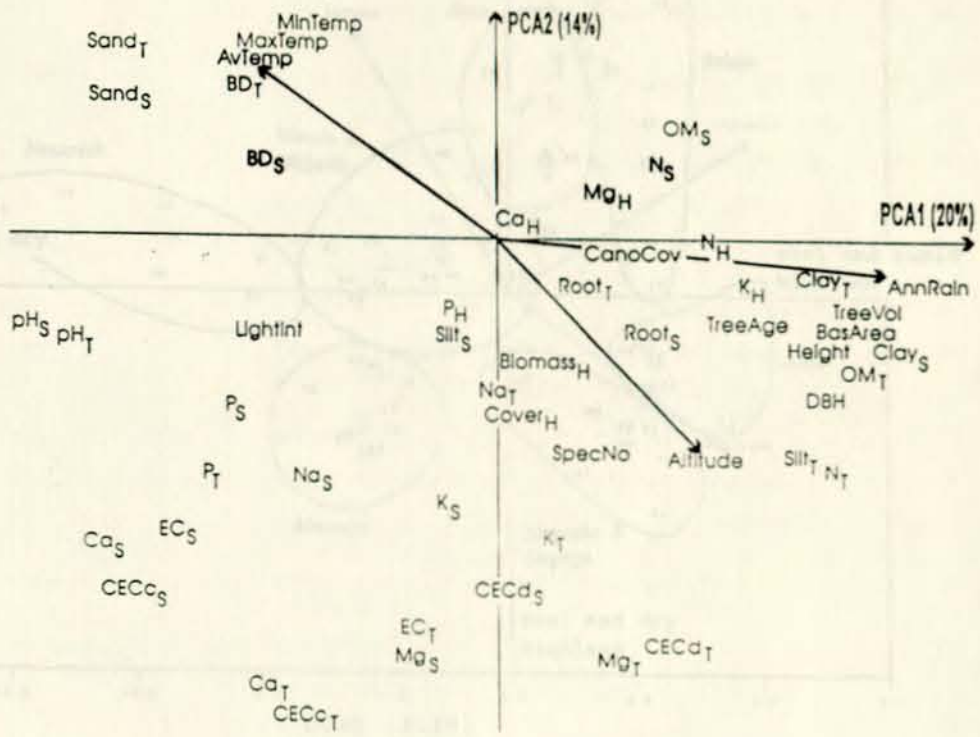


FIG. 2. Principal Component analysis (PCA) on 52 environmental variables in 92 forest sites. The variables most distant from the origin show the highest variation within the dataset; the degree of correlation between variables is revealed by the angle between variables as seen from the origin. The three variables describing the climate have been drawn as vectors to guide the interpretation. The variable-indices T, S and H refer to topsoil, subsoil and herbaceous plants, respectively

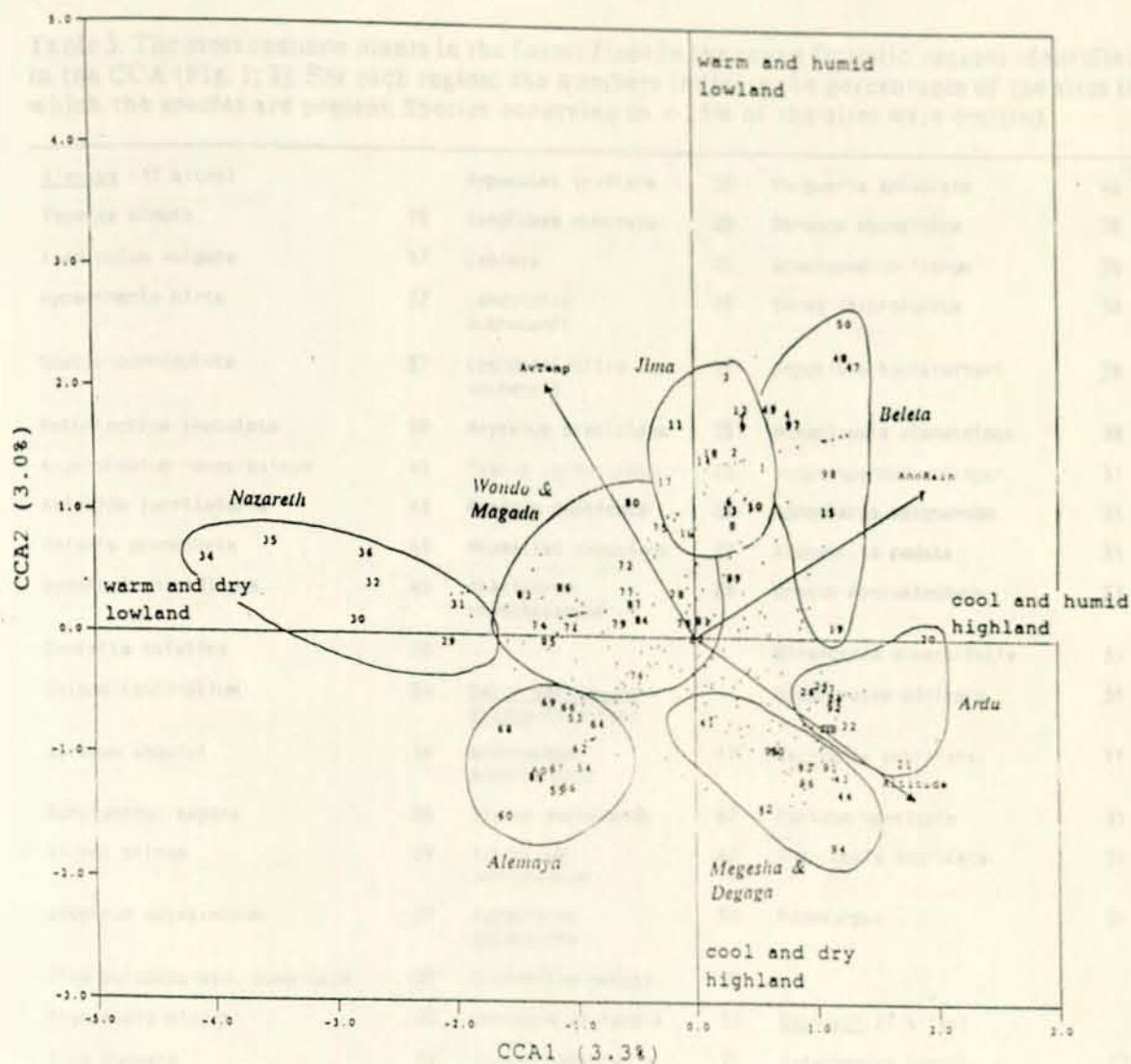


Fig. 3. Canonical correspondence analysis (CCA) triplot showing positions of plant species and sites on the major environmental gradients. Vectors show the direction of each climatic variable and the canonical axes are interpreted in terms of these. Names attributed to clusters of sites refer to geographic areas shown in Fig. 1; the numbers refer to sites. Plant species are shown as dots; a subset of the species are listed in Table 3. The six sites of Debre Brehan and Entoto, not included in the analysis, would lie in the direction of high altitude (right and downwards)

Table 3. The most common plants in the forest floor in the seven floristic regions identified in the CCA (Fig. 1; 3). For each region, the numbers indicate the percentages of the sites in which the species are present. Species occurring in < 25% of the sites were omitted.

Alemaya (17 sites)		Hypoestes triflora	25	Vangueria apiculata	46
Tagetes minuta	79	Isoglossa punctata	25	Bersama abyssinica	38
Foeniculum vulgare	57	Labiata	25	Brachypodium flexum	38
Hyparrhenia hirta	57	Landolphia buchananii	25	Carex chlorosaccus	38
Oxalis corniculata	57	Lepidotrichilia volkensis	25	Impatiens hochstetteri	38
Bothriochloa insculpta	50	Maytenus gracillipes	25	Mikaniopsis clematoides	38
Argyrobium ramosissimum	43	Oxalis corniculata	25	Achyrosermum schimper	31
Aristida ferrilateris	43	Panicum monticola	25	Agrocharis melanantha	31
Chloris pycnothrix	43	Physalix peruviana	25	Alchemilla pedata	31
Dyschoriste radicans	43	Thalictrum rhynchocarpum	25	Croton macrostachyus	31
Centella asiatica	36			Girardinia diversifolia	31
Ocimum lamiifolium	36	<u>Debre Berhan and Entoto</u> (6 sites)		Hippocratea africana	31
Solanum anguivi	36	Andropogon amethystinus	47	Kalanchoe petitiiana	31
Achyranthes aspera	29	Thymus serrulatus	67	Panicum monticola	31
Bidens pilosa	29	Trifolium semipilosum	67	Phaulopsis imbricata	31
Jasminum abyssinicum	29	Agrocharis melanantha	50	Podocarpus	31
Olea europaea ssp. cuspidata	29	Alchemilla pedata	50		
Rhynchosia minima	29	Anthemis tigrensis	50	<u>Nazareth</u> (7 sites)	
Sida cuneata	29	Crepis carbonaria	50	Heteropogon contortus	57
		Dichrocephala chrysanthemifolia	50	Hypoestes forsskaolii	57
Ardu (9 sites)		Orobanche minor	50	Aristida adoensis	43
Achyranthes aspera	67	Pseudognaphalium melanosphaerum	50	Aristida adoensis	43
Digitaria abyssinica	56	Stureia simensis	50	Cynodon dactylon	43
Kalanchoe petitiiana	56	Trifolium cryptopodium	50	Hibiscus 2	43
Agrocharis melanantha	44	Bidens macroptera	33	Hyparrhenia antihistricoides	43
Alchemilla pedata	44	Carduus sp.	33	Hyparrhenia rufa	43
Centella asiatica	44	Cyanotis barbata	33	Indigofera sp. 1	43
Cyperus fischerianus	44	Eragrostis sp.3	33	Euphorbia hirta	29
Hypericum peplidifolium	44	Geranium sp.	33	Sida sp. 1	29
Hypoestes triflora	44	Hebenstretia dentata	33	Solanum anguivi	29
Jasminum abyssinicum	44	Helichrysum sp.2	33	Tagetes minuta	29
Laggera pterodonta	44	Hypericum revolutum	33		

Table 3 count.

<i>Mikaniopsis clematoides</i>	44	<i>Pennisetum sphacelatum</i>	33	<u>Wondo and Megada (17 sites)</u>		
<i>Sporobolus africanus</i>	44	<i>Plantago lanceolata</i>	33	<i>Achyranthes aspera</i>	53	
<i>Stephania abyssinica</i>	44	<i>Rumex steudellii</i>	33	<i>Ageratum conyzoides</i>	53	
<i>Tagetes minuta</i>	44	<i>Vermifrux abyssinica</i>	33	<i>Phaulopsis imbricata</i>	53	
<i>Tagetes minuta</i>	44	<i>Vermifrux abyssinica</i>	33	<i>Celtis africana</i>	47	
<i>Diclis ovata</i>	33			<i>Digitaria abyssinica</i>	47	
<i>Eragrostis botryoides</i>	33	<u>Jimma (17 sites)</u>		<i>Setaria plicatilis</i>	47	
<i>Geranium arabicum</i>	33	<i>Phaulopsis imbricata</i>	88	<i>Oplismenus compositus</i>	41	
<i>Monopsis stellaroides</i>	33	<i>Centella asiatica</i>	71	<i>Centella asiatica</i>	35	
<i>Pennisetum sphacelatum</i>	33	<i>Hyparrhenia sp.1</i>	53	<i>Cynodon dactylon</i>	35	
<i>Phaulopsis imbricata</i>	33	<i>Oplismenus compositus</i>	53	<i>Maytenus arbutifolia</i>	35	
<i>Plantago lanceolata</i>	33	<i>Pennisetum sphacelatum</i>	41	<i>Sida ovata</i>	35	
<i>Poa schimperiana</i>	33	<i>Triumfetta rhomboidea</i>	41	<i>Tragia volubilis</i>	35	
		88	<i>Ageratum conyzoides</i>	35	<i>Calpurnia aurea</i>	29
<u>Beleta (8 sites)</u>			<i>Sida cuneata</i>	35	<i>Conyza sp.8</i>	29
<i>Oplismenus compositus</i>	88	<i>Brachiaria brizantha</i>	29	<i>Panicum monticola</i>	29	
<i>Setaria plicatilis</i>	75	<i>Setaria plicatilis</i>	29	<i>Rhynchosia minima</i>	29	
<i>Droguetia iners</i>	50			<i>Vernonia theophrastifolia</i>	29	
<i>Acritochaete volkensisii</i>	38	<u>Menagesha and Degaga (13 sites)</u>				
<i>Garyophyllaceae 1</i>	38	<i>Achyranthes aspera</i>	62			
<i>Geranium sp.</i>	38	<i>Cyperus fischerianus</i>	62			
<i>Malvaceae sp.</i>	38	<i>Hypoestes forsskaolii</i>	62			
<i>Phyllanthus sp.1</i>	38	<i>Hypoestes triflora</i>	62			
<i>Acanthaceae 4</i>	25	<i>Droguetia iners</i>	54			
<i>Achyranthes aspera</i>	25	<i>Stephania abyssinica</i>	54			
<i>Cyperus fischerianus</i>	25	<i>Acritochae volkensisii</i>	46			
<i>Embelia schimperi</i>	25	<i>Oplismenus compositus</i>	46			

seen to have a high sand content, whereas in the cooler highland the top soil is characterized by high scores on silt content, nitrogen, organic matter, magnesium, CEC determined (CECdet), and a high number of herbaceous- and large tree- species. Other variables of importance are unrelated to climatic gradients: Ca, EC and phosphorus. Generally, measurements of topsoil and subsoil properties give corresponding results, and nutrient contents of herbs show only little variation.

4.2. Gradient analysis of the ground vegetation in the forests

CCA was performed to reveal the variation in the ground flora which could be attributed to climate. The first CCA was performed on the full set of 92 sites. It showed the four Entoto sites and the two Debre Berhan sites to deviate distinctly from the other sites with respect to their ground flora. This was attributed to the high altitude of these sites. To get a better picture of the variation among the other sites, a new CCA was performed using 86 sites only, as shown in Fig. 3. Among the 52 site variables, the three environmental variables shown (altitude, rainfall and temperature) explained most of the variance ($P < 0.01$ for all three). More variables were also found significant but they were left out in the figure in order to emphasize the patterns of the undergrowth vegetation explained by climate and topography only. Sites with different sampling areas are seen to cluster depending on their flora. At the same time these sites are characterized by the canonical axes (CCA1 and CCA2), the interpretation of which followed directly from the chosen three environmental variables as shown in the CCA scattergram (Fig. 3). The plant species dominant in the seven regions shown in Fig. 3, together with the highland areas of Debre Berhan and Entoto, are listed in Table 3. A total of 523 plant species were recorded in the plantations and the natural forests belonging to 64 families of which three families: *Poaceae*, *Fabaceae* and *Acanthaceae* predominate in that order. Some characteristically invading and tolerant plant species, e.g. *Achyranthes aspera* L., were frequent in almost

Table 4. Stand characteristics of plantation stands of age older than 9 years, and of the adjacent natural forests.

	Dominant height (m)	DBH (cm)	Basal area (m ² /ha)	Volume (m ³ /ha)	Canopy cover (%)	Light (% of ambient)	Fine roots in topsoil (g/m ²)	Fine roots in subsoil (g/m ²)
<i>C. lusitanica</i>	16.8 a	19.4 a	46.7 a	377 a	88 a	4.5 b	725 a	94 a
<i>E. globulus</i>	19.8 a	15.3 a	49.4 a	583 a	41 c	30.7 a	277 ab	102 a
<i>E. grandis</i>	27.7 a	26.6 a	49.9 a	687 a	48 c	18.0 ab	189 b	66 a
<i>E. saligna</i>	22.3 a	14.5 a	49.7 a	670 a	52 c	34.4 a	345 ab	129 a
<i>P. patula</i>	20.8 a	20.5 a	44.7 a	396 a	70 b	16.4 ab	313 ab	87 a
Natural Forest	34.3 a	28.2 a	58.1 a	.	70 b	34.4 a	753 a	163 a
P in ANOVA	0.1914	0.1681	0.9982	0.8295	0.001	0.005	0.0283	0.4030

Table 5. The most common herbaceous plants of six forest types. For each forest type, the numbers indicate the percentage of sites in which the species are present; species occurring in one site only were omitted. Species marked with an * occur outside Africa (with Arabia and Madagascar) as listed in Cufodontis (1953-1972).

<u>Cupressus lusitanica</u>		<u>Eucalyptus saligna</u>	
*Oplismenus compositus	50	*Centella asiatica	67
*Achyranthes aspera	25	Dyschorisite radicans	67
Cyperus fischerianus	25	*Achyranthes aspera	50
*Gerbera piloselloides	25	*Oplismenus compositus	50
Mikaniopsis clematoides	25	Acanthus pubescens	33
*Oxalis corniculata	25	*Brachiaria brizantha	33
Panicum monticola	25	Clematis hirsuta	33
*Phaulopsis imbricata	25	*Digitaria abyssinica	33
*Rhus ruspolii	25	Jasminum abyssinicum	33
*Tagetes minuta	25	*Phaulopsis imbricata	33
		*Rubia cordifolia	33
		Stephania abyssinica	33
<u>Eucalyptus globulus</u>		*Tragia volubilis	33
*Centella asiatica	44	*Triumfetta rhomboidea	33
Cyperus fischerianus	44		
*Digitaria abyssinica	44		
*Achyranthes aspera	33	<u>Pinus patula</u>	
Agrocharis melanantha	33	*Oplismenus compositus	100
Alchemilla pedata	33	*Achyranthes aspera	75
*Bidens pilosa	33	*Mukia maderaspatana	50
*Droguetia iners	33	Monopsis stellaroides	50
*Hypoestes triflora	33	*Phaulopsis imbricata	50

<i>Pennisetum sphacelatum</i>	33	<i>Hypericum peplidifolium</i>	50
* <i>Phaulopsis imbricata</i>	33	* <i>Ageratum conyzoides</i>	50
<i>Achyrospermum schimperi</i>	22	* <i>Digitaria abyssinica</i>	50
* <i>Cyanotis barbata</i>	22	<i>Kalanchoe petitiiana</i>	50
* <i>Ehrharta erecta</i>	22	* <i>Centella asiatica</i>	50
<i>Eragrostis sp. 3</i>	22	* <i>Tagetes minuta</i>	50
* <i>Eragrostis tenuifolia</i>	22		
<i>Helichrysum sp. 2</i>	22	Natural forest	
<i>Jasminum abyssinicum</i>	22	* <i>Achyranthes aspera</i>	80
<i>Kosteletzkya adoensis</i>	22	<i>Acritochaete volkensii</i>	60
Lamiaceae	22	<i>Hypoestes forskalii</i>	60
<i>Lactuca paradoxa</i>	22	* <i>Hypoestes triflora</i>	60
<i>Mikaniopsis clematoides</i>	22	<i>Jasminum abyssinicum</i>	60
* <i>Oplismenus compositus</i>	22	* <i>Oplismenus compositus</i>	60
* <i>Physalis peruviana</i>	22	<i>Peperomia abyssinica</i>	60
<i>Rosa abyssinica</i>	22	<i>Brechypodium flexum</i>	40
<i>Senecio ochrocarpus</i>	22	<i>Carex chlorosaccus</i>	40
<i>Stephania abyssinica</i>	22	<i>Clematis sinensis</i>	40
		<i>Mimulopsis solmsii</i>	40
<u><i>Eucalyptus grandis</i></u>		<i>Panicum monticola</i>	40
* <i>Achyranthes aspera</i>	50	<i>Periploca linearifolia</i>	40
<i>Alchemilla pedata</i>	50	* <i>Phaulopsis imbricata</i>	40
<i>Cyathula uncinulata</i>	50	<i>Stephania abyssinica</i>	40
<i>Hyparrhenia sp. 1</i>	50		
* <i>Oplismenus compositus</i>	50		
* <i>Phaulopsis imbricata</i>	50		
* <i>Sida cuneifolia</i>	50		
* <i>Sporobolus africanus</i>	50		
<i>Stephania abyssinica</i>	50		
* <i>Tragia volubilis</i>	50		

all site groups, whereas other species were frequent in one site group only, e.g. *Andropogon amethystinus* Steud., *Thymus serrulatus* Hochst. ex Benth and *Trifolium semipilosum* Fres. in the high altitude Debre Berhan and Entoto sites, and *Heteropogon contortus* (L.) R. & S. in the lower altitude Nazareth site

4.3. The tree stands and their effect on the ground vegetation

As the aim was to study the long-term effects of plantation establishment and young plantations are assumed not to have affected the environment as much as older plantations, the following analysis included only data from the 36 plantation sites with *C. lusitanica*, *E. globulus*, *E. grandis*, *E. saligna* and *P. patula* with age older than 9 years, and adjacent natural forests.

In Table 4 the characteristics of the stands are shown. No significant differences in height, DBH or basal area were revealed, partly because some of the eucalypts had been coppiced (see Table 2). Other factors contributing to the large variation within plantations with the same species of plantation tree are the climatic conditions at the different sites (Table 1). The canopy was nearly closed in the *C. lusitanica* plantation, intermediate in the natural forest and the *P. patula* plantation and most open in the three eucalypt plantations. The light intensity at the forest floor was mostly inversely correlated with the canopy cover; it was significantly lower in the *C. lusitanica* plantation than in the *E. globulus* and *E. saligna* plantations, and in the natural forest (Table 4). The fine root biomass in the upper 10 cm soil layer was higher in *C. lusitanica* sites than the other plantation and natural forest sites. In both plantation and natural forest sites the majority of the fine root biomass were in the upper 10 cm of soil than in the 50-60 cm soil depth; with least concentration of fine root biomass in the latter depth of the soil.



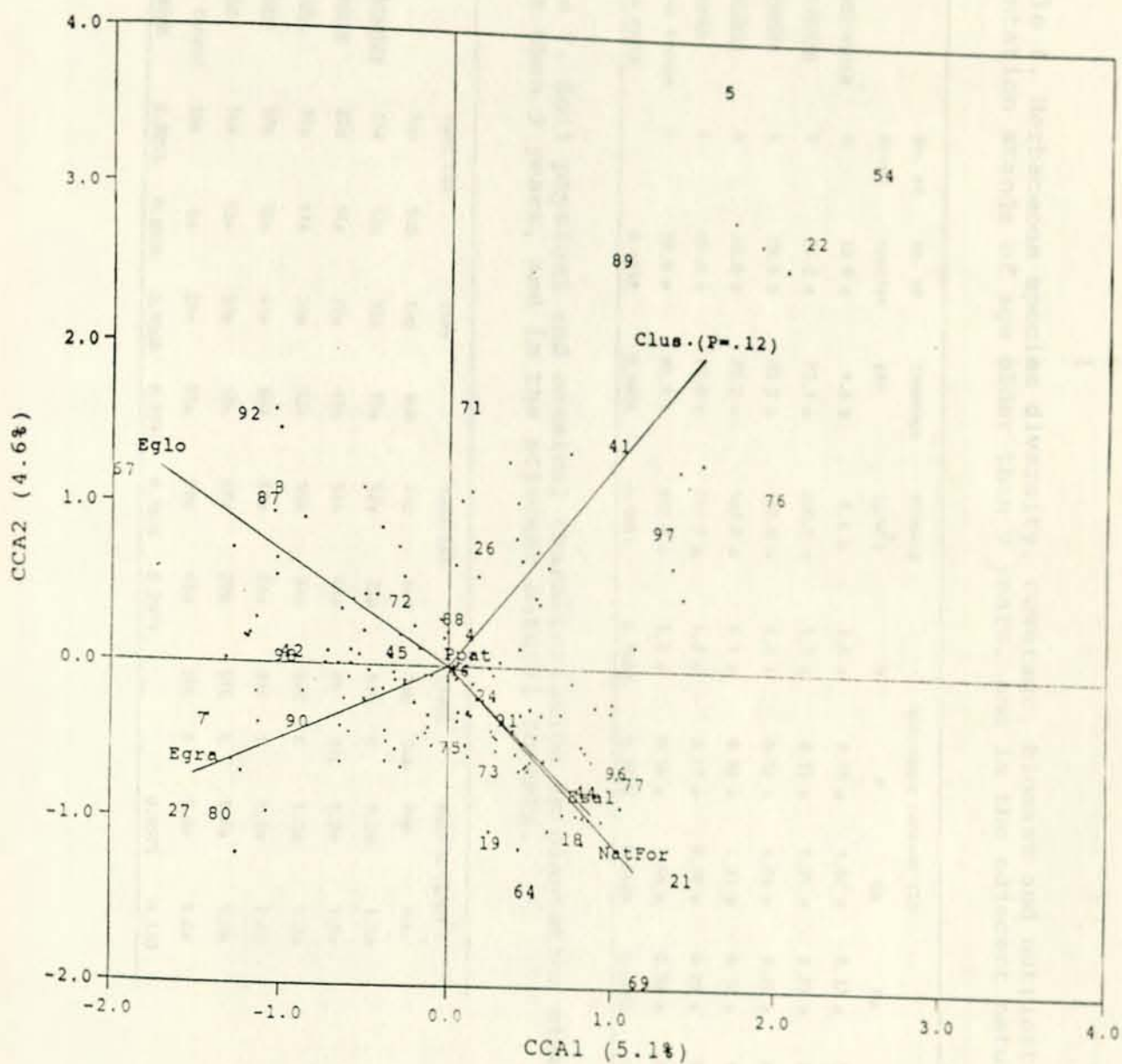


Fig. 4. Canonical correspondence analysis (CCA) triplot showing the effect of *C. lusitanica*, *E. globulus*, *E. grandis*, *E. saligna*, *P. patula* (older than 9 years) and natural forest on the ground vegetation; analyzed on the residual variation after removing the effects altitude, temperature, rainfall and area. P values less than 20% are indicated.

