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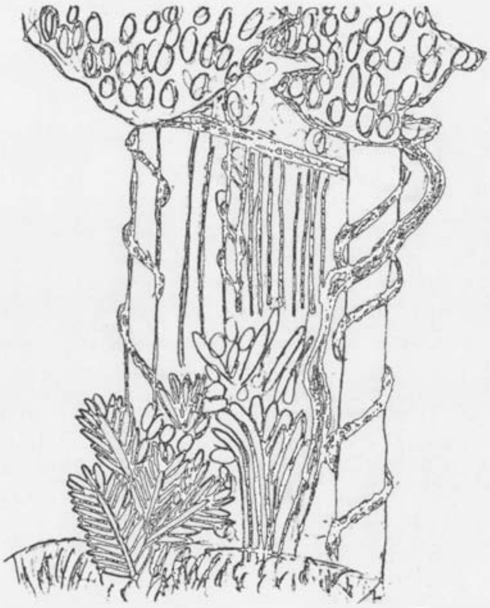
Tamrat Bekele

Vegetation ecology of remnant Afromontane forests on the Central Plateau of Shewa, Ethiopia



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The floristic composition and structure of the vegetation of Afromontane forest remnants on the Central Plateau of Shewa, Ethiopia are described and related to environmental factors. The study was conducted in four forests: one humid forest, the Jibat forest, and three dry forests, the Chilimo, Menagesha Suba and Wof-Washa forests. 146 relevés were analysed, 77 in Jibat, 30 in Chilimo, 20 in Menagesha Suba, and 19 in Wof-Washa.

The sample plots were usually 30 m × 30 m for trees and shrubs, and 2 m × 2 m for herbaceous plants. For each species the cover/abundance value was estimated. Height and diameter at breast height of all woody individuals taller than 2 m and thicker than 2 cm were measured. Profile diagrams were made in selected transects in two of the forests, Menagesha and Wof-Washa.

The following environmental variables were measured in each sample plot: altitude, slope, and exposure. Representative soil samples from each sample plot were analysed for chemical properties: pH, Electrical conductivity, Na, K, Ca, Mg, N, P, Cation exchange capacity, and Organic matter, and for physical properties: Sand, Silt and Clay.

The relevés were classified with the clustering and relocation program TABORD, and the two-way indicator species analysis program TWINSPAN. The resulting clusters were interpreted as community types and given provisional names after usually two dominant or characteristic species. Community-environment relationships were analysed with the ordination program Canonical Correspondence Analysis (CANOCO program) and the Discriminant Analysis program DISCRIM.

Eighteen community types were described: *Arundinaria alpina* type, *Ilex mitis-Rapanea simensis* type, *Syzygium guineense-Psychotria orophila* type, *Olea hochstetteri-Olinia aequipetala* type, *Croton macrostachyus-Ficus sur* type, *Olea welwitschii-Carissa edulis* type, *Syzygium guineense-Vepris dainelli* type, *Erica arborea* type, *Juniperus procera-Myrsine africana-Ehrharta erecta* type, *Juniperus procera-Maytenus arbutifolia-Peucedanum winkleri* type, *Erica arborea-Myrica salicifolia* type, *Spiniluma oxyacantha-Scolopia theifolia* type, *Scolopia theifolia-Podocarpus gracilior* type, *Podocarpus gracilior-Olea europaea* type, *Podocarpus gracilior-Allophylus abyssinicus* type, *Juniperus procera-Sideroxylon gillettii* type, *Podocarpus gracilior-Maytenus arbutifolia* type and *Euphorbia obovalifolia-Podocarpus gracilior* type. There is a strong contrast in species composition between the humid and dry forests: the humid forest is characterized by a mixture of deciduous species while the dry forests are dominated mainly by the two conifers *Juniperus procera* and *Podocarpus gracilior*.