Table 6. Herbaceous species diversity, coverage, biomass and nutrient content in plantation stands of age older than 9 years, and in the adjacent natural forests.

	No. of Sites	No. of Species	Coverage (%)	Biomass (g/m ²)	-----Nutrient content (%)-----				
					N	P	Ca	Mg	K
<i>C. lusitanica</i>	8	10.9 a	1.6 b	4.4 b	1.6 a	0.15 a	1.82 a	0.32 a	3.3 a
<i>E. globulus</i>	9	24.2 a	73.1 a	200.1 a	1.3 a	0.15 a	0.95 a	0.21 a	2.7 a
<i>E. grandis</i>	4	25.5 a	63.5 a	182.0 a	1.3 a	0.12 a	0.94 a	0.25 a	2.5 a
<i>E. saligna</i>	6	23.0 a	73.2 a	167.0 a	1.1 a	0.10 a	1.21 a	0.37 a	1.8 a
<i>P. patula</i>	4	20.8 a	47.0 a	231.3 a	1.2 a	0.13 a	0.79 a	0.23 a	3.1 a
Natural Forest	5	30.8 a	62.8 a	192.0 a	1.2 a	0.14 a	1.46 a	0.30 a	3.6 a
P in ANOVA		0.1352	0.0006	0.0001	0.7463	0.7720	0.5449	0.6680	0.3273

Table 7. Soil physical and chemical characteristics in plantation stands of age older than 9 years, and in the adjacent natural forests.

	Sand (%)		Clay		Silt (%)		Class		Bulk d (g/cm ³)	
	Top	Sub	Top	Sub	Top	Sub	Top	Sub	Top	Sub
<i>C. lusitanica</i>	15a	12a	33a	55a	52a	33a	SiC	C	1.2a	1.5a
<i>E. globulus</i>	22a	14a	27a	41a	51a	45a	CL	SiC	1.2a	1.5a
<i>E. grandis</i>	15a	11a	30a	52a	55a	37a	SiC	C	1.0a	1.2a
<i>E. saligna</i>	19a	12a	41a	64a	40a	24a	SiC	C	1.1a	1.4a
<i>P. patula</i>	16a	18a	37a	53a	47a	29a	SiL	C	1.2a	1.9a
Natural forest	18a	6a	23a	51a	59a	43a	SiL	C	1.0a	1.6a
P. in ANOVA	0.9213	0.8024	0.1568	0.7337	0.7628	0.2091			0.9675	0.360

Table 7. (cont.)

pH		EC (mS/cm)		Org. mat. (%)		Total N (%)		Avail P (ppm)		Na (me/100 g)	
Top	Sub	Top	Sub	Top	Sub	Top	Sub	Top	Sub	Top	Sub
5.8ab	5.6a	0.18a	0.13a	4.2a	3.3a	0.25a	0.10a	1.7b	0.99b	0.62a	0.69a
5.5ab	5.6a	0.26a	0.15a	5.0a	2.4a	0.26a	0.12a	3.5b	2.43b	0.66a	0.85a
5.7ab	6.1a	0.17a	0.19a	4.2a	3.1a	0.30a	0.10a	2.3b	1.22b	0.85a	0.96a
5.9ab	5.9a	0.20a	0.17a	3.9a	3.0a	0.23a	0.11a	8.8b	0.86b	0.79a	0.82a
5.2b	5.3a	0.13a	0.09a	3.8a	3.9a	0.20a	0.14a	2.7b	0.41b	0.71a	0.81a
6.8a	5.7a	0.26a	0.15a	5.3a	2.4a	0.42a	0.10a	26.8a	10.03a	0.64a	0.47a
0.0595	0.8456	0.8711	0.9635	0.7928	0.7955	0.2142	0.7599	0.0003	0.0021	0.0574	0.7975

Table 7. (cont.)

Ca (me/100 g)		Mg (me/100 g)		K (me/100 g)		CEC calculated		CEC determined	
Top	Sub	Top	Sub	Top	Sub	Top	Sub	Top	Sub
12.79 b	9.9 a	4.4 a	3.8 a	0.84 a	0.54 a	18.6 a	15.0 a	31.5 a	31.9 a
11.88 b	10.7 a	3.5 a	3.5 a	0.94 a	0.72 a	17.0 a	15.7 a	26.1 a	27.4 a
14.49 b	12.0 a	3.7 a	5.1 a	1.17 a	2.09 a	20.2 a	20.2 a	39.0 a	32.4 a
12.34 b	9.3 a	3.7 a	3.4 a	0.94 a	0.76 a	17.7 a	14.3 a	27.8 a	30.3 a
11.21 b	9.7 a	2.8 a	2.4 a	0.75 a	0.52 a	15.5 a	13.4 a	32.5 a	30.1 a
29.75 a	12.4 a	6.3 a	5.2 a	1.29 a	1.33 a	37.9 a	19.9 a	36.6 a	37.4 a
0.0474	0.9946	0.2750	0.7432	0.7779	0.1423	0.0635	0.9492	0.3434	0.7630

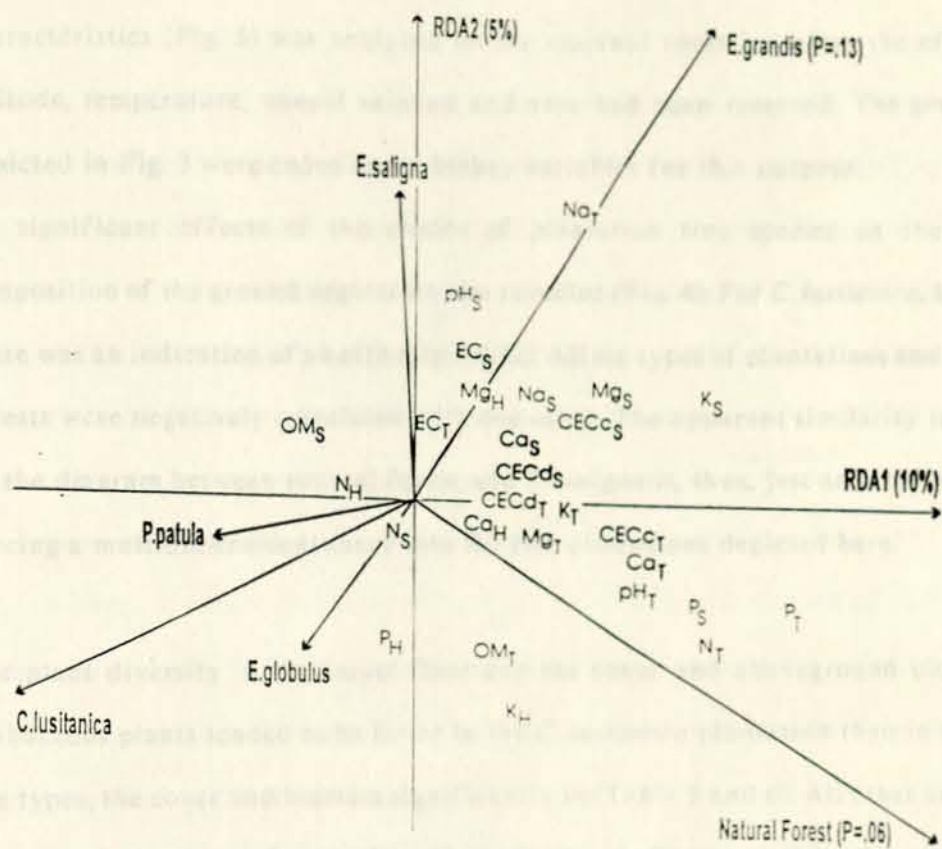


Fig. 5. Partial redundancy analysis (RDA) biplot showing the effect of *C. lusitanica*, *E. globulus*, *E. grandis*, *E. saligna*, *P. patula* (older than 9 years) and natural forests on soil physical and chemical properties; analyzed on the residual variation after removing the effects of altitude, temperature, annual rainfall and area. Interpretation in the manner of Fig. 2, i.e. correlation between any two factors is judged from their angle as seen from the origin, the most significant factors as these most distant from the origin. P values less than 20 % are indicated

The effect of plantation tree species on the ground vegetation (fig. 4) and the soil characteristics (Fig. 5) was analyzed on the residual variation after the effects of altitude, temperature, annual rainfall and area had been removed. The seven axes depicted in Fig. 3 were coded as six binary variables for this purpose.

No significant effects of the choice of plantation tree species on the species composition of the ground vegetation was revealed (Fig. 4). For *C. lusitânica*, however, there was an indication of an effect ($p = 0.12$). All six types of plantations and natural forests were negatively correlated with one other. The apparent similarity indicated by the diagram between natural forest and *E. saligna* is, thus, just an artefact due to forcing a multidimensional space into the two dimensions depicted here.

The plant diversity in the forest floor and the cover and aboveground biomass of herbaceous plants tended to be lower in the *C. lusitânica* plantation than in all other site types, the cover and biomass significantly so (Table 5 and 6). All other site types, including the natural forest, showed similarity in those variables. No significant differences in nutrient concentration of the herbaceous plants were found between sites. On the contrary, large variation was found within species among sites (Table 2); as an example the herbaceous cover in the *E. globulus* sites at Entoto ranged from 2 to 100% due to differences in exploitation by the local people and their livestock as well as the relatively smaller inter-planting distances observed in these plantation sites.

4.4. The effect of tree species selection on soil characteristics

In order to test the effects of the various plantation tree species on soil properties a RDA was performed on the residual variation leaving out the same effects as above, climate and area (Fig. 5). The natural forest had a near-significant effect ($P = 0.06$) on the soil and *E. grandis* less so ($P = 0.13$). These two forest types both showed higher potassium content in the topsoil than the other forest types. Natural forest is further characterized by higher scores on topsoil of phosphorus, nitrogen and pH, and subsoil

phosphorus, while *E. grandis* showed a high content of sodium in the topsoil.

5. Discussion

The distribution of the ground flora in plantations and natural forests is highly dependent on the factors altitude, temperature and rainfall, parallel to the distribution of natural forest trees and other floristic elements in Ethiopia (Zerihun *et al.*, 1989; Friis, 1992). Using CCA (Fig. 3) eight different and rather distinct groups of sites could be identified, which to a larger extent were identical with the different areas of sampling (Fig. 1). The sites most distant on the canonical axes, i.e. the sites with the most distinct flora, were the very high altitude sites of Debre Berhan and Entoto, and the low altitude sites at Nazareth (Fig. 3; Table 3). The partitioning of the sites into distinct, regionally based floristic groups confirmed the necessity of analyzing the floristic composition of the ground cover in plantations on the residual variation after the effects of altitude, temperature, annual rainfall and geographical regions had been removed ("partial" CCA, ter Braak (1992)).

This analysis suggested that plantations of *C. lusitanica* differed from plantations of other species as well as from the natural forests ($P = 0.12$), with respect to floristic composition in the forests (Fig. 4). The species number, cover and above ground biomass of the herbaceous plants were highly reduced (although biomass and cover showed a significant decrease) in *C. lusitanica* plantations (Tables 2, 5 and 6), confirming the observations of Michelsen *et al.* (1993). These may be due to the dense canopy cover formed by *C. lusitanica* which leads to low light intensity reaching the forest floor (Table 4), combined with allelopathic agents which suppress the ground vegetation (Lisanework & Michelsen 1993a). The poor growth of herbaceous plants in *C. lusitanica* plantations can not be explained by low nutrient content in such soils as the nutrient content of soils from *C. lusitanica* sites did not differ from that of other plantation types (Table 7).

The result of CCA did not reveal any difference in the diversity of the ground vegetation of the natural forests and plantations of *E. globulus*, *E. grandis*, *E. saligna* and *P. patula* older than 9 years (Fig. 4), and these forest types did not differ with respect to herbaceous diversity, cover and biomass (Table 6). Although it should be kept in mind that some of the stands with *E. globulus* and *E. saligna* had been coppiced recently (a practice which leads to a reduced canopy cover and increased light intensity at the forest floor, and, hence benefits the ground flora) it seems that plantations with eucalypts (and pines) may not have a reduced diversity and biomass of herbaceous plants in Ethiopia. This contrasts the frequent generalizations based on studies of eucalypts in S. Europe, India and elsewhere (Poore & Fries, 1985; Bhaskar & Dasappa, 1986; Florence 1986). Eucalypts, e.g. the species *E. globulus* and *E. saligna*, may have a higher allelopathic potential (Lisanework & Michelsen, 1993a), but the effect is reduced in areas with relatively high rainfall and the resulting high leaching of the allelochemicals from the topsoil. Ground vegetation under *Eucalyptus* plantations is less affected in wet conditions than in the dry, where it may be greatly reduced leaving the soil bare and prone to erosion (Poore & Fries, 1985)

The biomass of fine roots of the upper 10 cm soil was similar to or higher than those reported from tropical forests (Lundgren, 1978; Cavelier, 1992; Michelsen *et al.* 1993). Concentrations of fine roots in the upper 10 cm soil layer is a frequently observed phenomenon (e.g. Klinge, 1973; Gower, 1987; Berish & Ewel, 1988; Cavelier, 1992) caused mainly by the nutrient availability from decomposing litter. High live root biomass is often the result of low available soil nutrients (Cavelier, 1992). The presence of a higher amount of dead roots in the top 10 cm soil of the *C. lusitanica* plantation forests may, however, have contributed to the apparently very high biomass of the fine roots. A relatively slower decomposition of the roots and a concomitant release of nutrients, similar to the fine litterfall decomposition (Lisanework &

Michelsen, 1993b), could be the reason for such an accumulation of dead root mass in the *C. lusitânica* soil.

The species richness, herbaceous cover and biomass in plantations (except those of *C. lusitânica*) was high and similar to that of the natural forests. This is parallel to the results of Lugo (1992) from Puerto Rican plantations and secondary forests and is promising from the conservation point of view. However, in contrast to the natural forest many of the most common species in the Ethiopian plantations were weeds or species invading from montane grassland and wooded grassland replacing the most specialized plant species of the original vegetation. The observations were in agreement with the findings of Mathur & Soni (1983). Furthermore, the species diversity of the trees themselves, as well as their associated epiphytic plant communities is high in the natural forests (Zerihun *et al.*, 1989; Friis, 1992; Michelsen, 1993b). Consequently, the species diversity in the natural forests as a whole is higher than in plantations where epiphytes are rare and the upper tree stratum is dominated by the tree monoculture.

The survey of the soil, climatic and stand characteristics in the areas of study (Fig. 2) revealed that the trees in plantation stands showed larger basal area and height in the sites of higher altitudes and adequate moisture, thus confirming that Ethiopian plantations, from the point of view of wood production, should be established at higher altitudes where rainfall is favourable (Pohjonen, 1989; Pohjonen & Pukkala, 1990; 1992). The topsoils of these forests of higher altitudes were characterized by low pH and high content of organic matter and total N (Fig. 2), possibly due to a lower rate of decomposition and nutrient release from litter with lower temperature (Vitousek, 1984; Vogt *et al.*, 1986).

When natural forests and plantations of *C. lusitanica*, *E. globulus*, *E. grandis*, *E. saligna* and *P. patula* older than 9 years only were considered, the soil characteristics of the natural forests, followed by *E. grandis*, segregated most clearly from those of the other forest types (Fig. 5). From the RDA, the natural forests were characterized by a high content of available P, in top- and sub-soil, as well as high pH, total N and exchangeable Ca in the topsoil. These results are confirmed by the ANOVAs, significantly so with respect to P in the top- and sub-soil, and Ca in topsoil (Table 7). The much (3-16 times) higher P content in the natural forests than in the plantations may be explained by the fast growth and high nutrient demand by the exotics in comparison with the trees of the natural forest, leading to the reduced availability of P in the plantation soil. Based on the data on nutrient use efficiency, plant performance and litter decomposition, P was recently suggested to be limiting for plant growth and decomposition in the Ethiopian plantations with *C. lusitanica* and *E. globulus* (Lisanework & Michelsen, 1993b; Michelsen *et al.*, 1993). The present results from a high number of planted and natural forest stands in Ethiopia suggest that this may be a general phenomenon in such forests.

The study cannot exclude the possibility that management of plantation forests, i.e. site preparation prior to tree planting and silviculture, could have contributed to the differences in the soil properties between the forest sites. Subsequent to the removal of the natural vegetation for tree plantings, soil erosion could be enhanced with considerable loss of important soil nutrients from the sites. There is evidence that site soil nutrient depletion occurs when plantation forests are established following removal of the natural vegetation (Lundgren, 1978; Madeira, 1989; Bargali *et al.*, 1993). After plantations are established a considerable portion of plant total nutrient stock could be immobilized in the growing above ground tree biomass and the standing litter mass on the forest floor. Export of nutrients with trees following harvesting of plantation trees on short rotation may contribute to decreasing soil nutrient levels

from the sites (Parrotta, 1992; Bargali *et al.*, 1993). A further substantial drain on the soil nutrients may occur if the forest floor litter is removed regularly; a common feature where plantations of eucalypts are established. The foregoing attributes should be taken into account when evaluating the influence of plantation tree species, notably *Eucalyptus*, on the soil.

The results of this study indicate that plantation forests of conifers and eucalypts, established following the natural vegetation clearance, almost invariably seem to be associated with deterioration in the nutrient levels of the soils. No significant differences were found between the soil characteristics of the species examined in greater details: *C. lusitanica*, *E. globulus*, *E. grandis*, *E. saligna* and *P. patula*. Accordingly, it appears that no recommendations on species selection for tree planting in the Ethiopian highlands can be given based on the nutrient status of the plantation soils. The species abundance, cover and biomass of the ground vegetation was less in the *C. lusitanica* plantations than in the other plantation types. Consequently, the planting of *C. lusitanica* should be limited or avoided as these forests will be more prone to soil erosion and furthermore, sustain a markedly less diverse flora. The impact of *C. lusitanica* on the conditions of the soil will be much aggravated when the plantation stands are clear-felled for timber uses. This species does not regenerate or coppice under Ethiopian climatic conditions. As an alternative to *C. lusitanica* the local, medium productive gymnosperm *J. procera* could be planted (Pohjonen & Pukkala, 1992; Lisanework & Michelsen, 1993b), as well as several other indigenous species (Michelsen 1992). At lower altitudes a range of local, drought tolerant *Acacia* species should be included in species trials as they may prove equally productive as the exotics used most often, *E. camaldulensis* and *Prosopis juliflora* (Sw.) DC. (Pohjonen, 1989; Michelsen, 1993a).

Summary

The floristic composition, cover and biomass production of the undergrowth vegetation, and soil properties were studied in established plantations and adjacent natural forest sites.

Vegetation and environmental data were collected from ninety-two plantation and natural forest sites in SW, NE, S and central parts of the Ethiopian highlands and in the central and NE lowlands of the country. The measured variables included altitude, stand characteristics as basal area and canopy cover, fine root biomass, diversity, cover and biomass of herbaceous plants, and the light intensity at the forest floor, together with chemical (pH, EC, OM, N, P, K, Ca, Mg, CEC) and Physical (bulk density, texture) properties of top- and sub-soil. Multivariate analyses were applied to identify the environmental variables responsible for species distribution, the effects of trees on herbaceous plant cover and on soil characteristics.

Using canonical correspondence analysis (CCA) the floristic composition of the ground cover in the forests was shown to differ among regions. These were segregated with regard to the environmental gradients governing the species distribution as identified by CCA: altitude, temperature and rainfall. Principal components analysis (PCA) showed that tree basal area was positively correlated with altitude and rainfall, and that the sites with high basal area were characterized by a relatively high content of organic matter and nitrogen in topsoil, and low pH.

After the variation between sites due to climate, topography and regional position had been removed a CCA showed that plantations of *C. lusitanica* older than 9 years tended to affect the species composition of the ground cover, and ANOVAs showed that this

tree species had significantly reduced cover and biomass of the undergrowth species compared to *E. globulus*, *E. grandis*, *E. saligna*, *P. patula* plantations and natural forests.

ASPECTS OF NUTRIENT CYCLING IN THREE PLANTATIONS

Using Redundancy analysis (RDA) and ANOVAs it was shown that the soil characteristics of the natural forests differed from that of the five most common plantation tree species: natural forest soil had higher content of exchangeable Ca and available P. The much (3-16) higher available P may be explained by the fast growth and high nutrient demand by the exotics in comparison with the trees of the natural forest, leading to a reduced availability of P in the plantation soils.

No significant differences were found between soil characteristics of the above mentioned plantation tree species. Hence, no recommendations on species selection for tree planting in Ethiopian highlands can be given based on the nutrient status of the plantation soils. However, based on data of herbaceous cover and diversity, the planting of *C. lusitanea* should be restricted due to the risk of soil erosion in such forests

Large scale plantation forests have been established in tropical regions under a wide range of climatic conditions, but how effects of nutrient cycling in tropical forests have been conducted in areas with a rainfall exceeding 2000 mm (Thorn & Long, 1982). The extensive studies of Lugo et al. (1989) include an extensive study of differences in accumulated litter masses between different plantation tree species. Factors which should affect the availability of nutrients, also, comparative studies of the nutrient cycling in natural and planted forests are needed, especially in higher altitudes (Sandgren, 1983), although natural or secondary forests may provide important opportunities for investigations of the environmental effects of plantation establishment (Lugo, 1992).

In Ethiopia, many plantations of exotic tree species have been established at altitudes above 2000 m, where the climate is favourable for fast growing tree species

ASPECTS OF NUTRIENT CYCLING IN THREE PLANTATIONS COMPARED TO A NATURAL FOREST IN THE ETHIOPIAN HIGHLAND

1. Introduction

Litterfall and litter decomposition are important processes influencing the function of forest ecosystems. The quantity and quality of litter and its decomposition are important for the study of energy flow, primary production and nutrient cycling and are, as such, indicative of the function of forest ecosystems (Bray & Gorham, 1964; Swift *et al.*, 1979; Proctor, 1983; Vitousek, 1984).

Both litter production and litter decomposition rates in tropical forests are often higher than in forests in other parts of the world, although large variations occur between forest types and within sites (Bray & Gorham, 1964; Anderson & Swift, 1983; Swift & Anderson, 1989). Large scale plantation forests have been established in tropical countries under a wide range of climatic conditions, but most studies of nutrient cycling in tropical forests have been conducted in areas with a rainfall exceeding 2000 mm (Brown & Lugo, 1982). The extensive studies of Lugo *et al.* (1990) in such an area showed differences in accumulated litter masses between different plantation tree species, factors which could affect the sustainability of plantations. Also, comparative studies of the nutrient cycling in natural and planted forests are rare, especially in higher altitudes (Lundgren, 1978), although natural or secondary forests may serve as important reference areas for investigations of the environmental effects of plantation establishment (Lugo, 1992).

In Ethiopia, many plantations of mainly exotic species have been established at altitudes above 1500 m, where the rainfall is favourable for fast growing tree species

(Pohjonen, 1989; Pohjonen & Pukkala, 1990). However, planting of selected tree species may lead to undesirable environmental effects. The larger part of the plantation forests consists of *Eucalyptus* species managed on short rotation; *E. globulus* ssp. *globulus* alone covers more than 100,000 ha. *Eucalyptus* species have widely been criticized for their potential role in soil degradation through reduction of soil fertility, but such effects are rarely demonstrated (Poore & Fries, 1985). In plantations of another fast growing exotic, *C. lusitanica*, the herbaceous cover is sparse (Michelsen *et al.*, 1993) and the topsoil thus vulnerable to erosion.

Despite these hazards, no studies of the dynamics of nutrient elements have been made in the plantation forests of Ethiopia. A knowledge of the amounts of nutrients cycled through litterfall is considered useful because litterfall represents a major process for transferring nutrients from the above ground vegetation to soils, and the relative rate at which forest vegetation loses organic matter versus particular nutrients provides an index of the efficiency of nutrient use within vegetation (Vitousek, 1982; Vitousek & Sanford, 1986). Moreover, a comparison of the nutrient cycling in planted and natural forests may contribute information regarding productivity, site fertility, choice of species and sustainability of forests.

The aims of this study, covering a two year period, were

- (i) to quantify the annual litterfall and its nutrient element content, its seasonal pattern and the relative contribution of each component of the litter,
- (ii) to study the rate of dry weight loss and nutrient element release from decomposing litter to the soil.

The study was conducted in three plantations with the most common plantation tree species in Ethiopia: The exotics *C. lusitanica* and *E. globulus*, and the indigenous *J. procera*. As a reference, parallel studies were also carried out in an adjacent natural

montane forest dominated by *J. procera*, *Olea europaea* ssp. *cuspidata* (DC.) Ciffieri and *P. falcatus*.

2. Study area

Menagesha State Forest is located on the gentle slope of Mt. Wochacha in the central highland of Ethiopia, at 8° 52' N, 38° 32' E. The altitudinal range of the areas covered by trees (plantations and natural forests) is from c. 2300 to 3300 m. The climate is subhumid tropical montane, with an average annual rainfall of 1019 mm recorded at Holleta Genet, on the plateau at 2380 m above sea level and 12 Km northwest of the study area. The air temperatures fluctuate highly between night and day: In November-December the night minimum temperature is 2°C, whereas the day maximum temperature reaches 24°C in February-May (Fig. 6). The parent material of the soil is volcanic, mainly fissural (Mohr, 1971) and the soil is classified as chromic luvisol (Anonymous, 1988).

The four study sites, located at about 3 km up the mountain slope, were selected (i) to represent mature forest stands, (ii) to encompass the variation of the stands in the general area and (iii) to avoid possible marginal effects. The forest may to some (relatively small) extent be influenced by the inhabitants of the neighbouring villages (some illegal felling of trees for domestic use, collection of fallen branches and leaves for fuel, and grazing by livestock may take place). Hence, each site, 10 m by 10 m for the plantations and 20 m by 20 m for the natural forest, was fenced off with barbed wire and guarded intensively.

Various characteristics of the four sites are described in Table 8. The natural forest site included, in addition to the tall dominants, mature individuals of *Allophylus abyssinicus* (Hochst.) Radlk., *Apodytes dimidiata* Arn., *Bersama abyssinica* Fresen., *Ekebergia capensis* Sparrm. and *Maytenus arbutifolia* (A. Rich.) Wilczek. According to Friis (1992) this is classified as an undifferentiated evergreen afro-montane forest. The

Climate

Holleta, alt. 2380 m (1984-91)

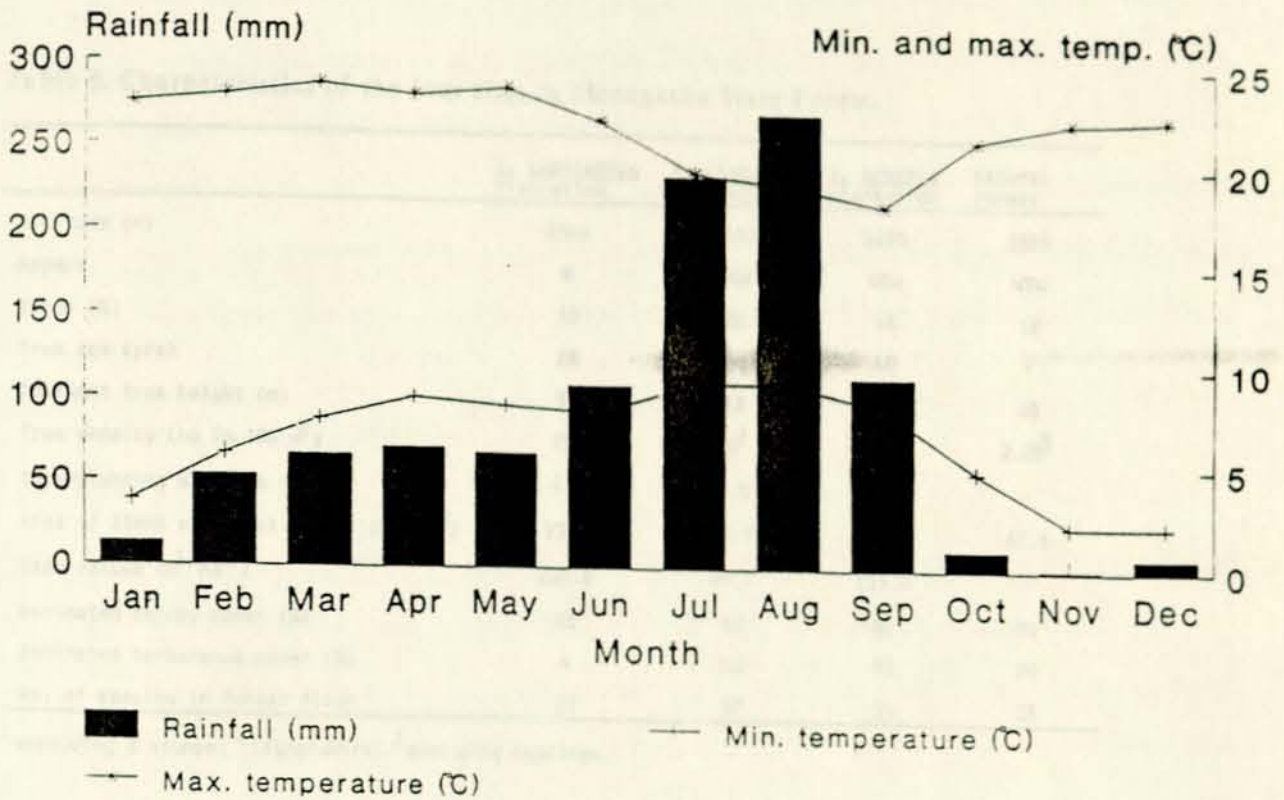


Fig. 6. Monthly rainfall, min. and max. temperatures (1984-91) at Holleta Genet, altitude 2380 m. Data from the Ethiopian National Meteorological Stations Office

Table 8. Characteristics of the four sites in Menagesha State Forest.

	<i>G. lusitanica</i> Plantation	<i>E. globulus</i> plantation	<i>J. procera</i> plantation	Natural forest
Altitude (m)	2360	2420	2450	2630
Aspect	N	NNW	WSW	WSW
Slope (%)	10	20	18	12
Tree age (yrs)	28	40	40	-
Dominant tree height (m)	15	12	15	40
Tree density (no in 100 m ²)	15 ¹	14 ²	10 ¹	2.25 ³
Interplanting distance (m)	1.5	1.5	2.0	-
Area of stems at breast height (m ² ha ⁻¹)	33.0	13.9	37.4	63.8
Stem volume (m ³ ha ⁻¹)	207.8	69.1	235.6	-
Estimated canopy cover (%)	95	30	80	70
Estimated herbaceous cover (%)	4	100	98	90
No. of species in forest floor	21	57	31	35

¹excluding 8 stumps; ²lignotubers; ³excluding saplings.

areas which are now plantation forests were, before planting, covered by natural forest similar to the one studied here (von Breitenbach, 1961; Friis, 1992). The trees in the plantation sites of *C. lusitanica* and *J. procera* were, in 1990, 28 and 40 years old respectively, whereas the lignotubers in the *E. globulus* site were 40 years old. Originally the plantation tree spacing seemed to have been 1.5 - 2.0 m, but some trees had been cut at an early stage and the trees in the plantations now appeared to be distributed rather irregularly. According to the management practice all *E. globulus* had been cut, and the regrowth (coppice) from the lignotubers was from 2-6 years old.

3. Materials and Methods

3.1. Litterfall

In February 1990, ten cotton cloth bags, 75 cm deep and with an opening of approximately 28 cm diameter (area = 0.06 m²), were placed in each forest site. The bags were fixed by wooden pegs at the corners, and were slightly raised aboveground. The litter in each bag was collected at approximately monthly intervals for 24 months, except in two cases (February-March and september-October 1991) where two months of litterfall were collected together and the dry weight was considered equal for the two months. The litter was dried at 80°C and sorted into the following litter components: leaves; small branches and bark (≤ 2 cm diameter); miscellaneous fraction (mainly reproductive parts, but also fine plant fragments, etc.). The litter components were comparable to the "fine litter" of Proctor (1983). After weighing, the components of each sample were bulked for subsequent chemical analysis, performed on the first 17 months of litter collection.

3.2. Decomposition

The litter bag technique (Bocock *et al.*, 1960; Anderson and Swift, 1983) was used to study the pattern and rate of litter decomposition and nutrient release. Senescent leaves were collected from mature trees of the species characterizing the respective

sites. The leaf litter of *C. lusitanica* and *J. procera* consists of fine non-woody twigs with small scaly leaves still attached; this material was, hence, used in the sites with these species. In the natural forest the proportion of plant material used of the different tree species was equivalent to the species' respective canopy cover in the site. Twenty-five grams of leaves were put into each 20 cm X 20 cm nylon-mesh bag, mesh-size 2 mm. Thirty-two bags were randomly placed in each of the sites in February 1990. The litter of the current year was removed, the bags were pinned to the forest floor and the removed litter was placed back to cover the bags. In each site, four bags were collected randomly every three months over a period of two years. The bags were carefully brushed free of foreign material. The decomposing litter was removed from the bags, fine roots penetrating the mesh were excluded and the litter was oven dried at 80°C and weighed. The first 12 months' collections of decomposing litter were analyzed chemically for N, P, Ca, Mg and K. For each time of collection the dry weight and amount of nutrient elements remaining in the decomposing litter was calculated as a percentage of the initial pool size in the litter bags.

A single exponential equation (Olson, 1963) $x/x_0 = e^{-kt}$ was used to estimate the weight and nutrient loss from the litter: x is the weight (mass of nutrient element) remaining at time t , x_0 the initial weight (mass of nutrient element) at the beginning of the experiment and k the decomposition constant. The half time of mass and nutrient loss ($0.693/k$) and the time after which 95% mass and nutrient were lost ($3/k$) were then calculated using this model.

4.1. Litterfall

Furthermore, the annual amount of nutrients released from decomposing litter equivalent to one year of litterfall was calculated and compared with the annual input of nutrients with litterfall.

3.3. Chemical analysis

The chemical analysis of plant material was done at the Department of Plant Ecology, Univ. of Copenhagen. Analytical procedures followed Allen (1989). Five samples of litterfall (the ten samples were bulked in pairs to yield five samples) and four samples of decomposing litter from each site and time of collection were ground in a Cyclotec 1093 Sample Mill (Tecator, Sweden). Sub-samples of 0.25 g were wet ashed in conc. HNO_3 , analyzed by atomic absorption spectrophotometry for Ca, Mg, and K using a Perkin-Elmer 5000 atomic absorption spectrophotometer, and for P by the Molybdenum Blue method using Tector Aquatec 5400 Analyzer. N was determined by the semi-micro Kjeldahl method with a kjeltec Auto 1030 Analyzer (Tecator, Sweden) after digesting 0.5 g sub-samples in concentrated H_2SO_4 with a selenium catalyst using Digestion System 40 (Tecator, Sweden).

3.4. Statistical analysis

The weight and nutrient content of litterfall and decomposing litter were analyzed statistically using one-way analysis of variance (ANOVA) and the multiple comparison Tuendt-Newman-Keuls (SNK) test with $p < 0.05$ (Sokal & Rohlf, 1981; Day & Quinn, 1989) in order to investigate if significant differences occurred in litterfall and decomposition rate among sites. Statistical analysis of data expressed as percentage was performed after square root-arc sine transformation.

4. Results

4.1. Litterfall

The total litterfall in the four sites (calculated from the two year period \pm standard error of the mean) was 501 ± 76 , 583 ± 102 , 653 ± 99 , and $1087 \pm 219 \text{ g m}^{-2} \text{ year}^{-1}$ in *C. lusitanica*, *E. globulus*, *J. procera* and the natural forest, respectively. The annual litterfall in the first year was much lower than in the second year: 326, 416, 576, and 961 g m^{-2} , respectively, compared with 677, 750, 749, 1213 g m^{-2} in the second year.

Table 9. Pearson product-moment correlation between monthly average rainfall (Hollela Genet, 1990-92) and total monthly litterfall in the four sites. n = 24; *: p < 0.05, **: p < 0.01; ns: non significant.

	Correlation coefficient
<u>Cupressus lusitanica</u>	0.0347 ns
<u>Eucalyptus globulus</u>	- 0.4421 *
<u>Juniperus procera</u>	- 0.6469 **
Natural forest	- 0.5660 **

Table 10. Rate of loss of dry matter and nutrient elements, half time (yrs) and time (yrs) required for 95% loss from litter mesh bags on the forest floor of the four sites. Loss of elements estimated from a 12 months period, dry matter from both 12 and 24 months (m).

		Dry matter		N	P	Ca	K	Mg
		24 m	12m					
k value	<u>C. lusitanica</u>	1.121	1.896	1.743	1.790	2.498	3.518	2.818
	<u>E. globulus</u>	1.317	1.467	1.245	1.309	1.760	2.940	2.420
	<u>J. procera</u>	1.540	2.250	2.331	1.664	2.683	3.854	3.212
	Natural forest	1.067	1.490	1.133	1.266	1.770	2.914	2.392
Half time	<u>C. lusitanica</u>	0.618	0.366	0.398	0.387	0.277	0.194	0.246
	<u>E. globulus</u>	0.526	0.472	0.557	0.530	0.394	0.236	0.286
	<u>J. procera</u>	0.450	0.308	0.297	0.417	0.258	0.180	0.216
	Natural forest	0.649	0.465	0.612	0.547	0.392	0.238	0.290
95% loss	<u>C. lusitanica</u>	2.676	1.582	1.721	1.676	1.201	0.838	1.065
	<u>E. globulus</u>	2.277	2.045	2.410	2.292	1.705	1.020	1.240
	<u>J. procera</u>	1.948	1.334	1.287	1.803	1.118	0.778	0.934
	Natural forest	2.810	2.013	2.648	2.369	1.695	1.029	1.254

Total litterfall in the forests (g/m²)

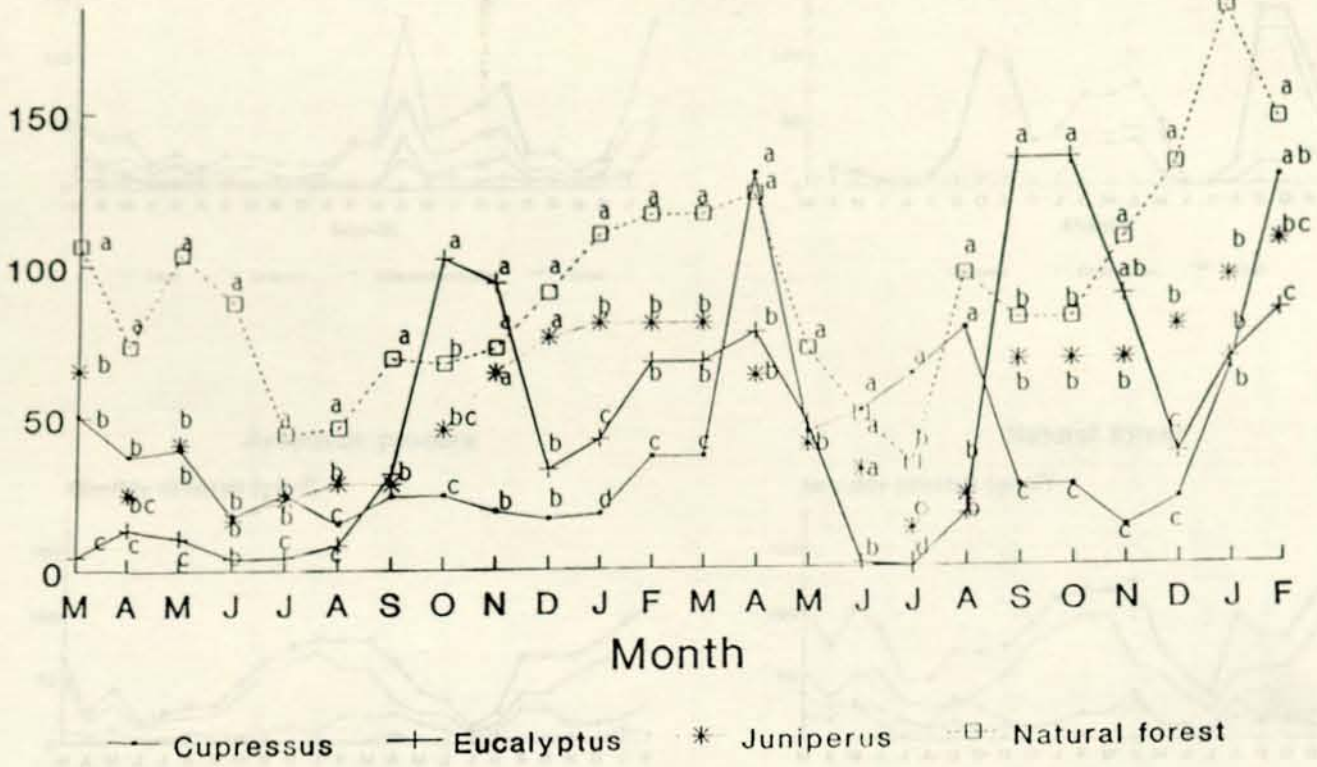
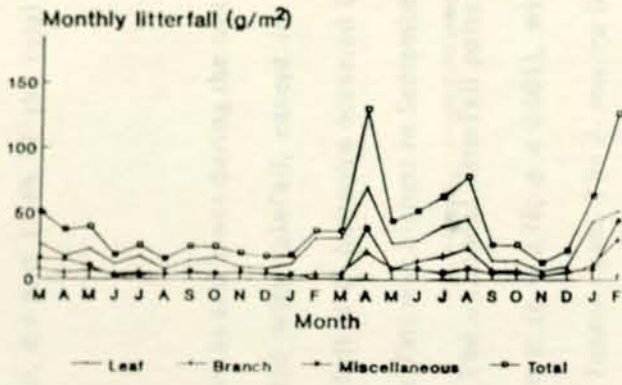
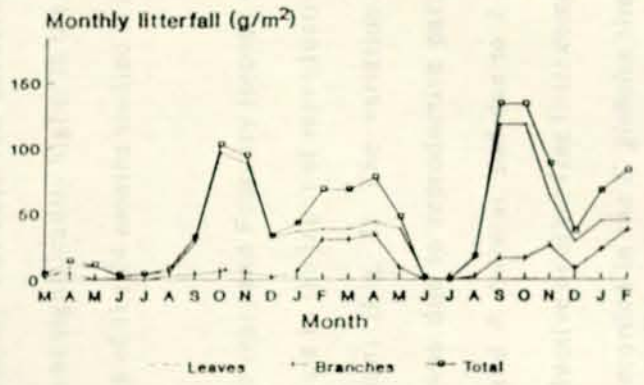


Fig. 7. Monthly variation in total litterfall in the four sites over a 24 month period. n = 10 per site. For each month, sites with means with the same letter do not have significantly different litterfall at p < 0.05 (SNK test)

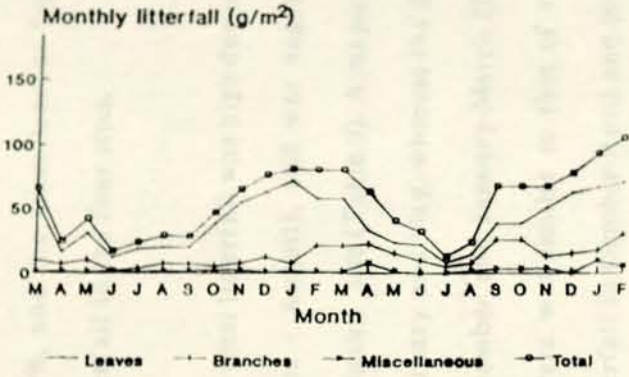
Cupressus lusitanica



Eucalyptus globulus



Juniperus procera



Natural forest

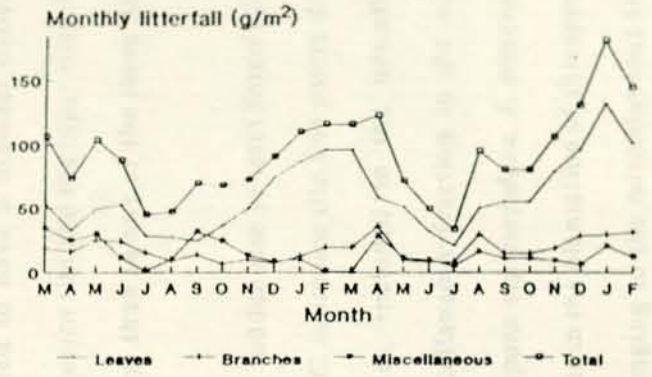


Fig. 8. Monthly variation in litterfall components (leaf, branch, miscellaneous, total) in the four sites. n = 10 per site.

The leaf litter constituted 57.6, 77.2, 71.9 and 65.5%, branches 20.9, 22.8, 23.7 and 19.2%, and the miscellaneous fraction 21.5, 0.0, 4.4 and 15.4% of the total annual litterfall in the four sites.

The total litterfall was high during the drier months and lower during the wet months (June - August), and was negatively correlated with rainfall, except in the *C. lusitanica* site (Table 9). A major peak of litterfall of *C. lusitanica* occurred between February and May, whereas the *E. globulus* litterfall was highest in September-November and January-March (Fig. 7, Fig. 8). The unimodal litterfall pattern of *J. procera* was similar to that of the natural forest ($r = 0.78$; $p < 0.001$), with high litterfall in October-April and low litterfall in June-August. The *J. procera* litterfall showed some similarity to that of *E. globulus* ($r = 0.59$; $p < 0.01$), although this species tended to have a bimodal pattern. Little similarity was observed between the *C. lusitanica* site and the other sites. The litterfall was significantly higher in the natural forest than in any of the three plantations in 18 of the 24 months studied (Fig. 7).

The sudden rise in total litterfall in April (first year) and February (second year) in the *C. lusitanica* site was partly due to the increase in the input of reproductive parts (cones, included in the miscellaneous fraction) (Fig. 8). The variation in the miscellaneous fraction in the natural forest was due to reproductive parts of *O. europaea* ssp *cuspidata*, *J. procera*, *E. capensis* and *P. falcatus*, and due to *J. procera* cones in the plantation of this species. No reproductive or other fine litter components belonging to the miscellaneous fraction were recorded in the *E. globulus* site as this consisted of eucalypt lignotubers with younger coppices.

The N and Mg concentrations in the litterfall from the four sites ranked: *C. lusitanica* < *E. globulus* < *J. procera* < natural forest (Fig. 9). K followed the same trend, except that the concentrations in *E. globulus* and *J. procera* litter were similar. P concentrations in *C. lusitanica* and *E. globulus* litter were similar and lower than in

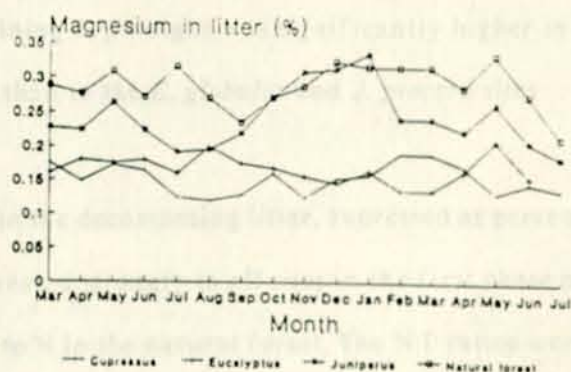
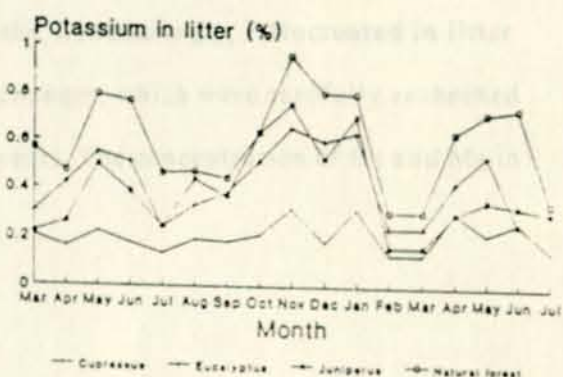
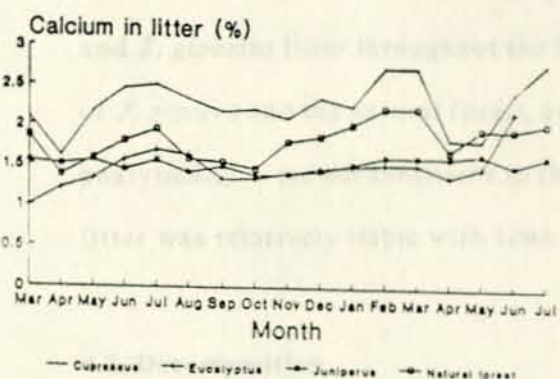
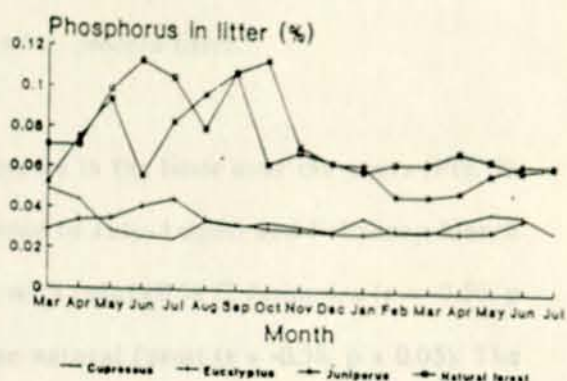
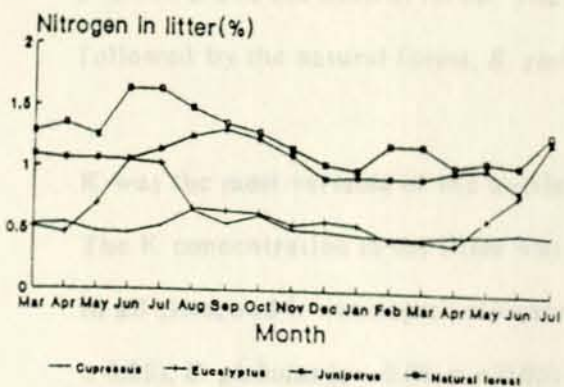


Fig. 9. Monthly variation in nutrient element concentration (% N, P, Ca, K, Mg) in litter. $n = 5$ per site. Mean 95% confidence limits are: for N 22.6, P 40.9, Ca 26.4, K 39.1, and for Mg 27.8% of mean monthly concentrations. Results of SNK tests are available upon request.

J. procera and the natural forest. The concentration of Ca was higher in *C. lusitanica* followed by the natural forest, *E. globulus* and *J. procera* litter.

K was the most variable of the nutrient elements in the litter over the years (Fig. 9). The K concentration in the litter was depressed in July-August and February-March in all sites, and it was negatively correlated with rainfall in *C. lusitanica* ($r = -0.56$, $p < 0.05$), *E. globulus* ($r = -0.56$, $p < 0.05$) and the natural forest ($r = -0.58$, $p < 0.05$). The N concentration in the litter showed little or no variation throughout the year, with the exception of the increase for *E. globulus* in May-July. P was stable in *C. lusitanica* and *E. globulus* litter throughout the 17 months. Contrastingly, P fluctuated in litter of *J. procera* and the natural forest, and the changes, which were carefully rechecked analytically, were not consistent in the two years. The concentration of Ca and Mg in litter was relatively stable with time.

4.2. Decomposition

The loss of dry weight in litter over the 24-months period followed the same trend in all sites (Fig. 10). The slowest decomposition was found in the natural forest. After 24 months, the remaining dry weight was significantly higher in the natural forest and *C. lusitanica* sites than in the *E. globulus* and *J. procera* sites

The content of P in the decomposing litter, expressed as percentage of the initial pool size (Fig. 11), increased strongly in all sites in the first phase of litter decomposition. The same applies to N in the natural forest. The N:P ratios were between 22 and 28 at the start of decomposition, dropped to between 6 and 8 (16 for *E. globulus*) at month 3 and increased to between 15 and 27 at month 12 (Fig. 12). The amount of N, Ca, Mg and K remaining after 12 months of litter decomposition (Fig. 11) was significantly higher in the litter of *E. globulus* and in that of the natural forest than in the litter in

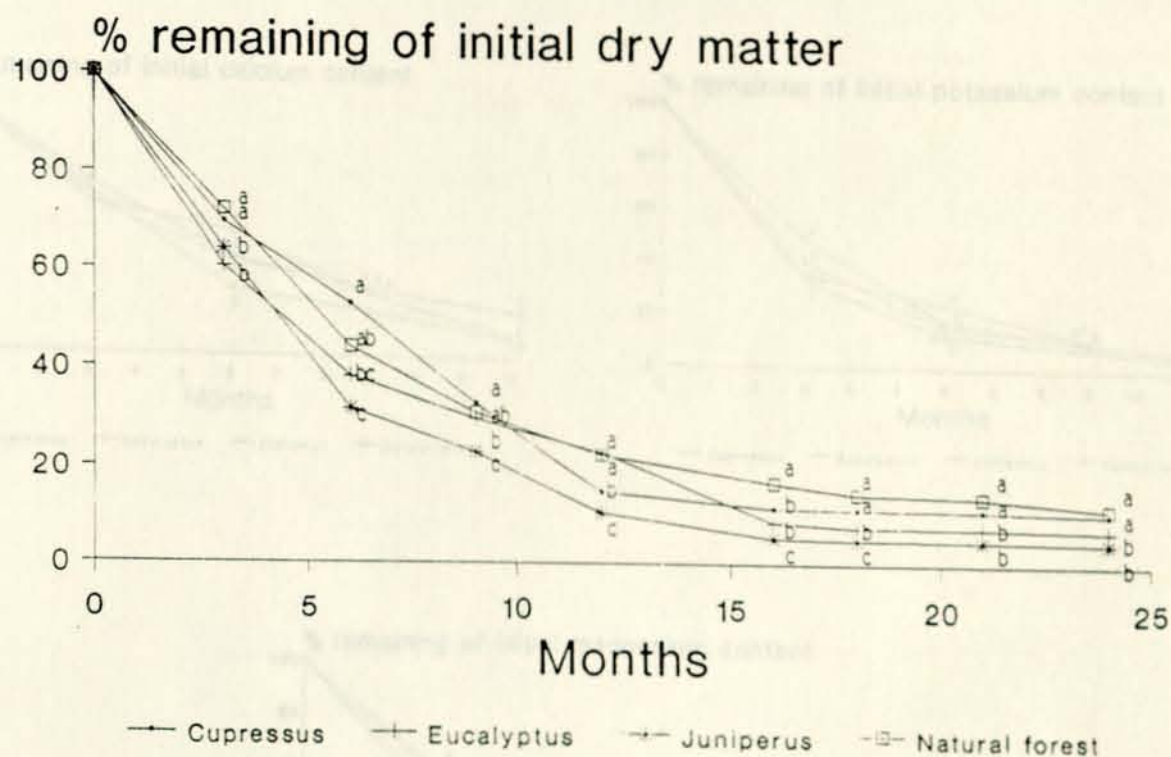


Fig. 10. Dry matter remaining as % of the initial content in litter mesh bags on the forest floor, over 24-months period, $n = 4$ per site. For each month of sampling, site means with the same letter are not significantly different at $p < 0.05$ (SNK test).

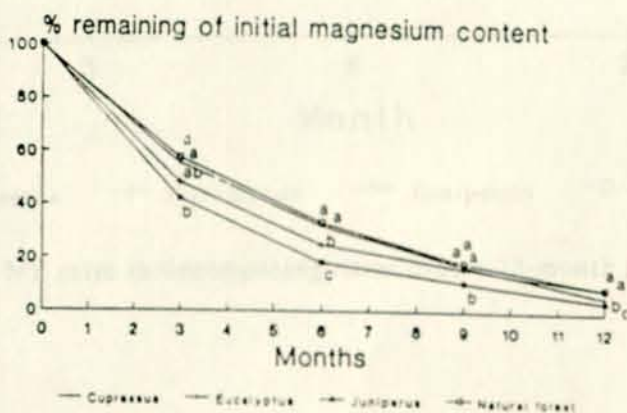
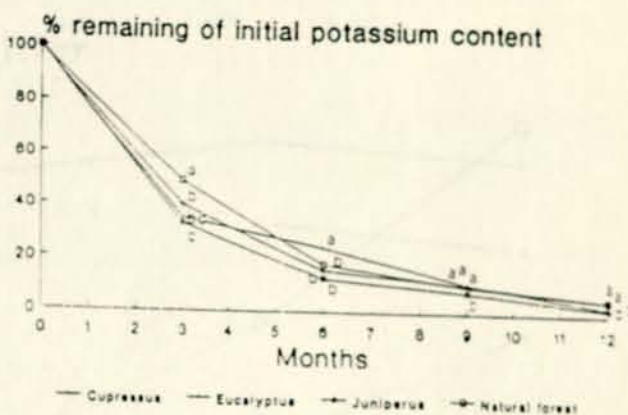
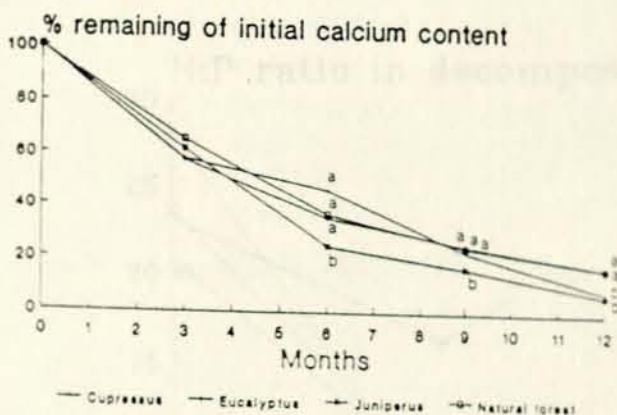
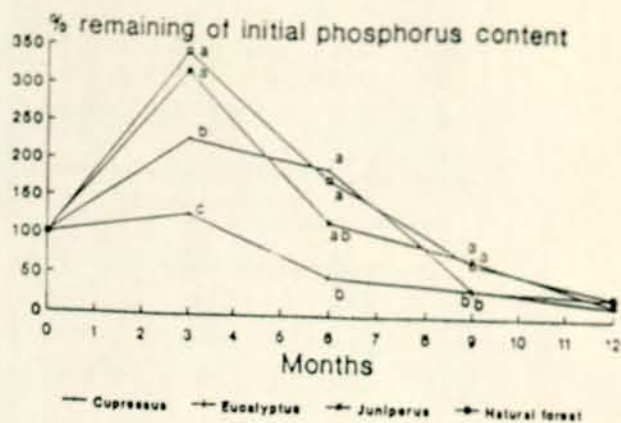
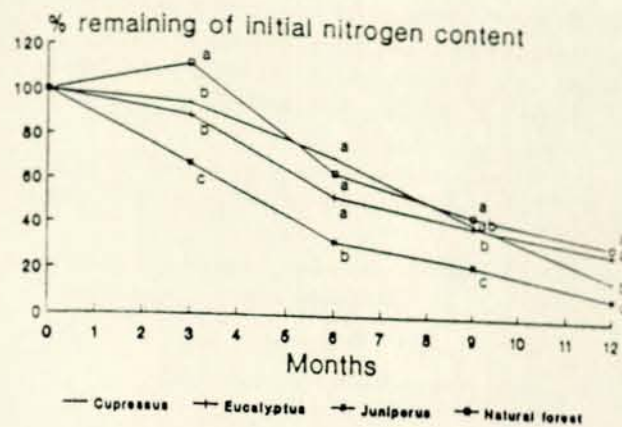


Fig. 11. Nutrient elements (N, P, Ca, K, Mg) remaining as % of the initial content in the litter mesh bags over 12-months period.

... litter during the year of decomposition. ...
 Pool sizes are based on data from Malhotra et al. (1972). For the soil, Σ is total N,
 available fraction and C_o, K and Mg is the exchangeable fraction.

		Elemental composition of litter (g kg ⁻¹)				
		C	N	P	K	Mg
Juniper	Leaf with litter	487	6.00	0.40	0.00	0.00
	Litter from litter	420	4.70	0.30	0.00	0.00
	Pool 20 top 40 in well	420	4.70	0.30	0.00	0.00
Eucalypt	Leaf with litter	470	6.10	0.40	0.00	0.00
	Litter from litter	420	4.70	0.30	0.00	0.00
	Pool 20 top 40 in well	420	4.70	0.30	0.00	0.00
Cupressus	Leaf with litter	470	6.10	0.40	0.00	0.00
	Litter from litter	420	4.70	0.30	0.00	0.00
	Pool 20 top 40 in well	420	4.70	0.30	0.00	0.00

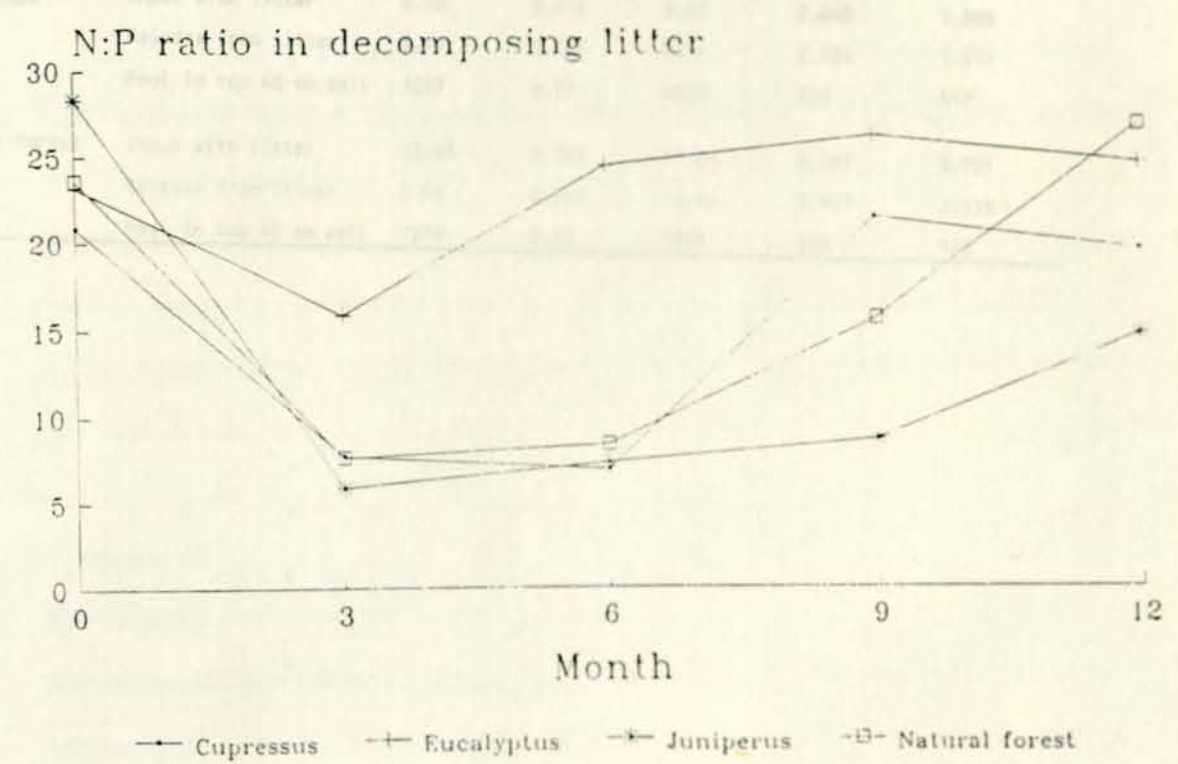


Fig. 12. N:P ratio in decomposing litter over a 12-month period.

Table 11. Annual input of nutrient elements from leaf and fine branch fall, and amounts released from litter during one year of decomposition, and element pool sizes in the top 40 cm soil. Pool sizes are based on data from Michelsen et al. (1993). For the soil, N is total N, P is the available fraction and Ca, K and Mg is the exchangeable fraction.

Site		Fluxes ($\text{g m}^{-2} \text{ year}^{-1}$) and pool sizes (g m^{-2})				
		N	P	Ca	K	Mg
<i>C. lusitanica</i>	Input with litter	2.27	0.151	9.69	0.996	0.656
	Release from litter	1.87	0.126	8.89	0.968	0.617
	Pool in top 40 cm soil	1274	1.24	3670	193	574
<i>E. globulus</i>	Input with litter	2.12	0.116	5.22	1.785	0.594
	Release from litter	1.51	0.085	4.32	1.691	0.541
	Pool in top 40 cm soil	1344	2.06	2916	153	620
<i>J. procera</i>	Input with litter	6.06	0.416	8.58	2.640	1.540
	Release from litter	5.47	0.337	7.99	2.584	1.477
	Pool in top 40 cm soil	1297	6.77	4020	230	517
Natural forest	Input with litter	12.60	0.780	17.84	6.267	2.901
	Release from litter	8.55	0.560	14.80	5.927	2.636
	Pool in top 40 cm soil	1279	2.60	3905	232	568

the two other species, whereas the amount of P remaining was equal in all four sites. The sites could be arranged in this sequence with respect to the rate of nutrient element release after 12 months: *J. procera* > *C. lusitanica* > *E. globulus* > natural forest (Table 10). The exception was P, which had similar release rates in *J. procera* and *C. lusitanica* litter. The rate of nutrient element release and dry weight loss in the four sites was: K > Mg > Ca > dry weight > P = N, except in *J. procera* where N > P.

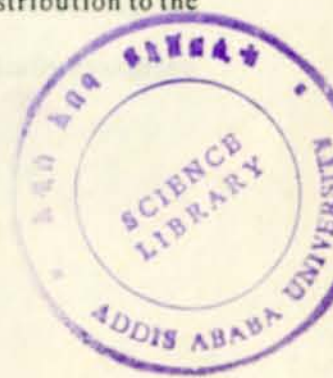
4.3. Nutrient return

The annual input of nutrients in litterfall, and the net amount of nutrients released in the first year following litterfall from decomposing litter in an amount equivalent to one year of litterfall is given in Table 11, together with the nutrient element pool sizes in the top 40 cm of soil (based on data from Michelsen *et al.*, 1993). The nutrient input to the soil by litter of the two exotic tree species was generally much lower than for *J. procera* and, notably, the natural forest. As a consequence of the relatively high rate of release of Ca, Mg, and K the input of these elements was nearly balanced with release after one year in all sites, whereas the proportion of N and P released was less than the input.

5. Discussion

5.1. Litterfall

The observed litterfall in the natural forest ($10.9 \text{ t ha}^{-1} \text{ yr}^{-1}$) is in the upper part of the range ($3.6\text{-}12.4 \text{ t ha}^{-1} \text{ yr}^{-1}$) recorded for tropical forests (Bray & Gorham, 1964; Tanner, 1980; Anderson & Swift, 1983; Songwe *et al.*, 1988; Schmidt, 1991; Scott *et al.*, 1992), also when the inverse linear relationship between litterfall and latitude in the tropics (Lugo & Brown, 1991) is considered. However, few figures exist of litter fall in montane forests exposed to rainfall comparable in size and seasonal distribution to the forest studied here.



The litter production in three plantations was lower ($5.0 - 6.5 \text{ t ha}^{-1} \text{ yr}^{-1}$) than that in the natural forest but similar to that recorded in climatically comparable plantations (Bray & Gorham, 1964; Lundgren, 1978; Egunjobi & Onweluzo, 1979). Lundgren (1978) recorded a litterfall similar to that of the present study: $5.2 \text{ t ha}^{-1} \text{ yr}^{-1}$ in a 20 year old *C. lusitanica* plantation in Tanzania as opposed to a litterfall of $8.8 \text{ t ha}^{-1} \text{ yr}^{-1}$ in a natural forest. The high standing crop and species diversity of trees in natural forests compared with younger monocultures may explain the higher litterfall in the natural forests. Total litterfall is linearly related to the standing crop (Brown & Lugo, 1982). As the plantations were still in a rather early successional stage, the potential litterfall in mature plantations could be higher than results obtained from younger plantations (or coppiced plantation in *E. globulus*) suggest. Some of the few other comparisons between litterfall in plantations and natural tropical forests show similar litterfall in the two types (Brasell & Sinclair, 1983), or even higher litterfall in plantations than in secondary forests (Lugo, 1992). This is probably partly due to the occurrence of natural forest tree species regenerating in the plantations investigated by these authors, and partly due to species characteristics. In the plantation sites in Menagesha such species were at the seedling or sapling stage and did not contribute much to litterfall.

The negative correlation between litterfall and rainfall in the sites (except in the *C. lusitanica* site) (Table 9) corresponds with most results from litterfall studies in tropical forests (Lundgren, 1978; Songwe *et al.*, 1988; Martinez-Yrizar & Sarukhan, 1990; Schmidt, 1991). This correlation is explained by the effect of water stress on abscission of leaves and smaller branches (Songwe *et al.*, 1988; Swift & Anderson, 1989). Nevertheless, the plantation trees as well as almost all species in the natural forest retained the majority of their leaves throughout the year, and the assumption of Friis (1992) of the natural *Juniperus-Olea-Podocarpus* forest as basically evergreen is therefore corroborated.

The higher litterfall in the second than in the first year of data collection, notably in the *C. lusitanica* and *E. globulus* sites, is unlikely to be attributed to the rainfall pattern which, however, often causes strong between-year variation (Songwe *et al.*, 1988). This is because the annual rainfall varied little, being 1083 and 977 mm in the first and second year, respectively. Also, the pattern of rainfall distribution did not vary much in these two years. Higher wind velocities in the second year seems to be a more probable factor because the branch fraction increased (fig. 8), but no meteorological data are available to confirm this suggestion. Other studies (e.g. Egunjobi & Onweluzo, 1979; Songwe *et al.*, 1988; Dantas & Phillipson, 1989) also show considerable variation in litterfall between years, but the presented variations are among the highest recorded between years (Proctor, 1983; 1984). This emphasizes the need for long-term litterfall studies.

5.2. Decomposition

The high precipitation and temperature of tropical climates yield a generally high rate of decomposition (Esser & Lieth, 1989). The decomposition rates in the four sites (Fig. 10, Table 10) were in the upper part of the range recorded for similar climate in the tropics (Swift & Anderson, 1989; Palm & Sanchez, 1990). Locally decomposition rates are modified by differences in substrate quality (Meentemeyer, 1978; Anderson & Swift, 1983; Vitousek, 1984). Since the four sites in the present study were exposed to similar climatic conditions, the among-site differences in litter decomposition rates should relate to the substrate quality.

After 24 months, the remaining dry weight was significantly higher in the natural forest and the *C. lusitanica* sites than in the *E. globulus* and *J. procera* sites. The relatively slow decomposition in the natural forest is perhaps surprising as *J. procera* (with the fastest decomposition) was an important element in this site. However, sclerophyllous leaf litter of other trees in the site (e.g. *O. europaea* spp *cuspidata* and

P. falcatus) were included in the bags, and this litter may have been decomposing relatively slowly.

Dry mass and nutrient elements may be lost from litter bags by leaching, mineralization and direct transfer of litter fragments to the mineral soil (Swift *et al.*, 1979; O'Connell, 1988b; Palm & Sanchez, 1990). The amount of cations remaining (as compared with the original pool size in the litter bags) showed a similar trend of decline in all sites. However, K had the most rapid rate of release, followed by Mg and then Ca (Fig. 11). This order confirms reports from other tropical forests (Swift *et al.*, 1981; Anderson & Swift, 1983; Palm & Sanchez, 1990). Of the initial amount of K, 32-49% was lost from decomposing litter during the first three months as compared with a weight loss of 28-40%; this indicates initial leaching loss of K. This element is not highly associated with the structural material of litter and mineralization is not a prerequisite for release (O'Connell, 1988b; Sharma & Ambasht, 1987) as it is generally leached in advance of microbial decay (Swift *et al.*, 1981; O'Connell, 1988b). Leaching also appeared to contribute to the loss of Mg during the initial phase of decomposition because its rate of release exceeded the rate of weight loss, whereas the release of Ca, approximated the loss rate of mass, seemed primarily to be related to the cellular decay.

In all sites net accumulation of P, and N in the natural forest, was observed during the first three months of decomposition (Fig. 11). In subsequent months the N and P concentration decreased in decomposing litter. Both early N and P immobilization (Anderson & Swift, 1983) and decreases in N and P concentration following mass loss have been found (Swift *et al.*, 1981; Sharma & Ambasht, 1987). The high accumulation of P in decomposing litter in the first months have been observed in forests elsewhere (Upadhyay & Singh, 1989; Palm & Sanchez, 1990) The accumulation could be from falling litter, herbivore frass, precipitation, throughfall, stemflow, the soil substrate,

and from ingrowth of fungal hyphae (Swift *et al.*, 1979; O'Connell, 1988b). Mycorrhizal fungi were abundant in roots and soil of the sites (Michelsen *et al.*, 1993), and, could, together with saprotrophic fungi, account for a major part of the P accumulation, through fungal ingrowth and P translocation in the hyphae. The N:P ratios in fresh litter were relatively high compared with most other studies (Lugo & Murphy, 1986; Nadkarni & Matelson, 1992). This suggests P limitation in the soil substrates, a hypothesis supported by the low available P found in all the soils (Michelsen *et al.*, 1993). The changes in N:P ratios in decomposing litter with time (Fig. 12) followed a similar trend as those reported by Palm & Sanchez (1990). As 10 is the ideal N:P ratio for decomposers (Vogt *et al.*, 1986) the high ratios indicate that P was limiting the litter decomposition in the *C. lusitanica* and the natural forest sites in the beginning and at the end. P seemed to limit decomposition of *J. procera* litter in the beginning only; this site had the highest amount of available P in the soil of the four sites (Michelsen *et al.*, 1993), and litter decomposition was fastest for this species (Table 10; Fig. 10). *E. globulus* litter decomposition appeared to be P-limited during the whole period.

5.3. Nutrient return

The soil properties in the three plantation sites prior to the establishment of plantations 28 to 40 years ago are assumed to have been similar to those presently recorded from the nearby natural forest because the sites are well within the area of the characteristic forest type of the central highlands of Ethiopia which covered the sites before the forest was cleared for plantation establishment (von Breitenbach, 1961; Friis, 1992). The soil types of the sites were similar and only smaller differences in soil nutrient content were found between sites (Michelsen *et al.*, 1993). These cannot alone explain the large differences in nutrient element content of litter between sites, which primarily must be attributed to the characteristics of the species involved.

The litter amount in the four sites showed the same trend as the litter quality, both

were relatively low in the *C. lusitanica* and *E. globulus* sites and higher in the *J. procera* site and, notably, the natural forest. Adding estimates of fine root production (Michelsen *et al.*, 1993) to the estimates on litter production (a procedure proposed by Vogt *et al.*, 1986) does not change the picture on productivity in the sites. For *E. globulus* the low litter production is partly a result of site consisting of young coppice, and for *C. lusitanica* partly because the stand age is 28 years, or 12 years less than the *J. procera* stand to which it was compared. Nevertheless, the considerably smaller nutrient input (Table 11) to the soil in the two sites with exotics than in the *J. procera* plantation and the natural forest is probably to a large extent due to species characteristics.

The nutrient input to the soil with litterfall from the exotics and from the natural forest was comparable with that of Lundgren (1978) in *C. lusitanica* and *P. patula* plantations and in a natural montane forest, respectively. The natural forest site furthermore had a nutrient input close to that of lowland rain forests (Scott *et al.*, 1992), montane rain forest (Edwards, 1982) and disturbed natural forests (Lugo, 1992). The input from the exotics in the present study was rather high compared with less productive areas: the input from the *E. globulus* coppice was twice as large as that of an *E. camaldulensis* forest (Briggs and Maher, 1983), and of that of a 40 years old *E. diversicolor* stand (O'Connell, 1988a). In the latter the input furthermore highly exceeded release as the rate of decomposition and nutrient return was relatively slow, perhaps due to lower substrate quality.

The precision of the account on nutrient input and release (Table 11) is affected by the limitations of litterfall and decomposition studies. As an example, decomposition in mesh bags may under estimate actual decomposition of undisturbed litter on the forest floor (Wieder and Lang, 1982; Anderson and Swift, 1983; Proctor, 1983). Also, the litter material for the decomposition studies was senescent leaves collected directly

from the trees, and consequently the litter was generally of a higher quality than fallen litter in which nutrient retranslocation may have taken place prior to abscission. Finally, Table 11 does not account for nutrient input to soil with fall of branches > 2 cm, stem flow and throughfall. Some leaching, especially of K, may have taken place before fall of litter and/or litter collection as K concentration in fallen litter was negatively correlated with rainfall. Nevertheless, it appears from Table 11 that the input of Ca, Mg and K was nearly balanced with release after one year in all sites, whereas the proportion of N and P released was less than the input. This indicates that N and P were more strongly immobilized than Ca, K and Mg by the litter dwelling biota.

Export of nutrients from the sites with logging was not determined but would be expected to influence the nutrient cycling considerably. This may especially be the case for the sites where input of important nutrient elements as N, P and Mg with fine litterfall is low, i.e. in the *C. lusitanica* and *E. globulus* sites, and a major part of the nutrient pool thus may be found in the wood, as it was the case in other studies (Lugo & Murphy, 1986)

From the data on pool sizes of nutrient elements in the top 40 cm soil (Table 11; based on data from Michelsen *et al.*, 1993) it is evident that the quantities of total N and exchangeable Ca, K and Mg present in soil are far larger than the amounts cycled annually in fine litter. Hence, the data do not point to a rapid cycling of K such as that observed by Edwards (1982) in montane rain forest in New Guinea. However, the quantity of available P in soil of the natural montane forest in the present study is only three times larger than the annual litter content of P, which suggests rapid cycling of this element here.

The dimensionless ratio of mass of litterfall input ($\text{Kg h}^{-1} \text{yr}^{-1}$) to the quantity of nutrients contained in litterfall ($\text{kg ha}^{-1} \text{yr}^{-1}$) (Vitousek, 1982; 1984) was an index of within stand nutrient use efficiency, was for N 221 and 275 in *C. lusitanica* and *E. globulus* compared to 108 and 86 in *J. procera* and the natural forest, and for P 3318 and 5026 compared to 1570 and 1394, respectively. Vitousek (1984) has estimated that the systems showing values > 130 for N and > 3000 for P could be efficient in that relatively large amount of organic matter could be fixed per unit of nutrient taken up. Although the ratios, in the present study, are obtained from comparisons of non-replicated stands of different tree species, the pattern suggests that the two exotics have much more efficient within-stand cycling of nutrient elements than *J. procera* and the natural forest, similar to the results of Lugo (1992) from plantations and paired secondary forests. Contrastingly, both input of mass and, especially, nutrients with litter, and the subsequent release of nutrient elements in *J. procera* plantation and the natural forest were high (Table 10), i.e. these stands had more "inefficient" within-stand cycling (sensu Vitousek, 1984).

Herbs, shrubs and tree seedlings in *J. procera* and the natural forest may benefit from the high degree of nutrient release to the soil. A vigorous herbaceous cover may protect the soil from erosion, a desirable property of plantation trees in the Ethiopian highland. With such characteristics, the planting of *J. procera* may be recommended. Although the herbaceous biomass and cover was similar in the *E. globulus* and *J. procera* sites, this could be attributed to the relatively high light intensity in the coppiced *E. globulus* site; the growth of bioassay plants in soil from the *E. globulus* site under controlled experimental conditions was strongly reduced as compared with their growth in soil of *J. procera* (Michelsen *et al.*, 1993). However, if the objective of plantation establishment is primarily fast production of wood biomass, the planting of *E. globulus* and *C. lusitanica* is suggested (Poschen-Eiche, 1987; Pohjonen, 1989; Pohjonen & Pukkala, 1990; 1992). Although these species may reduce the germination

and growth of herbaceous species in the ground cover through release of allelopathic substances from leaves, eucalypts as *E. camaldulensis* and *E. saligna* seem more damaging in this respect (Lisanework & Michelsen, 1993a).

In view of the obvious lack of studies on nutrient cycling in montane forests in Eastern Africa, this study considered neighbouring plantations of three most commonly planted species in Ethiopia as well as an adjacent undisturbed natural montane forest, instead of selecting one species and having replicated sites. This lack of site replication in the present study should be taken into account when the results are evaluated. There are also difficulties inherent in comparing forest ecosystems such as plantations and native forests, e.g. due to their differences in age and structure, but this does not justify ignoring the need for information (Lugo, 1992). Especially this holds true in countries as Ethiopia, where the remnants of the natural montane forests are threatened by complete destruction. More studies on aspects of nutrient cycling in plantations of exotic and indigenous tree species as compared with natural forests are needed to evaluate the sustainability of plantations in the Ethiopian highlands. Such investigations should include comparative studies of plantation species in replicated stands in a range of climatic and edaphic conditions.

Summary

The pattern of litterfall, its nutrient element content, rate of weight loss and release of nutrient elements were investigated in 28-40 years old plantations of *C. lusitanica*, *E. globulus*, and *J. procera*, and compared with that of an adjacent *Juniperus-Olea-Podocarpus* montane forest in the Ethiopian highland.

The total annual fine litterfall was 501, 583, 653, and 1087 g m⁻² year⁻¹ in the *C. lusitanica*, the *E. globulus*, the *J. procera* plantation and the natural forest, of which leaves constituted 57.6, 77.2, 71.9 and 65.5%, respectively. Litterfall was higher in the

IMPACTS OF TREE PLANTATIONS IN THE ETHIOPIAN HIGHLAND ON SOIL FERTILITY AND PLANT PERFORMANCE: FIELD SURVEYS AND BIOASSAYS

1. Introduction

The current degradation of the natural forests, woodlands and bushlands of the tropical region emphasizes the need of tree planting. Ethiopia is one of the NE African countries most badly struck by the environmental crisis. Many plantations with fast growing exotic tree species, mainly *E. globulus* ssp. *globulus* (Poschen-Eiche, 1987; Pohjonen & Pukkala, 1990), have been established here since the end of the last century to meet the demand for fuelwood, timber and other tree products.

It has been suggested that old Ethiopian plantations in the long run undergo a succession in which indigenous trees such as *Acacia abyssinica* Hochst. ex. Benth. and *J. procera* establish and ultimately replace the exotic plantation species (Tewoldeberhan, 1974; Pohjonen & Pukkala, 1990; 1992). Such development would make the recent trend of forest degradation less deleterious. However, fast growing *Eucalyptus* species have a high demand of water and nutrients and, furthermore, may release allelopathic substances from leaves, barks and roots. In some areas such effects reduce herbaceous plant growth and lead to soil erosion (Poore & Fries, 1985). Consequently, the indigenous tree seedlings may not be able to establish, and attempts to intercrop trees with pasture grasses (Singh *et al.*, 1989) may fail. The question is therefore: should the use of *Eucalyptus* be restricted and planting of other fast growing trees promoted? Little research on the ecological effect of eucalypts has been undertaken in NE Africa to answer this question.

The aim of this study was to investigate ecological effects of *C. lusitanica*, *E. globulus*

and *J. procera* plantations in the central highlands of Ethiopia. The physical and chemical characteristics of the soil, the species composition, the above ground herbaceous biomass and nutrient content and the fine root production of herbs and grasses were studied in three types of planted forests as well as an adjacent natural montane forest. Productivity of herbaceous plants in forest stands may, however, be influenced by several co-occurring factors. Erroneous conclusions on the potential productivity of soils in plantations could thus easily be reached from such data alone. Therefore, the field studies were combined with bioassays under controlled conditions using three indigenous plant species: one tree, *A. abyssinica*, the forage grass *Chloris virgata* Sw., and teff (*Eragrostis tef* (Zucc.) Trotter), one of the most important cereal crops in Ethiopia.

2. Materials and methods

This study was conducted concurrently with the investigation of the aspects of nutrient cycling in the four forest sites. Further details of the sites are presented in Table 12, and a list of species in the ground cover (forbs, graminoids and seedlings of shrubs and trees) is, together with a visual estimate of their cover, given in Table 13.

2.1. Sampling in the forest sites

Soil sample collections to investigate soil properties and fine root biomass were based on the procedures described in chapter II.

The above ground biomass of herbs and grasses was collected in four randomly placed 1 m² quadrats in each of the four sites. The collection was performed in February and repeated in June and October 1990.

In order to estimate the growth potential of fine roots in the upper 10 cm soil depth, ten soil cores of 10 cm depth and 5 cm diameter were randomly drilled in each site.

Table 12. Characteristics of the four sites in Menagesha State Forest.

	<i>Cupressus lusitanica</i> plantation	<i>Eucalyptus globulus</i> plantation	<i>Juniperus procera</i> plantation	Natural forest
Altitude (m)	2360	2420	2450	2630
Aspect	N	NNW	WSW	WSW
Slope (%)	10	20	18	12
Tree age (yr)	28	40	40	-
Dominant tree height (m)	15	6	15	40
Tree density (no. in 100m ²)	15 ¹	14 ²	10 ¹	2.25 ³
Interplanting distance (m)	1.5	1.5	2.0	-
Area of stems at breast height (m ² ha ⁻¹)	33.0	13.9	37.4	63.8
Stem volume (m ³ ha ⁻¹)	207.8	69.1	235.6	-
Estimated canopy cover (%)	95	30	80	70
Estimated herbaceous cover (%)	4	100	98	90
Annual fine litterfall (g m ⁻²)	501	583	653	1087
No. of species in forest floor	21	57	31	35
Light intensity in % of that in the open	14.1	51.5	12.3	20.5

¹excluding stumps; ²lignotubers; ³excluding sapling;

Table 13. list of species in the ground cover of the four sites, including seedlings of shrubs and trees less than 0.5 m tall, and the percentage coverage of the species. + present, coverage less than 1%.

C. lusitanica site Most plants poorly developed and/or sterile.

<i>Achyranthes aspera</i>	+	<i>Cyperus fischerianus</i>	-	<i>Olea europaea</i> spp. <i>cuspidata</i>	+
<i>Alchemilla</i> sp.	+	<i>Dovyalis abyssinica</i>	+	<i>Oplismun compositus</i>	+
<i>Asparagus africanus</i>	+	<i>Ehrharta erecta</i>	+	<i>Panicum pusillum</i>	+
<i>Asplenium aethiopicum</i>	+	Fern	+	<i>Panicum hochstetteri</i>	+
<i>Bidens pilosa</i>	+	<i>Helichrysum</i> sp.	+	<i>Phaulopsis imbricata</i>	4
<i>Carissa edulis</i>	+	<i>Kalanchoe</i> sp.	+	<i>Rhus ruspolii</i>	+
<i>Conyza</i> sp.	+	<i>Maytenus arbutifolia</i>	+	<i>Schrophulariaceae</i> indet	+

E. globulus site Most plants normally developed.

<i>Achyranthes aspera</i>	+	<i>Dichrocephala chrysanthemifolia</i>	+	<i>Mikaniopsis clematoides</i>	+
<i>Agrocharis melanantha</i>	+	<i>Digitaria abyssinica</i>	10	<i>Myrsine africana</i>	-
<i>Alchemilla pedata</i>	+	<i>Dregea</i> sp	+	<i>Olea europaea</i> ssp. <i>cuspidata</i>	+
<i>Andropogon abyssinicus</i>	5	<i>Dyschoriste clinopodioides</i>	+	<i>Pennisetum thunbergii</i>	1
<i>Asparagus africanus</i>	+	<i>Ehrharta erecta</i>	+	<i>Periploca linearifolia</i>	+
<i>Barleria ventricosa</i>	+	<i>Eragrostis tenuifolia</i>	+	<i>Phaulopsis imbricata</i>	35
<i>Bersama abyssinica</i>	+	<i>Festuca abyssinica</i>	-	<i>Plectrocephalus varians</i>	-
<i>Bidens pilosa</i>	+	<i>Hyparrhenia arrhenobasis</i>	5	<i>Rhynchosia</i> sp	+
<i>Brachypodium flexum</i>	30	<i>Hypericum peploidifolium</i>	+	<i>Satureja abyssinica</i>	+
<i>Carex chlorosaccus</i>	+	<i>Hypoestes forskalii</i>	4	<i>Satureja biflora</i>	+
<i>Carissa edulis</i>	+	<i>Juniperus procera</i>	+	<i>Senecio ochrocarpus</i>	+
<i>Cassia mimosoides</i>	+	<i>Jasminum floribundum</i>	-	<i>Sida</i> sp.	-
<i>Centella asiatica</i>	1	<i>Justicia ledanoides</i>	+	<i>Sium simense</i>	+
<i>Cheilanthes farinosa</i>	+	<i>Kalanchoe densiflora</i>	+	<i>Solanum incanum</i>	+
<i>Conyza schimperii</i>	+	<i>Kosteletzkya adoensis</i>	+	<i>Stephania abyssinica</i>	+
<i>Croton macrostachyus</i>	+	<i>Laggera pterodonta</i>	+	<i>Tagetes minutus</i>	+
<i>Cynanotus</i> sp.	+	<i>Laggera tonentosa</i>	-	<i>Trifolium simense</i>	-
<i>Cynoglossum lanceolatum</i>	+	<i>Maytenus undata</i>	+	<i>Vernonia bipontinii</i>	+
<i>Cyperus fischerianus</i>	2	<i>Maytenus gracilipes</i>	+	<i>Vernonia leopoldi</i>	+

J. procera site Most plants normally developed.

<i>Achyranthes aspera</i>	+	<i>Dovyalis abyssinica</i>	+	<i>Mikaniopsis clematoides</i>	-
<i>Acritochaete volkensii</i>	50	<i>Ehretia cymosa</i>	+	<i>Oxalis corniculata</i>	+
<i>Agrocharis melanantha</i>	+	Fern	+	<i>Olea europaea</i> ssp. <i>cuspidata</i>	+
<i>Alchemilla pedata</i>	+	<i>Galium spurium</i> spp. <i>africanum</i>	+	<i>Phaulopsis imbricata</i>	20
<i>Asclepiadaceae</i> , climber	+	<i>Geranium arabicum</i>	+	<i>Rhynchosia</i> sp.	+
<i>Asplenium</i> sp.	+	<i>Geranium aculeolatum</i>	+	<i>Scadoxus multiflorus</i>	+
<i>Bersama abyssinica</i>	+	<i>Hypoestes triflora</i>	20	<i>Senecio ochrocarpus</i>	+

<i>Brachypodium flexum</i>	+	<i>Impatiens hochstetteri</i>	+	<i>Teclea nobilis</i>	+
<i>Carex chlorosaccus</i>	7	<i>Jasminum floribundum</i>	+	<i>Thalictrum rhynchocarpum</i>	+
<i>Carissa edulis</i>	+	<i>Kalanchoe petitiiana</i>	+		

Natural Juniperus-Olea-Podocarpus site Most plants normally developed.

<i>Achyranthes aspera</i>	1	<i>Ehrharta erecta</i>	+	<i>Mimulopsis solmsii</i>	+
<i>Acrilochoaete volkensis</i>	2	<i>Ekebergia capensis</i>	+	<i>Olea europaea</i> spp. <i>cuspidata</i>	+
<i>Allophyllus rubifolius</i>	+	<i>Galium spurium</i> ssp. <i>africanum</i>	+	<i>Oxalis corniculata</i>	+
<i>Apodytes dimidiata</i>	+	<i>Hypoestes forskalii</i>	85	<i>Periploca linearifolia</i>	+
<i>Bersama abyssinica</i>	+	<i>Hypoestes triflora</i>	+	<i>Phaulopsis imbricata</i>	+
<i>Brachypodium flexum</i>	+	<i>Jasminum floribundum</i>	+	<i>Podocarpus falcatus</i>	+
<i>Cardamine africana</i>	+	<i>Juniperus procera</i>	+	<i>Sanicula elata</i>	+
<i>Carex chlorosaccus</i>	1	<i>Kalanchoe</i> sp.	+	<i>Senecio ochrocarpus</i>	+
<i>Carex Johnstonii</i>	+	<i>Kyllinga erecta</i>	+	<i>Smilax Krassiana</i>	+
<i>Cheilantes farinosa</i>	+	<i>Maytenus</i> sp.	+	<i>Sonchus schweinfurthii</i>	+
<i>Clematis simensis</i>	+	<i>Mikania cordata</i>	+	<i>Stephania abyssinica</i>	+
<i>Cyperus fischerianus</i>	1	<i>Mikaniopsis clematoides</i>	+		

All roots were carefully removed from these soil cores by sieving and collection with forceps. The soil was packed in nylon cloth bags with 2 mm mesh size so that the original bulk density was approximated. The bags with soil of the respective sites were fit tightly into the holes, after which their upper part was covered with litter.

For the bioassay study, soil sample (0-10 cm) covering 3 m² was collected from each of the sites in December 1990, after removal of herbs and litter. The soil was passed through a 4 mm sieve to remove stones, coarse roots and rhizomes.

2.2. Soil and plant analysis

Extractable micronutrients (Cu, Fe, Mn and Zn) were determined by the EDTA titration method (Allen, 1989). The procedures for the analyses of the other soil physical and chemical properties, fine root biomass estimation, and the biomass and nutrient contents of the aboveground herbaceous plants follow those described in chapter II.

The bags, buried for measurement of fine root growth potential, were carefully collected after one year, after roots penetrating the mesh from the outside had been cut with a knife. Their contents (i.e. roots) were immediately separated from the soil and debris by wet sieving, decantation and collection with forceps. These roots never exceeded 2 mm in diameter. The fine roots were then separated into roots of plantation trees and herbaceous plants using colour and morphological characteristics: *C. lusitanica* brown, *J. procera* reddish-brown with orange-red tips, and *P. falcatus*, beaded with numerous uniform short roots. Fine roots of *E. globulus* and the herbaceous plants were morphologically similar and could not be separated with sufficient precision. The root categories types were dried at 80 °C and weighed.

2.3. Experimental Design of the bioassay

After transportation to Copenhagen and storage for two months, the fertility of the soils collected from the four different sites were tested by using them as substrate for three plant species.

The seeds for the test were obtained from Ethiopia. The seeds of *A. abyssinica* were collected from a single mother tree close to Menagesha State Forest. They were treated with 96% H_2SO_4 for two hours before incubation. The seeds of the forage grass *C. virgata* were collected in the Mojo nursery, Shoa, whereas the seeds of the grain crop *E. tef* were obtained from the market in Mojo. The grass seeds were surface sterilized in 10% H_2O_2 for two minutes.

The soil was mixed with an inactive growth medium (expanded clay, 2-5 mm particle size) in the proportion 1:1 (v:v) in order to increase volume and aeration, and filled in 800 ml pots. Three-day-old germinating *A. abyssinica* seeds were placed in one third of the pots, with one seed in each pot. In another third of the pots 20 three-day-old seedlings of *C. virgata* were planted and in the remaining third 20 three-day-old seedlings of *E. tef*. In the first two weeks the grass seedlings failing to establish were replaced in order to maintain a plant density of 20 per pot. Each of the 12 treatments, a combination of four soils and three test plants, consisted of 9 replicates. The pots were placed in completely randomized arrangement in a greenhouse with a night temperature of 12°C and a day temperature of 19°C. The day light was supplemented with 16 hours of artificial light. The pots were watered to a field capacity every second day.

2.4. Harvest and analysis of the bioassay plants

After three months the plants were harvested. Approximately one-quarter of the root system was separated in order to estimate the total root length following Newman (1966) procedure, and weighed. The rest of the root system and shoots were dried for two days at 80°C, and weighed. The shoots were analyzed for content of nutrient elements following the methods indicated above, except that N was analyzed using the Dumas method. The total root length and the total root dry weight were calculated to represent the respective values per pot.

2.5. Computation and statistical analysis

The plant growth variables were subjected to analysis of variance (ANOVA) with SAS Proc GLM, and differences between sites or treatment means were examined with Tukey's studentized range (HSD) test used on the condition that the ANOVA F tests were significant (SAS Institute, 1988; Day & Quinn, 1989). Two way ANOVAs with forest sites and time as the main effects were conducted for the field studies, together with one way ANOVAs to reveal differences between sites for each harvest time separately. In the bioassay, soil type and bioassay species were considered as main effects in the two-way ANOVAs, and ANOVAs were further performed with each species separately in order to examine the effects of the soils in more detail.

The floristic similarity between the ground vegetation cover in the four sites was calculated with NTSYS-PC (Rohlf, 1987) using presence/absence data from Table 13. Jaccard's similarity quotient (ratio) was calculated for each pair of sites, and clustering was done with the unweighted pair-group method, arithmetic averages (UPGMA) (Dunn & Everitt, 1982; Rohlf, 1987). Other coefficients and clustering methods were used as well; these gave similar results, but UPGMA gave the best fit (co-phenetic correlation coefficient = 0.9772).

Table 14. Physical and Chemical properties of the soils of the four forest sites.

	Depth (cm)	Texture (%)			Class	Bulk density g/cm ³	PH in KCL	EC (ms cm ⁻¹)	Exchangeable cations (me 100g ⁻¹)			
		Sand	Silt	Clay					Na	K	Ca	Mg
<i>C. lusitanica</i>	0-40	4	63	33	siCL	1.188	4.91	0.229	0.669	1.04	19.26	4.97
	50-100	2	29	69	C	1.423	4.75	0.172	0.644	1.03	10.91	4.50
<i>E. globulus</i>	0-40	3	60	37	siCL	1.226	5.00	0.285	0.644	0.80	14.83	5.20
	50-100	4	41	55	C	2.194	4.97	0.139	0.666	0.90	5.87	4.85
<i>J. procera</i>	0-40	4	65	31	siCL	0.962	5.47	0.323	0.627	1.53	26.05	5.53
	50-100	7	48	45	siC	1.295	5.20	0.304	0.596	1.52	15.93	5.04
Natural forest	0-40	4	73	23	siL	0.943	5.86	0.404	0.604	1.57	25.82	6.20
	50-100	6	60	34	siCL	1.415	5.06	0.179	0.773	1.00	12.62	5.21

Table 14 (cont.)

CEC ¹ det. (me/100g)	Org. mat (OM) (%)	Total N (%)	Available P (ppm)	Extractable micronutrients (ppm)			
				Fe	Mn	Zn	Cu
33.52	6.13	0.268	2.6	15.50	44.68	1.98	1.04
26.48	1.02	0.059	0.8	5.04	9.95	0.28	0.59
23.30	5.70	0.274	4.2	22.40	64.81	2.50	0.86
11.16	0.80	0.052	2.3	3.77	9.31	0.51	0.14
49.86	6.76	0.337	17.6	18.60	61.63	8.75	0.83
38.02	1.68	0.112	6.8	9.98	30.16	0.64	0.57
45.62	6.94	0.339	6.9	16.30	63.05	13.88	0.60
39.06	0.82	0.053	4.8	5.17	6.68	1.14	0.12

¹ Cation exchange capacity, determined

The overall floristic composition of all sites had a high proportion of species native, N, P and low species diversity. Although the soil cation content and cation exchange capacity were high (Table 14). The vegetation at the natural forest site was similar to all sites, whereas the other natural forest site (20-100 m) differed from the natural forest, whereas the *C. lusitana* plantation. The floristic composition of the different sites in the red soil between sites were also found in the natural forest. The sites in *C. lusitana* and *E. globulus* plantations generally had the lowest nutrient content, Ca, and N, together with the sites in *E. globulus* and *C. lusitana* plantations. The sites in *E. globulus* and *C. lusitana* plantations generally had the lowest nutrient content, Ca, and N, together with the sites in *E. globulus* and *C. lusitana* plantations. The sites in *E. globulus* and *C. lusitana* plantations generally had the lowest nutrient content, Ca, and N, together with the sites in *E. globulus* and *C. lusitana* plantations. The sites in *E. globulus* and *C. lusitana* plantations generally had the lowest nutrient content, Ca, and N, together with the sites in *E. globulus* and *C. lusitana* plantations.

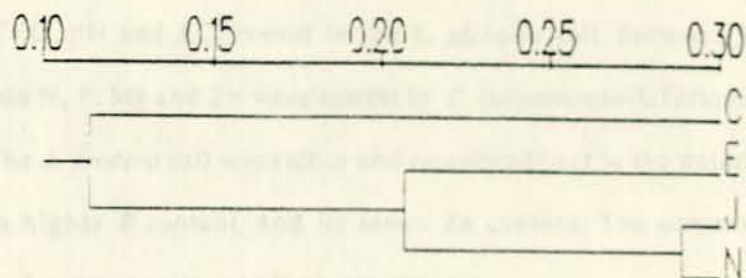


Fig. 13. Cluster analysis showing the floristic similarity of the ground cover at the four forest sites. The phenogram was calculated with the unweighted pair-group method, arithmetic averages (UPGMA) using Jacard's quotient of similarity. C: *Cupressus lusitana* plantation, E: *Eucalyptus globulus* plantation, J: *Juniperus procera* plantation, N: Natural forest.

The floristic composition of the ground cover was floristically different from that of the natural forest in the presence of *E. globulus*, *E. globulus* and *C. lusitana* (Fig. 13). The *C. lusitana* site had a higher content of herbaceous plants and significantly lower forested dry matter than the other sites (Fig. 14). Contrarily, the herbs content of the *C. lusitana* site generally had higher content of N, Ca, and Mg than other sites. These sites were generally similar with respect to nutrient content in the herbaceous plants except that N and K was less in plants from the *E. globulus* (Fig. 14). Little similarity between natural

3. Results

3.1. Field surveys

The topsoil (0-40 cm) of all sites had a low content of organic matter, N, P and low electric conductivity, whereas the cation content and cation exchange capacity were high (Table 14). The texture of the topsoil was similar in all sites, whereas the clay content in the subsoils (50-100 cm) increased from the natural forest towards the *C. lusitanica* plantation. For all other soil variables the differences existing in the top soil between sites were also found in the subsoils. The soils in *C. lusitanica* and *E. globulus* plantations generally had the lowest nutrient content. Ca, and K were, together with OM, CEC, pH and EC, lowest in the *E. globulus* soil, followed by *C. lusitanica* soil, whereas N, P, Mg and Zn were lowest in *C. lusitanica* soil, followed by the *E. globulus* soil. The *J. procera* soil was richer and resembled that in the natural forest soil, except for its higher P content, and its lower Zn content. The content of micronutrients, except Zn, was similar in all plantation soil.

The intensity of light reaching the forest floor and the species richness of forbs and graminoids were higher in the *E. globulus* plantation than in the other sites due to a less dense canopy (Table 12 and 13). The floristic composition of the ground cover was increasingly different from that of the natural forest in the sequence: *J. procera*, *E. globulus* and *C. lusitanica* (Fig. 13). The *C. lusitanica* site had a sparse cover of herbaceous plants and significantly lower harvested dry matter than the other sites (Fig. 14). Contrastingly, the herbaceous plants in the *C. lusitanica* site generally had higher content of N, Ca, and Mg than those in other sites. These sites were generally similar with respect to nutrient content in the herbaceous plants except that N and K was less in plants from the *E. globulus* site (Fig. 14). Little interaction between site and

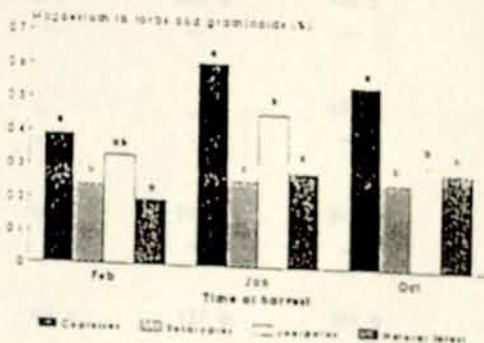
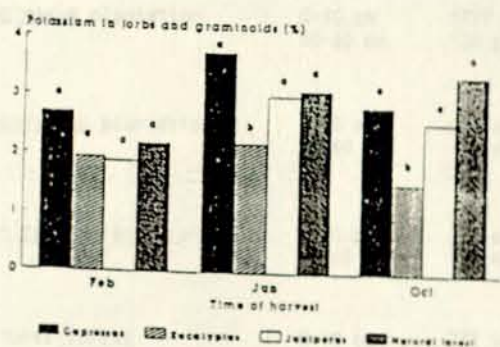
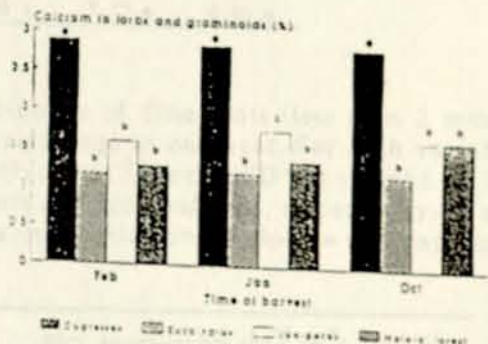
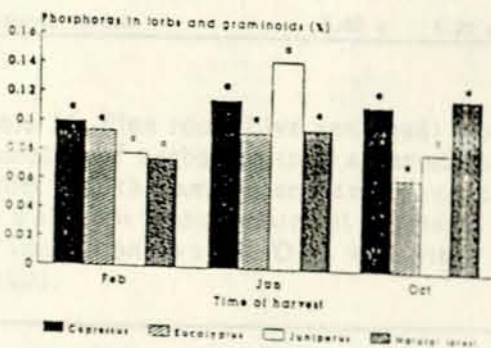
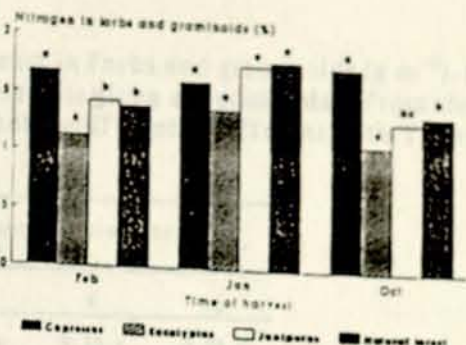
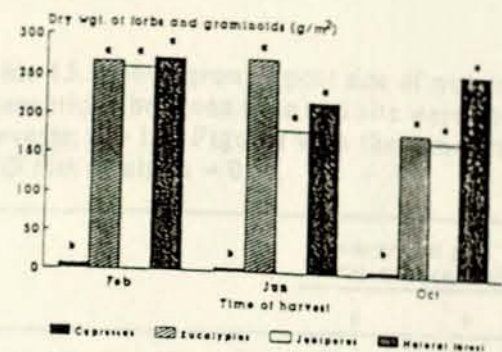


Fig. 14. Dry matter (g m^{-2}) and percentage nitrogen, phosphorus, calcium, potassium and magnesium of the above-ground parts of forbs and graminoids in four sites. Time of harvest of the 1 m^2 quadrats was February, June and October. $n = 4$ per harvest and site. For each harvest, columns with the same letter are not significantly different with Tukey's HSD test at $\alpha = 0.05$.

Table 15. Above-ground pool size of nutrient elements in forbs and graminoids (g m^{-2}). No interactions between time and site were found and results given are pooled data from three harvests; $n = 12$. Figures with the same letter are not significantly different with Tukey's HSD test at $\alpha = 0.05$.

	Above-ground pool size of nutrient elements in forbs and graminoids (g m^{-2})				
	N	P	Ca	K	Hg
<u>Cupressus</u> plantation	0.10 b	0.01 b	0.17 c	0.18 c	0.03 b
<u>Eucalyptus</u> plantation	2.92 a	0.20 a	2.71 b	4.77 b	0.57 a
<u>Juniperus</u> plantation	3.07 a	0.20 a	3.34 a	4.96 b	0.72 a
Natural forest	3.80 a	0.25 a	3.55 a	7.10 a	0.64 a

Table 16. Fine root (Live and dead) biomass, biomass of fine roots (less than 2 mm in diameter) of herbs and trees accumulated in buried bags in one year. For each variable, values with the same letter are not significantly different (Tukey's HSD test at $\alpha = 0.05$), $n = 6$ and $n = 10$ per treatment in data on root mass and accumulation, respectively. ** and *** implies one-way ANOVA with site as main factor significant at $\alpha = 0.01$ and $\alpha = 0.001$.

		Fine root mass (g m^{-2})	Root accumulation ($\text{gm}^{-2} \text{yr}^{-1}$)		
			Herbs	Trees	Total
<u>Cupressus</u> plantation	0-10 cm	1777 a	0 b	148 b	148 b
	50-60 cm	128 c	—	—	—
<u>Eucalyptus</u> plantation	0-10 cm	664 b	1	1	305 a
	50-60 cm	28 d	—	—	—
<u>Juniperus</u> plantation	0-10 cm	702 b	53 a	287 a	340 a
	50-60 cm	112 c	—	—	—
Natural forest	0-10 cm	773 b	42 a	127 b	189 b
	50-60 cm	161 c	—	—	—
ANOVA		**	**	***	***

¹ Fine roots of Eucalyptus and herbaceous plants were morphologically alike and could not be separated.

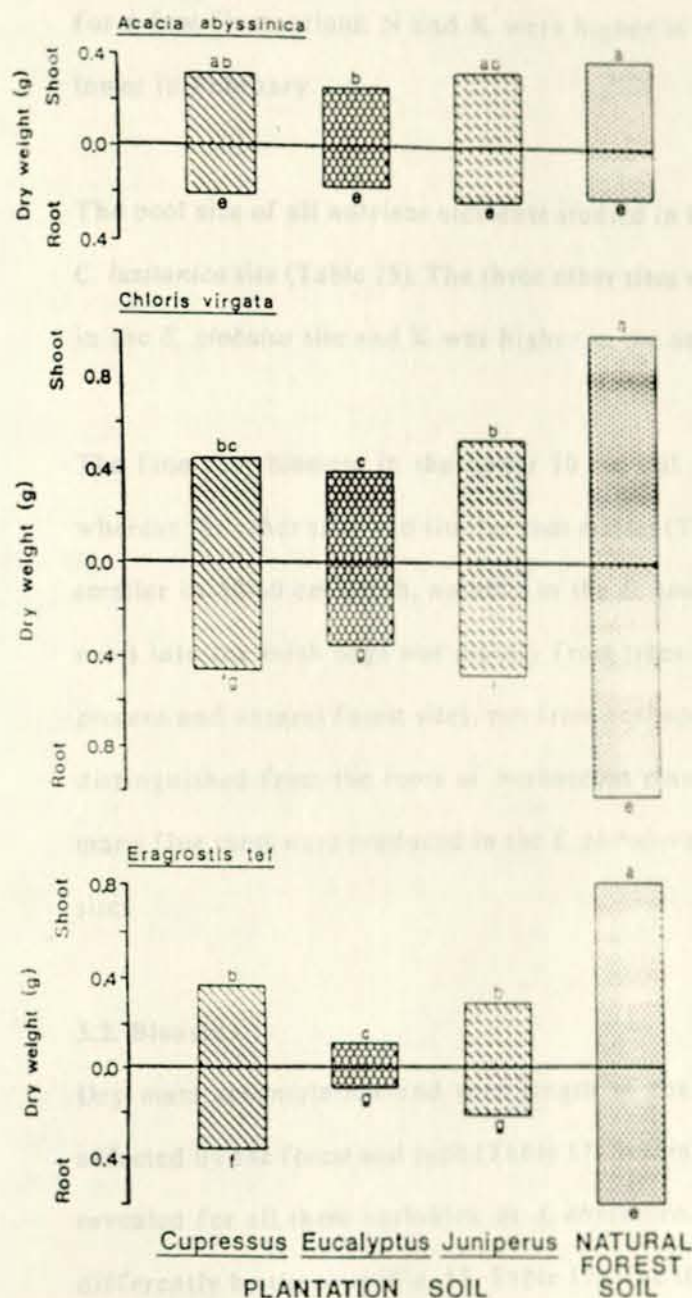


Fig. 15. Shoot and root dry weight of *Acacia abyssinica*, *Chloris virgata* and *Eragrostis tef* after three months' growth in the forest soils. Columns with the same letter are not significantly different with Tukey's HSD test at $\alpha = 0.05$, $n = 9$ per treatment.

time was revealed by two-way ANOVAs (no results presented) as little variation in dry mass and nutrient content was found between the different times of harvest, except for a few fluctuations: N and K were higher in June, and Mg and K contents were lower in February.

The pool size of all nutrient elements studied in herbaceous plants was smaller in the *C. lusitanica* site (Table 15). The three other sites were equal, except that Ca was lower in the *E. globulus* site and K was higher in the natural forest.

The fine root biomass in the upper 10 cm soil was highest in the *C. lusitanica* site, whereas the other sites had similar root masses (Table 16). The root masses were much smaller in 50-60 cm depth, notably in the *E. globulus* site. The ingrowth of the fine roots into the mesh bags was mainly from trees in plantation of the *C. lusitanica*, *J. procera* and natural forest sites, not from herbaceous plants (tree roots would not be distinguished from the roots of herbaceous plants in the *E. globulus* site). Twice as many fine roots were produced in the *E. globulus* and the *J. procera* sites as in the other sites.

3.2. Bioassay

Dry mass accumulation and root length of the bioassay plants were significantly affected by the forest soil type (Table 17). Interactions between soil and species were revealed for all these variables, as *A. abyssinica*, *C. virgata* and *E. tef* were affected differently by the soils (Fig. 15, Table 17). The shoot dry weight was higher in plants grown in the natural forest soil than in the plantation soils, with the exception of *A. abyssinica* dry weight, which was similar in the natural forest soil and in *C. lusitanica* and *J. procera* soils. The shoot dry weight was lower in *E. globulus* soil than all other soils, except for *C. virgata* in *C. lusitanica* soil and *A. abyssinica* in *C. lusitanica* and *J. procera* soil. The growth pattern was similar in *C. lusitanica* and *J. procera* soil, except

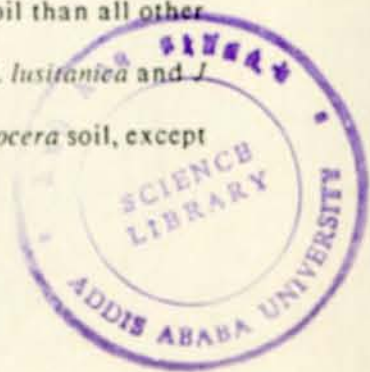


Table 17. Growth characteristics of *Acacia abyssinica*, *Chloris virgata* and *Eragrostis tef* after three months in the four forest soils. Values with the same Letter are not significantly different with Tukey's HSD test at alpha = 0.05 n = 9 per treatment. In the two-way ANOVA, site and bioassay species were main factors; *, ** and *** implies factors significant at alpha = 0.05, 0.01 and 0.001, respectively.

	Total dry weight (g)	Root / shoot ratio	Root Length (cm)	Specific root Length (m/g)
ANOVA				
Soil	***	*	***	***
Bioassay species	***	***	***	***
Soil * species	***	**	***	***
<u>A. abyssinica</u>				
<u>Cupressus</u> soil	0.52 a	0.67 a	692 a	33.55 a
<u>Eucalyptus</u> soil	0.44 a	0.68 a	481 a	30.72 a
<u>Juniperus</u> soil	0.56 a	0.72 a	670 a	29.22 a
Natural forest soil	0.60 a	0.53 b	700 a	35.44 a
<u>C. virgata</u>				
<u>Cupressus</u> soil	0.91 b	1.03 a	6185 c	134.90 c
<u>Eucalyptus</u> soil	0.74 c	0.91 a	6187 c	178.66 bc
<u>Juniperus</u> soil	1.01 b	0.93 a	13106 b	265.71 a
Natural forest soil	2.01 a	1.03 a	21921 a	217.06 ab
<u>E. tef</u>				
<u>Cupressus</u> soil	0.73 b	0.97 a	8257 b	234.41 b
<u>Eucalyptus</u> soil	0.20 c	0.78 ab	2333 c	234.10 b
<u>Juniperus</u> soil	0.51 b	0.74 b	7919 b	340.61 b
Natural forest soil	1.41 a	0.72 b	28530 a	497.66 a

Table 18. Concentration of nutrient elements in *Acacia abyssinica*, *Chloris virgata* and *Eragrostis tef* after three months in the four Ethiopian forest soils. Values with the same letter are not significantly different with Tukey's HSD test at alpha = 0.05 n = 9 per treatment, except for the grasses where n = 5. In the two-way ANOVA, site and bioassay species were main factors; *, ** and *** implies factors significant at alpha = 0.05, 0.01 and 0.001; ns = non significant.

	N conc. (%)		P conc. (%)		Ca conc. (%)		K conc. (%)		Mg conc. (%)	
	Shoot	Root	Shoot	Root	Shoot	Root	Shoot	Root	Shoot	Root
ANOVA										
Soil	***	***	***	ns	ns	ns	**	ns	***	ns
Bioassay species	***	***	***	***	***	ns	*	***	***	***
Soil * Species	***	***	ns	ns	**	*	***	ns	ns	ns
<i>A. abyssinica</i>										
<i>Cupressus</i> soil	3.99 a	2.37 a	0.22 a	0.17 a	1.06 a	0.82 a	1.49 a	1.49 a	0.21 a	0.34 a
<i>Eucalyptus</i> soil	4.26 a	2.74 a	0.23 a	0.17 a	0.92 a	0.88 a	1.74 a	1.53 a	0.22 a	0.35 a
<i>Juniperus</i> soil	4.06 a	2.39 a	0.26 a	0.18 a	1.12 a	0.93 a	1.46 a	1.52 a	0.22 a	0.38 a
Natural forest soil	4.78 a	2.74 a	0.22 a	0.18 a	0.94 a	0.96 a	1.50 a	1.48 a	0.18 a	0.41 a
<i>C. virgata</i>										
<i>Cupressus</i> soil	1.84 bc	1.34 b	0.15 a	0.15 a	0.60 a	0.98 a	1.45 b	1.34 a	0.29 b	0.14 b
<i>Eucalyptus</i> soil	2.92 a	1.89 a	0.15 a	0.15 a	0.66 a	0.91 a	1.46 b	1.33 a	0.38 a	0.21 a
<i>Juniperus</i> soil	1.65 c	1.35 b	0.17 a	0.15 a	0.67 a	0.78 b	1.48 b	1.38 a	0.30 b	0.14 b
Natural forest soil	2.04 b	1.38 b	0.12 b	0.14 a	0.61 a	0.93 a	2.04 a	1.34 a	0.26 b	0.16 b
<i>E. tef</i>										
<i>Cupressus</i> soil	2.49 b	1.58 b	0.16 a	0.17 a	0.87 a	1.35 a	1.73 b	1.39 a	0.30 b	0.22 a
<i>Eucalyptus</i> soil	4.47 a	3.13 a	0.20 a	0.16 a	0.81 ab	0.79 a	1.59 b	1.45 a	0.37 a	0.20 a
<i>Juniperus</i> soil	3.01 b	1.88 b	0.19 a	0.17 a	0.62 c	0.95 a	2.01 a	1.58 a	0.30 b	0.23 a
Natural forest soil	2.77 b	1.97 b	0.11 b	0.12 a	0.64 bc	0.89 a	1.80 ab	1.41 a	0.23 c	0.20 a

Table 19. Total nutrient element uptake (mg) of *Acacia abyssinica*, *Chloris virgata* and *Eragrostis tef* after three months in the four forest soils, and two-way ANOVA with site and bioassay species as main factors. *, ** and *** imply factors significant at alpha = 0.05, 0.01 and 0.001; ns = non significant. Different letters imply significant differences between treatments with Tukey's HSD test at alpha = 0.05. n = 9 per treatment, except for the grasses where n = 5.

	Total nutrient element uptake (mg)				
	N	P	Ca	K	Mg
ANOVA					
Soil	***	***	***	***	***
Bioassay species	**	***	***	***	***
Soil * Species	***	***	***	***	***
<i>A. abyssinica</i>					
Cupressus soil	17.77a	1.11ab	5.59a	8.55a	1.51a
Eucalyptus soil	16.36a	0.81b	3.69a	6.71a	1.06a
Juniperus soil	19.28a	1.21ab	5.66a	8.14a	1.48a
Natural forest soil	23.10a	1.27a	5.81a	9.12a	1.59a
<i>C. virgata</i>					
Cupressus soil	14.27c	1.33bc	7.17b	12.60bc	1.96b
Eucalyptus soil	17.82b	1.12c	5.78c	10.40c	2.21b
Juniperus soil	15.20c	1.58b	7.34b	14.47b	2.26b
Natural forest soil	134.33a	2.63a	15.44a	33.96a	4.26a
<i>E. tef</i>					
Cupressus soil	14.37b	1.20b	8.06a	11.62b	1.93b
Eucalyptus soil	5.17c	0.44c	1.95b	3.74c	0.73c
Juniperus soil	14.47b	0.74bc	3.02b	7.36c	1.10bc
Natural forest soil	133.76a	1.69a	10.81a	23.67a	3.17a

for a smaller root weight of *E. tef* in *J. procera* soil. In *C. virgata* the root to shoot ratios were similar for all soils, whereas that of *A. abyssinica* was smaller in the natural forest soil. The root length and dry weight generally followed the same trend in *A. abyssinica*, and no differences in the specific root length (SRL) were recorded. The SRL of *C. virgata* was higher in the *J. procera* and the natural forest soils than in the soil of the two exotics, whereas the SRL of *E. tef* was higher in the natural forest soil.

The two-way ANOVAs revealed significant effects of both soil and bioassay species on the concentrations of most nutrient elements in shoots, as well as interactions between species and soil (Table 18). Soil as a factor did not affect concentrations in roots, with the exception of N. In shoots, N and Mg concentrations were generally higher in plants grown in *E. globulus* soil than in soils of the other sites, whereas K was higher in the natural forest soil.

The total uptake of nutrient elements in grasses grown in soil of the natural forest was higher than in soils of the other sites, whereas grasses from the *E. globulus* plantation generally had the lowest uptake of P, Ca and K (Table 19). Also with respect to nutrient uptake, *A. abyssinica* was not sensitive to the origin of the soil.

4. Discussion

4.1. Physical and chemical soil properties

Generally, N, P, organic matter and electric conductivity in the four forest soils were medium-low, whereas cations were relatively high. However, differences in soil nutrient content between sites were found, although the sites formerly were covered by the same type of natural forest (von Breitenbach, 1961; Friis, 1992). The soils of the *C. lusitanica* and *E. globulus* sites generally had the lowest nutrient content, whereas the soil properties of *J. procera* site resembled those of the natural forest.

The study cannot exclude the possibility that variability in soil properties prior to

plantation establishment in the natural forest could have contributed to these differences. Furthermore, they could be due to differences in management and productivity. When the natural forest was cleared for plantation establishment, nutrient elements were removed with the original vegetation. After planting, immobilization of nutrient elements into the tree standing crop may have taken place. Export of nutrients with trees following logging (in the *E. globulus* site) and collection of branches and leaf litter (in the *C. lusitanica* and *E. globulus* sites) in the past may also have contributed to the reduced soil nutrient content in those sites; no significant logging or branch collection had occurred in the *J. procera* and natural forest sites. These conditions should be kept in mind when plant performance in the forest sites and their respective soils are analyzed.

4.2. Fine root biomass and accumulation

The fine root biomass of the upper 10 cm soil was similar to, or higher than previously reported from montane forests (Lundgren, 1978; Cavalier, 1992; Vance & Nadkarni, 1992). High live biomass of fine roots is interpreted as a response to low nutrient availability in soil (Cavalier, 1992). The very high biomass in the *C. lusitanica* site was, however, rather due to a large component of dead roots. This could be a result of a relatively low decomposition rate, as was the case with leaf litter of *C. lusitanica* (Lisanework & Michelsen, 1993b). The fine root biomass at 50-60 cm depth, however, was 7%, 4%, 16% and 21% of the 0-10 cm layer in the sites of *C. lusitanica*, *E. globulus*, *J. procera* and in the natural forest, respectively; indigenous trees thus seem to draw more resources from the subsoil than *C. lusitanica* and *E. globulus*.

Few accounts on fine root accumulation obtained by growth into buried bags are available for tropical forests, and results furthermore vary according to the methods used (Jordan & Escalante, 1980; Kummerow *et al.*, 1990; Sanford, 1990). The estimates in the present study are considerably higher than those of Sanford (1990) and similar

to those of Cuevas and Medina (1988), both for wet Amazonian forests, and similar to that of Kummerow *et al.* (1990) for a dry Mexican forest. Low nutrient availability in soil often correlates with high fine root production (Vogt *et al.*, 1986). *J. procera*, however, had the highest productivity of fine roots in the topsoil and a relatively high soil nutrient content. Species-specific differences in the pattern of fine root production between topsoil and subsoil are probably overlaying the effect of differences in soil nutrient content.

Fine roots constitute a considerable part of tree productivity: the mass ratio of tree fine roots accumulated in one year in the top 10 cm soil (Table 16) to the annual litter production (data from Lisanework and Michelsen (1993b)) was 0.30, 0.52 (including herb roots), 0.44 and 0.12 in the plantation of *C. lusitanica*, *E. globulus*, *J. procera* and in the natural forest sites, respectively. For the natural forest this is a low fine root to leaf production ratio compared to that reported in Kummerow *et al.* (1990), i.e. 0.62-1.07. In contrast to the present study, their data included the root productivity in deeper soil layers. In the natural forest of this study, root productivity could probably be high in subsoil, judging from the large fine root biomass estimated in the subsoil.

Assuming steady state of fine root biomass, i.e. that root accumulation is the same as root death and decay in sites, the fine root turnover time was 12.0 years, 2.2 years, 2.1 years and 4.1 years in the *C. lusitanica*, *E. globulus*, *J. procera* and natural forest, respectively. This is a rather long turnover time compared to the turnover of fine roots in other (temperate) forests (Vogt *et al.*, 1986), where turnover time ranged between 0.3 and 1.3 years. Since the estimates of fine root biomass in this study included dead roots, the turn over time appeared to be overestimated to an unknown degree, especially in the *C. lusitanica* plantation.

4.3. Herbaceous biomass in the sites

The *J. procera* site showed the closest similarity to the natural forest in the floristic composition of its ground cover (Fig. 13). The *C. lusitânica* plantation differed most strongly from the natural forest in this respect, and also had the lowest herbaceous cover and biomass. This can partly be ascribed to the reduced light intensity, a general phenomenon in *C. lusitânica* plantations. The *J. procera* site, however, had an equivalent light intensity at the forest floor. This suggests that factors in soil or litter, together with highly competitive tree roots, also influenced the herbs in the *C. lusitânica* plantation.

Although the soil of the *C. lusitânica* site was relatively poor in nutrient content, it was similar to that of the *E. globulus* site, in which the herbaceous standing crop and cover was high. The latter observation is in contrast to many reports on poor herbaceous cover in eucalypt forests in the tropics (Poore & Fries, 1985). This discrepancy could be the result of coppicing, leading to higher light intensity at the forest floor. Also, the results obtained in drier regions (Poore & Fries, 1985) may not apply to areas of higher rainfall where leaching and/or dilution of potentially allelopathic substances is more likely to occur. Finally, the dominant herbs in the *E. globulus* plantation may tolerate allelochemicals; plants differ in their tolerance to these substances (Lisanework & Michelsen, 1993a).

The differences among sites in nutrient concentration in the herbaceous biomass (Fig. 14), i.e. the higher N, Ca, and Mg concentration in herbs of *C. lusitânica* site and the lower N and K in herbs in the *E. globulus* site, were nearly consistent throughout the year. This could be due to the fact that the forbs and graminoids generally were growing the whole year, but with a reduced rate in the drier period. Exceptions were the bulbiferous plants as *Scadoxus multiflorus* (Martyn) Raf. and various short-lived annuals, but these did not have a large cover or biomass. The differences between sites

in nutrient concentration in the herbaceous biomass are probably largely caused by wide between-site differences in species composition of the ground cover.

The herbaceous plants contained an important part of the nutrient pool of the forest in all sites except in the *C. lusitanica* plantation (Table 15). Data on nutrient element pool size of the tree component in the system are not available, but a comparison of nutrient input due to litterfall and the amount of nutrients in herbaceous plants may be informative: annual input of N and P with fine litter (Lisanework & Michelsen, 1993b) was 60-70% of the pool sizes of N and P in aboveground herbaceous plant parts in *E. globulus* site, whereas the input was 2-3 times larger than the pools in the *J. procera* and in the natural forest sites. This supports the conclusion of Lisanework & Michelsen (1993b) that within-stand nutrient cycling in the *J. procera* plantation and in the natural forest is less tight than in the two sites with exotic species.

4.4. Bioassay

The soil type did not affect growth (Fig. 15, Table 17) or nutrient uptake (Table 19 and 20) of *A. abyssinica*. This tolerance to a range of soils is in accordance with its very wide distribution in Ethiopia (Friis, 1992). Therefore, if indigenous tree species are to be introduced, next to *J. procera* with its highest rate of spontaneous appearance, in old *E. globulus* plantations (Tewoldeberhan, 1974; Pohjonen & Pukkala, 1990; 1992), *A. abyssinica* seems to be a good choice, provided that the saplings would react in the same manner as the seedlings did in this study. Moreover, the planting of *A. abyssinica* seedlings in old plantations may be recommended due to their ability to improve soil N through N_2 -fixation.

The grasses, particularly *E. tef*, were very responsive to the origin of the soil (Fig. 15). Their growth was reduced in all plantation soils in comparison to that of the natural forest, seven-fold in the case of *E. tef* in the *E. globulus* soil. This indicates that establishment and management of the three plantations species affected soil fertility,

if the assumption is that the soil properties of the sites were similar before the plantation stands replaced the natural forest. The negative effect on growth was most severe in soil of the *E. globulus* site, but also striking for plants grown in *C. lusitanica* and *J. procera* soil. Former plantations, at least those of *E. globulus*, may not be useful areas for cereal crops or pastures.

The nutrient analysis of the bioassay plants gave some indications of the element(s) which potentially limited plant growth in the plantation soils. N and Mg are not among these, as their concentrations were higher in shoots of *C. virgata* and *E. tef* in the *E. globulus* soil. This is probably a reflection of the poor growth of the plants in that soil, resulting in luxury consumption of N and Mg when another factor was limiting growth. The factor could possibly be K. The K concentration in *C. virgata* shoots was 40% higher in the natural forest soil than in those grown in plantation soils, in spite of the biomass being twice as large. The total K uptake was, consequently, three times higher. However, this effect was not equally clear with *E. tef*.

The pH was lowest in the *C. lusitanica* and *E. globulus* soils, perhaps due to acidic substances in decomposing plant material. These may include allelochemicals which reduce the germination and growth of forage grasses and crops (Singh *et al.*, 1989; Lisanework & Michelsen, 1993a). The presence of such substances in the soil from *C. lusitanica* and *E. globulus* plantations could in part explain the retarded growth of grasses in the bioassay. Also, the lower pH in these soils may affect the availability of nutrients for plant growth. *E. tef* is very sensitive to soil acidity (Tekalign & Killham, 1987).

The stem volumes per unit area of the plantation trees were within the limits found for Ethiopian plantations of the same age and species (Pohjonen and Pukkala, 1990, 1992). The results of the study revealed that the diversity of the ground cover was

high in all sites, but the biomass and cover of forbs and graminoids were strikingly poor in the *C. lusitanica* sites, whereas it was high in the *E. globulus* and *J. procera* plantations and in the natural forest. The *C. lusitanica* and *E. globulus* sites had lower soil nutrient element content than the *J. procera* and the natural forest sites.

The interpretation of the results on nutrient element concentration and pool sizes in the herbaceous plants was hampered by between-site differences in species composition and abiotic conditions, e.g. light intensity at the forest floor. In the bioassay, however, the growth of the grasses *C. virgata* and *E. tef* was reduced in soil of all plantations compared with the natural, most strongly in *E. globulus* soil. No single soil factor could be identified as being the one responsible for the growth reduction; it was probably due to a combination of soil factors. Owing to the differences between the results obtained in the survey and the bioassay, it seems that the practice of productivity studies of herbaceous vegetation in the field combined with soil analyses only may lead to erroneous conclusions concerning the potential productivity of soils. The present results, therefore, suggest that field studies should be combined with bioassays in the surveys of the fertility of soils after plantation establishment.

Furthermore, the study indicates that establishment and management of the three plantation species affected soil fertility differently, if we assume that the soil properties of the sites were similar before the plantation stands replaced the natural forest. The poor growth of teff in soil from the *E. globulus* plantation has implications for future land use in Ethiopia, considering that they are respectively the most widely planted crop and tree in the country.

Summary

The soil physical and chemical characteristics, above ground herbaceous biomass and nutrient content, fine root biomass and productivity were studied in a natural montane forest and in adjacent 28-48 year old plantations of the exotic species *C. lusitana* and *E. globulus* and the indigenous *Juniperus procera*. The field studies were combined with bioassays of growth and nutrient uptake of *A. abyssinica*, *C. virgata*, and *E. tef* in soils taken from each site.

The *C. lusitana* and *E. globulus* soils had lower nutrient content than those of *J. procera* and the natural forest. The number of forbs and graminoids was high in all sites, but their biomass and cover were poor in the *C. lusitana* site. The production of fine roots in top soil was twice as large in *E. globulus* and *J. procera* sites than in other sites, whereas the standing crop of fine roots was higher in *C. lusitana* site. In the bioassay, growth of *C. virgata* and *E. tef* was reduced in the soils of all plantations, most strongly in *E. globulus* soil, compared to their growth in soil of the natural forest.

Nutrient concentration and pool sizes in herbaceous plants varied strongly between sites because of differences in species composition and herbaceous standing crop. Owing to the difference between herbaceous biomass harvested in the forest and biomass accumulation in the bioassay it is suggested that vegetation and soil analyses are combined with bioassays in the surveys of the fertility of soils after plantation establishment. The negative effect of *E. globulus* on growth of *E. tef* in the bioassay should be considered when plans for future land use in Ethiopia are elaborated as respectively these are the most widely planted tree and cultivated crop species here.

CHAPTER V

THE ALLELOPATHIC POTENTIALS OF *Cupressus lusitanica* AND THREE *Eucalyptus spp.* ON FOUR ETHIOPIAN CROPS

1. Introduction

The establishment of plantation forests and agroforestry systems in developing countries plays an important role in the restoration of the vegetation cover, and helps to meet the increasing demands for fuelwood and other wood products due to population growth. In Ethiopia long lasting deforestation has exposed large areas to serious erosion and created chronic shortage of wood for energy and timber. Large scale plantations as well as shelterbelts around cultivated fields and woodlots in peasants' homesteads have been established with fast growing exotic tree species, mainly *Eucalyptus*, *C. lusitanica* and *Pinus* species. Eucalypts are very common along field bunds, and *E. globulus* alone covers more than 100,000 ha of plantation forest (Poschen-Eiche, 1987; Pohjonen & Pukkala, 1990).

Exotic tree species have been introduced into Ethiopia without due consideration to their long-term effects on the environment. Elsewhere, eucalypts are claimed to suppress forbs and graminoids in plantations and crops adjoining shelterbelts (del Moral & Muller, 1970; Bahaskar & Dasappa, 1986), and consequently reduce the farmers' benefit from planting eucalypts (Saxena, 1991). Apart from their competitive effects on water and nutrient uptake (Florence, 1986; Malik & Sharma, 1990); eucalypts are alleged to reduce both the diversity and abundance of forbs and graminoids, and the productivity of adjoining crops through release of chemical substances - allelochemicals (Poore & Fries, 1985; May & Ash, 1990). Similar suppressive effects have been reported for indigenous trees used in agroforestry systems in the Himalayas (Bhatt & Todaria, 1990), and for conifers (del Moral & Cates,

1971; Harborne, 1988). Ultimately, this phenomenon may lead to exposure of the soil to erosion. Evaluation of the allelopathic potential may, therefore, be important for the assessment of the ecological impact of exotic tree species. The information is useful for species selection and plantation management, especially if the aim of tree planting is to implement an integrated land use. However, no such investigations have been undertaken in Ethiopia.

The present investigation was conducted in order to reveal whether aqueous extracts of leaves of *C. lusitanica*, *E. globulus* ssp. *globulus*, *E. camaldulensis* or *E. saligna* influence the germination and growth of four crops: *Cicer arietinum* L. (Chickpea), *Zea mays* L. (maize), *Pisum sativum* L. (pea) and *E. tef* (teff). The test species were selected due to their importance in crop production in Ethiopia and their ability to germinate rapidly.

2. Materials and methods

2.1. Preparation of aqueous extracts

Fresh leaves from several mature stands of *C. lusitanica*, *E. globulus*, *E. camaldulensis* and *E. saligna* were collected in various regions of Ethiopia, air dried and mixed. At the Institute of Plant Ecology, University of Copenhagen, the leaves were ground in a Tecator Cyclotec 1093 Sample Mill. Aqueous extracts were obtained using the extraction procedures of Stowe (1979). The extracts were prepared with distilled water and shaken for four hours. Following extraction, the solution was filtered through double layers of cheese cloth and filter paper and kept at 4°C until application. The leaf extracts from each species were prepared at 0%, 1%, 2.5%, 5% and 10% concentrations. All extracts were used for the germination bioassay, whereas concentrations of 0%, 1%, 2.5% and 5% were applied in the plant growth experiment. The osmotic effect of aqueous extracts of leaves may be capable of severe inhibition of germination and growth (Bell, 1974), and the osmotic potential of the extracts was,

Table 20. Osmotic potential of the aqueous leaf extracts (in per cent).

	Osmotic potential of leaf extracts (kPa)			
	1%	2.5%	5%	10%
<i>C. lusitanica</i>	-15	-40	-84	-140
<i>E. camaldulensis</i>	-10	-30	-50	-103
<i>E. globulus</i>	-10	-20	-48	-90
<i>E. saligna</i>	-17	-35	-63	-133

extract (-140 kPa) and compared to their germination in distilled water. The germination of the seeds in the extracts was generally lower than in distilled water. In the experiment, based on the results, it was concluded that the osmotic potential of the extracts of *E. globulus* and *E. saligna* was lower than that of the control. The osmotic potential of the extracts of *C. lusitanica* and *E. camaldulensis* was also lower than that of the control.

2.2. Germination bioassay

Seeds of Chickpea, maize, pea, red clover, vetch, alfalfa, lucerne, lupine, the groundnut, Leathers and Embellig (1961). The 100 mg seeds of each species were treated with extracts of 1%, 2.5%, 5%, and 10% and compared to the control. The seeds were sown in two rows of three seeds each in Petri-dishes. There were five replicates per treatment for each species. The Petri-dishes were incubated at 20°C in darkness in sealed bags. Seed germination and radicle length were recorded 48 h after the germination, which occurred after 24 h for alfalfa, and after three days for other crop seeds.

2.3. Growth experiment

500 ml pots were filled with expanded clay granules size 7-8 mm previously thoroughly with distilled water. Three pre-germinated seeds of chickpea, one

therefore, determined with a freezing-point osmometer, Gonotec Osmomat 030-D. The 10% extracts had potentials between -90 and -140 kPa (Table 20). According to del Moral and Cates (1971) and del Moral *et al.* (1978), this is generally not inhibitory to germination and radicle growth, although it may be in some cases (Stowe, 1979; Wardle *et al.*, 1992). In order to test if this could be the case with the prepared extracts, seeds of chickpea, maize, pea, and teff were germinated on Petri-dishes with a solution of mannitol (Bell, 1974) of an osmotic potential equivalent to the most concentrated extract (-140 kPa) and compared to their germination in distilled water. Neither the germination of the seeds nor the radicle length were affected by mannitol in this pilot experiment. Based on this, it was considered that any inhibition observed in germination and growth experiments would chiefly be due to allelopathic substances present in the extracts, and that distilled water could be used for the control treatments.

2.2. Germination bioassay

Seeds of Chickpea, maize, pea and teff were germinated following the procedure of Leather and Einhellig (1986). The filter paper was moistened with 5 ml of the aqueous extracts of 1%, 2.5%, 5%, and 10%, and distilled water in case of the control. Twenty seeds were spread out on two sheets of filter paper placed in Petri-dishes. There were five replicate Petri-dishes for each type of extract, concentration and recipient species. The Petri-dishes were randomized and incubated at 20°C in darkness in sealed plastic bags. Seed germination and radicle length were recorded 48 h after the onset of germination, which occurred after two days for teff, and after three days for the other crop seeds.

2.3. Growth experiment

800 ml pots were filled with expanded clay (particle size 2-5 mm) previously washed thoroughly with distilled water. Three pre-germinated seeds of chickpea, maize and

pea, were planted and 0.25 g of teff seeds were sown per pot. The pots were kept for ten weeks in a greenhouse with a 12 hours day-length and day and night temperatures of 24 and 18°C, respectively. There were five replicates for each treatment, and the pots were completely randomized. The pots were watered daily with a solution of 1 part nutrient solution to 5 parts aqueous extracts (0%, 1%, 2.5%, and 5%) (Abdul-Wahab & Rice, 1967; Rice 1972). The nutrient solution had the following properties: 6.5 pH, 1.76 EC mS cm⁻¹, 3.0 ppm P, 181 ppm NO₃-N, 257 ppm K, 32.6 ppm Mg, 139 ppm Ca. At harvest the oven-dry weights of shoots and roots of each pot were determined.

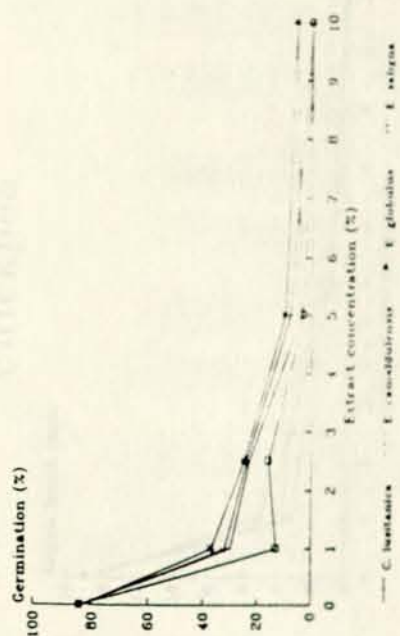
2.4. Statistical analysis

Seed germination, radicle length and dry weights of shoots and roots were, based on the condition of significant ANOVA's, tested by means of multiple comparison SNK tests with P= 0.05 (Day and Quinn, 1989) in order to investigate if significant differences existed among treatments. Analysis of data expressed as percentages was performed after square root-arc sine transformation (Sokal & Rohlf, 1981).

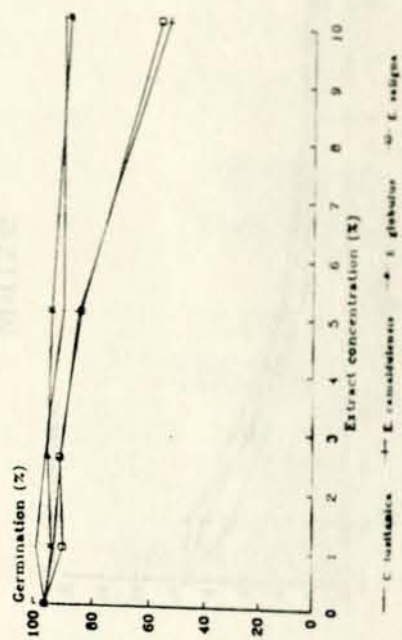
3. Results

The aqueous extracts of leaves of all the tested tree species, *C. lusitanica*, *E. camaldulensis*, *E. globulus* and *E. saligna*, significantly reduced both germination and radicle elongation of the majority of the crops, mostly starting from concentrations of 1% or 2.5% (Figs. 16 and 17). Chickpea was affected most strongly, with reduction of germination and radicle elongation by all 1% extracts. Teff germination was inhibited at 5%, whereas radicle elongation was affected at 1%. Pea germination was suppressed at 10%, 2.5%, 2.5%, and 2.5%, and radicle elongation at 5%, 1%, 1% and 2.5% for *C. lusitanica*, *E. globulus*, *E. camaldulensis* and *E. saligna* extracts, respectively. Seeds of maize showed no reduction in germination except with the 10% extracts of

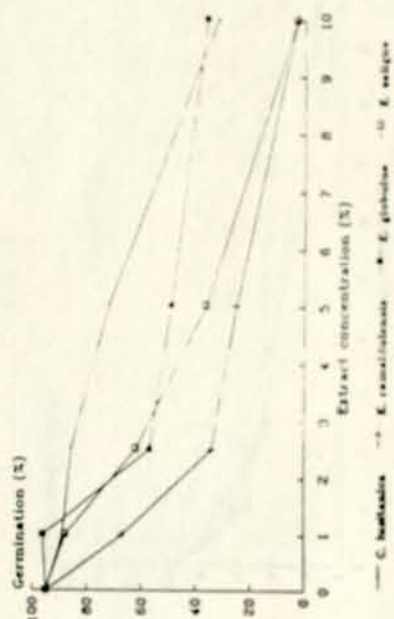
Chickpea



Maize



Pea



Teff

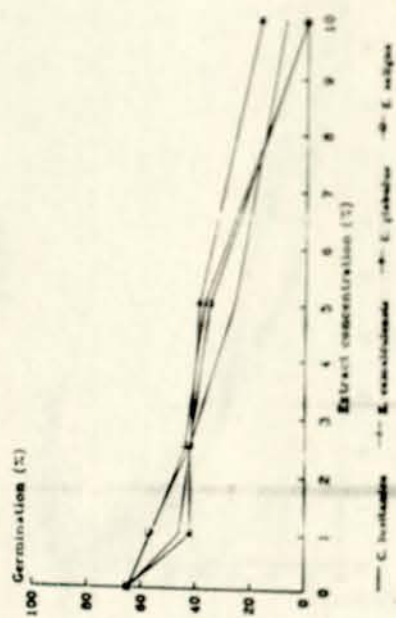
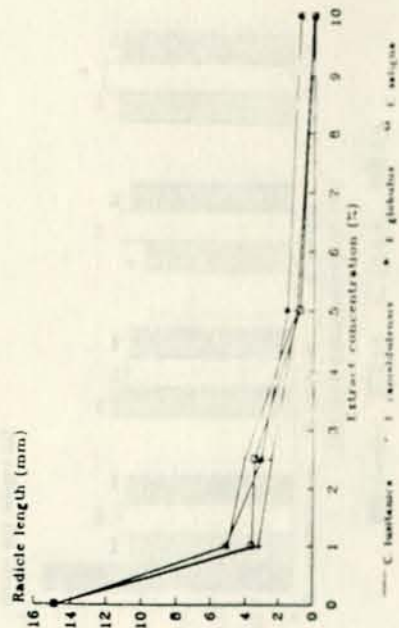
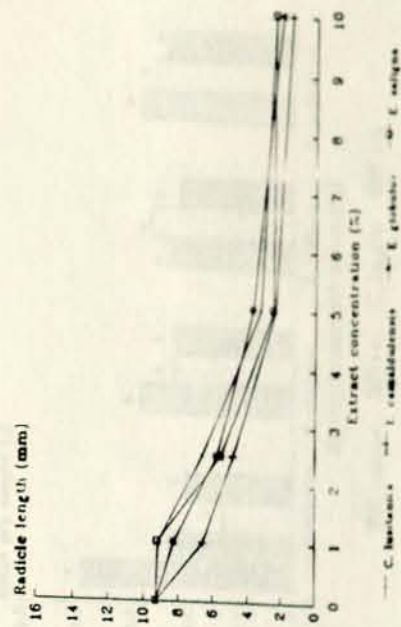


Fig. 16. The effects of aqueous extracts of leaves of *C. latifolia*, *E. globulus*, *E. camaldulensis* and *E. saligna* on the seed germination of four crops, N=5 per extract type and concentration. Results of the statistical analyses are not presented. The most important significant differences are mentioned in the results.

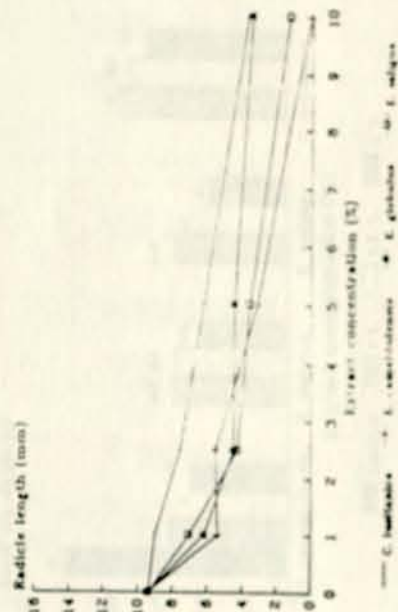
Chickpea



Maize



Pea



Teff

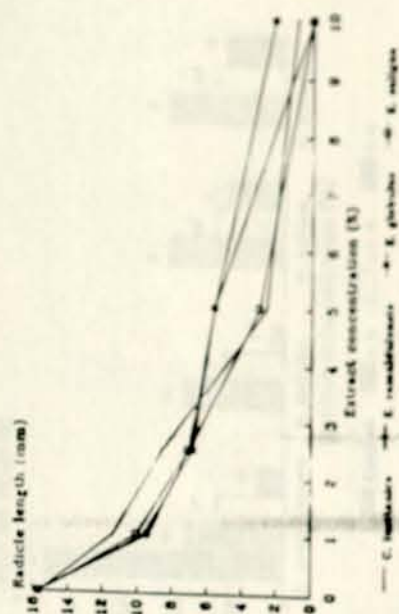
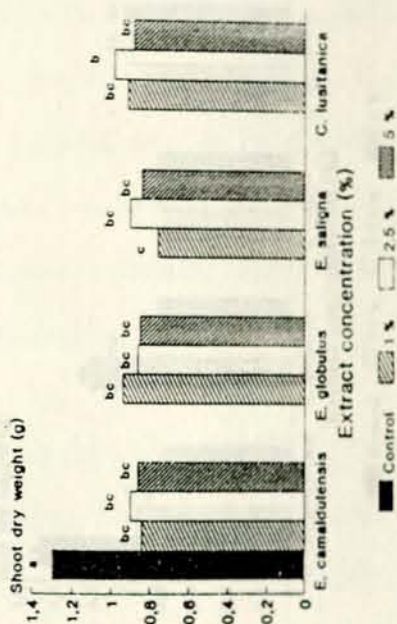
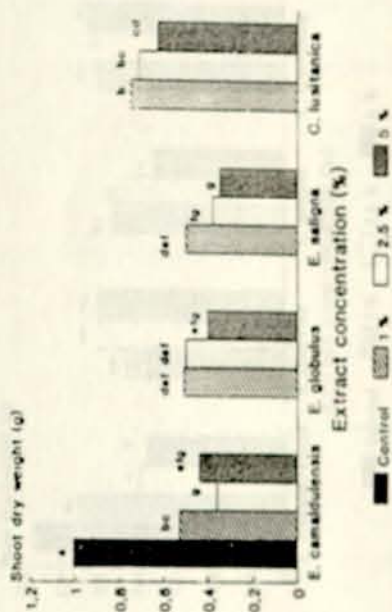


Fig. 17. The effects of aqueous extracts of leaves of *C. lusitanica*, *E. globulus*, *E. camaldulensis* and *E. saligna* on the radicle growth of four crops, N=5 per extract type and concentration. Results of the statistical analyses are not presented. The most important significant differences are mentioned in the results.

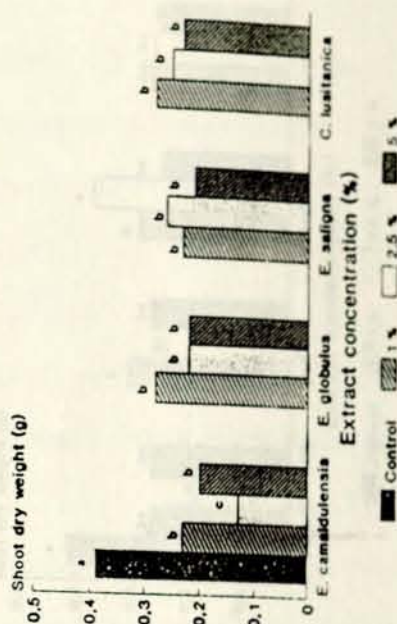
Chickpea



Pea



Maize



Teff

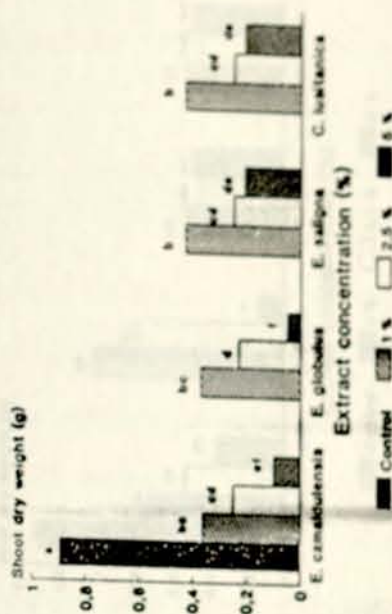
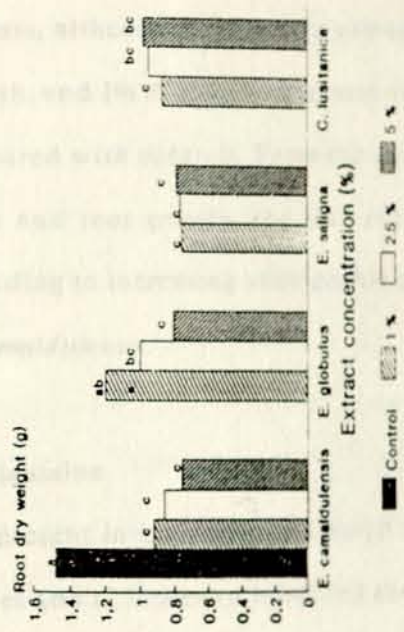
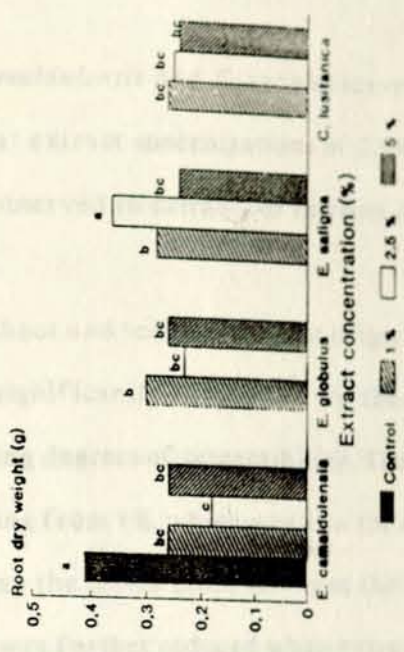


Fig. 18. The effects of aqueous extracts of *C. lusitânica*, *E. globulus*, *E. camaldulensis* and *E. saligna* on the shoot dry weight of four crops after ten weeks. Bars with the same letter are not significantly different at $p = 0.05$ (SNK test).

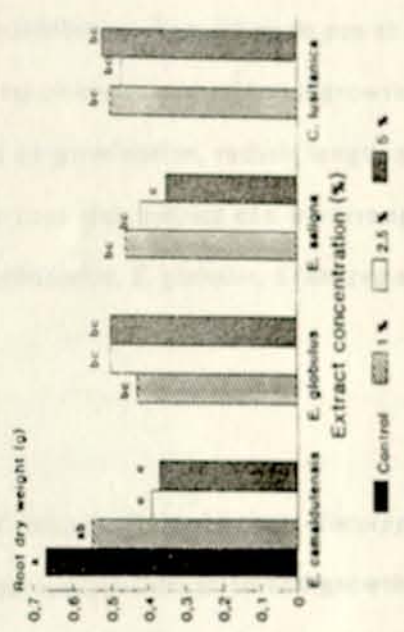
Chickpea



Maize



Pea



Teff

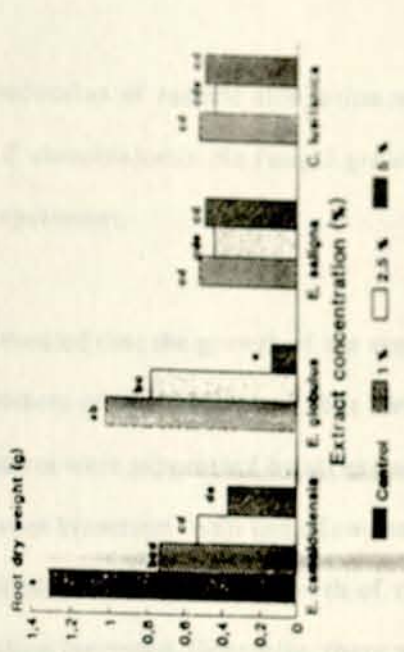


Fig. 19. The effects of aqueous extracts of leaves of *C. lusitanica*, *E. globulus*, *E. camaldulensis* and *E. saligna* on the root dry weight of four crops after ten weeks. Bars with the same letter are not significantly different at $p = 0.05$ (SNK test).

E. camaldulensis and *E. saligna* leaves, whereas reduction of radicle elongation was seen at extract concentrations of 2.5%, or 1% for *E. camaldulensis*. No fungal growth was observed in extracts or in roots during the experiment.

The shoot and root dry weights (Figs. 18 and 19) revealed that the growth of the crops was significantly suppressed by the aqueous extracts of the tree leaves, but with varying degrees of susceptibility. The shoot biomasses were suppressed by all extracts starting from 1%, which was also the case for the root biomasses in all but a few cases. Among the tested crops teff was the most susceptible. Also, the shoot growth of this crop was further reduced when extract concentration increased. Generally, there was only a slight difference between extracts with respect to their effect on shoot and root biomass, although *C. lusitana* extracts were less inhibitory than others to pea shoot growth, and 1% *E. globulus* extracts did not suppress chickpea and teff root growth as compared with controls. From the combined data on germination, radicle length and shoot and root growth, the leaf extracts of the four tree species can be arranged according to increasing allelopathic potential: *C. lusitana*, *E. globulus*, *E. saligna* and *E. camaldulensis*.

4. Discussion

The present investigation indicated that the leaf extracts from the three *Eucalyptus* species and *C. lusitana* inhibited the germination, radicle elongation and growth of the tested crops. This could be due to chemical substances in the extracts of the leaves, which again would suggest an allelopathic potential of the tree species under field conditions. Allelopathic effects of both *Eucalyptus* species (del Moral & Muller, 1969, 1970; Bhaskar & Dasappa, 1986; May & Ash, 1990; Kohli & Singh, 1991; Singh *et al.*, 1991) and *Cupressus* spp. (del Moral & Muller, 1969; del Moral & Cates, 1971) have been reported based on bioassays and field observations.

Inhibitory compounds such as essential volatile oils have been identified and isolated from the foliage of *Eucalypts* (del Moral & Muller, 1969, 1970; Singh *et al.*, 1991), and the occurrence of these compounds has been speculated for *Cupressus* (del Moral & Cates, 1971). Such essential oils may, when adsorbed to the soil particles, retain activity and inhibit germination of seeds and the ensuing radicle elongation (Singh *et al.*, 1991). The present results demonstrate that seed germination and radicle growth (and for teff, the shoot dry mass), are reduced to a higher extent by increasing the concentration of leaf extracts. This suggests that the potential allelopathic effects could be more pronounced in areas where rainfall is low or erratic and thus insufficient to dilute phytotoxic substances by run-off or leaching from top soil (May & Ash, 1990). Increasing extract concentrations did not decrease the growth of chickpea, maize and pea seedlings further; full growth reduction is probably reached by extract concentrations of 1%.

The stronger effect of leaf extracts of *E. camaldulensis* and *E. saligna* compared to those of *C. lusitanica* on germination of the test species could be the result of higher concentrations of allelopathic substances in leaves of most eucalypts. Dicotyledonous plants generally possess considerably greater concentrations of inhibitory substances than conifers (del Moral & Cates, 1971). Volatile mono- and sesquiterpenes are found in Myrtaceae and in gymnosperms (Harbone, 1988), and terpenoids have been identified as allelopathic agents in *E. globulus* and *E. camaldulensis* (del Moral & Muller, 1970; Rice, 1984). Within the eucalypts the different species differed widely in their allelopathic effect on the test species, with *E. camaldulensis* and *E. saligna* affecting the test species more adversely than *E. globulus*. This could be due to differences in composition and concentration of potential allelopathic substances between species of eucalypts (Kohli & Singh, 1991).

Allelopathic effects in natural systems are to a larger extent than laboratory experiments subjected to mitigation or intensification by the physico-chemical characteristics of the soil and the microbial activity (Harborne, 1991). It is thus not easy to relate results from bioassay studies with extracts of finely ground plant material to processes in natural forests and agroforestry systems (Stowe, 1979; May & Ash, 1991; Wardle *et al.*, 1992). As an example, only leaves were used for the preparation of extracts. Stem flow often appears to be a potent source of allelopathic chemicals in eucalypts, especially for *E. globulus*, and in addition to leaves, both bark and roots may contain allelopathic substances (del Moral & Muller, 1969; May & Ash, 1990). However, the present results show in all cases, strong reduction in crop growth with dilute extracts. This suggests that allelopathic substances from the tested tree species affect herbaceous plants and crops in Ethiopian land use systems. Bioassays with teff with soils from under mature *E. globulus*, *C. lusitanica* and *J. procera* plantations in Ethiopia support this conclusion (Michelsen *et al.*, 1993). In that study, the total dry weight of teff in the soil of *E. globulus* was reduced by 60-72% compared with teff in the soil from the two other plantation species, and by 86% in comparison with the natural forest, after three months of growth.

The crops varied in the degree of susceptibility to the tree leaf extracts. Of the four crops, chickpea and teff were clearly most strongly affected with respect to germination, and teff with respect to growth. This may have wide implications for land use in Ethiopia, considering the widespread planting of eucalypts along field bunds and the importance of teff in the Ethiopian highland; teff grain constitutes 19.8% of the total food crop production and occupies 24.3% of the agricultural area in Ethiopia (Anonymous, 1988).

Eucalypts and *C. lusitanica* are, under conditions as those prevailing in the Ethiopian highlands, highly productive tree species (Pohjonen, 1989; Pohjonen & Pukkala, 1990)

but seem to have long-term effects on soil properties (Michelsen *et al.*, 1993). The present results suggest that allelopathic substances are causes of the adverse effects of the planting of these tree species. In order to maintain the ground vegetation cover in plantations and improve the productivity of integrated land use systems, the planting of eucalypts and *C. lusitanica* should thus be avoided in areas prone to soil erosion; and with low rainfall, where there is strong competition between crops for water (Malik & Sharma, 1990), and where the potential of allelopathic effects is high. Furthermore, the use of *E. camaldulensis* and *E. saligna* should be minimized or avoided as they seem to affect crops the most strongly.

Although the present results demonstrated suppression of germination and growth by leaf extracts of *E. globulus* the effect was less than for the other eucalypts tested. *E. globulus* may be chosen for planting in areas with relatively high rainfall and fairly drainable soil, and where the main aim of tree planting is to increase short term tree production, as this species is characterized by fast growth (Pohjonen & Pukkala, 1990). In areas where conservation of land and soil resources through agroforestry is the main purpose of tree planting, species which do not suppress herbs and adjoining crops should be chosen. In the case of the Ethiopian highland such trees could be the local, medium productive hardwoods *A. abyssinica*, *Cordia africana* Lam., *Erythrina abyssinica* Lam. ex. Dc. and in the lowland drought resistant, multipurpose *Acacia* species such as *A. nilotica* (L.) Del., *A. seyal* Del., and *A. tortilis* (Forsk.) Hayne. Data on productivity, as well as competitive and environmental effects of indigenous species are, however, scarce (Poschen-Eiche, 1987; Pohjonen, 1989; Michelsen, 1992). In addition to measurements of productivity, long-term investigations of the ecological impact of exotic as well as local tree species should have merit in the process of species selection for integrated land use systems.

Summary

The potential allelopathic effect of *C. lusitanica*, *E. globulus*, *E. camaldulensis* and *E. saligna* on seed germination, radicle and seedling growth was investigated with four crops: *C. arietinum*, *Z. mays*, *P. sativum* and *E. tef*. Aqueous extracts of all the tree species significantly reduced both germination and radicle growth of the majority of the crops mostly starting from concentrations of 1% or 2.5%. The shoot and root dry weight increase of the crops was significantly reduced after 10 weeks of treatment with leaf extracts. Among the four crops, *C. arietinum* and *E. tef* were most susceptible with respect to germination, and *E. tef* with respect to growth. From the overall data the leaf extracts of the four tree species can be arranged according to increasing allelopathic potential: *C. lusitanica*, *E. globulus*, *E. saligna* and *E. camaldulensis*. It is suggested that the planting of *E. camaldulensis* and *E. saligna* in integrated land use systems should be minimized, whereas the use of *C. lusitanica* and *E. globulus* seems less environmentally damaging in this respect.

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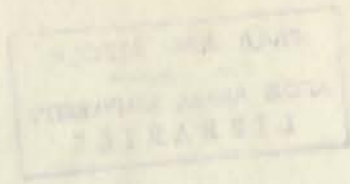
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D E C L A R A T I O N

I undersigned declare that this thesis is my work and that all sources of material used for the thesis have been duly acknowledged.

Lisanework Nigatu

Lisanework Nigatu

Addis Ababa
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