Analysis of community-environment relationships revealed strong correlations with altitude, soil chemical factors – especially organic matter and total cations – and the physical factors sand and clay content. It was deduced from the structural comparisons and vegetation history of the forests that Wof-Washa is an old forest while Jibat, Chilimo and Menagesha Suba are forests in different stages of secondary development.

Seven general patterns of species population structure were recognized for the forests, and interpreted in terms of the dynamics of the species: (1) good reproduction and continuous recruitment, (2) poor reproduction, but relatively many individuals in medium-size classes, (3) good reproduction but bad recruitment, (4) good reproduction but irregular recruitment, (5) good reproduction and continuous recruitment, but under-representation of medium-sized individuals, (6) poor reproduction but relatively many individuals in higher size classes, and (7) no reproduction, and only very large and old individuals present.

Floristic comparisons with other montane forests showed that the Jibat forest is more related to the southwestern humid forests of Ethiopia, while the forests of Chilimo, Menagesha and Wof-Washa were related to each other, and other dry forests on the Southeastern Plateau of Ethiopia.

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Contents

1 Introduction

Ethiopia is a mountainous country with remarkable contrasts: it comprises rugged mountains, flat-topped plateaux, deep gorges and river valleys, and rolling plains. The altitudinal variation ranges from 110 m below sea level at Kobar Sink (Dallol Depression) to 4620 m above sea level at the highest peak of Mt. Ras Dejen. The biological resources (flora, fauna and vegetation) of the country are still incompletely known. In other East-African countries, notably Kenya, Tanzania and Uganda, the overall composition and distribution of the vegetation have been better described, and Flora's are also available. Ethiopia has a long history and a rich cultural heritage, and it has been able to withstand foreign invasions which may be one of the explanations of our relatively poor knowledge of the country.

Given its unique physical setting and biogeographical position in Africa, a complete assessment of the vegetation of Ethiopia contributes significantly to the general understanding of African flora and vegetation. The ecological crisis the country is facing – drought, deforestation, soil erosion – has locally been catastrophic and detrimental to the biological richness of the country. Ethiopia is an agricultural country with about 85 % of the population earning its living in direct interaction with the biological and physical environment. A full understanding of the present remains of natural and semi-natural vegetation is required as a basis for the future design of a sound resource exploitation programme on a sustainable basis.

To meet such ends, two major projects were established with support from SAREC, the Swedish Agency for Research Cooperation with Developing Countries. The first project, which started in 1980, aims at a complete Flora of Ethiopia. One volume of this work has already been published (I. Hedberg & Edwards 1989) and subsequent volumes are in preparation. The second project, entitled 'Vegetation and land use study of the Central Plateau of Ethiopia' was launched in 1987. The first vegetation studies have been devoted to grasslands and shrublands (e.g. Zerihun & Backéus 1991). The present study forms part of the latter project and has the following specific objectives:

1. To study the floristic composition and structure of the natural forests of the Central Plateau of Shewa, Ethiopia, and to classify the forest vegetation;
2. To investigate the ecological relationships of the forest communities, with a special emphasis on the history of vegetation and climate, the present human impact, and the general dynamical status of the forest types.

In this study, the definition of forest given in two important studies of East-African vegetation (Greenway 1973; White 1983a) has been adapted: "Forest is a continuous stand of woody individuals, at least 5 m in height, with crowns touching or intermingling". This is a pragmatic definition, applicable to most of the vegetation of the forests described here. Where the term woodland is used, it refers to open woody vegetation with open space between crowns in the canopy. See further Eiten (1992), giving the same definitions, who discusses the variation and confusion regarding the names used for vegetation.

This study deals with the four major remnant forests left on the Central Plateau of Ethiopia: Jibat forest, Chilimo forest, Menagesha Suba forest and Wof-Washa forest. Jibat is the name of the mountain on which the forest occurs; Chilimo is the name given to the forest; Menagesha Suba derives its name from a nearby town and village (Menagesha & Suba respectively); Wof-Washa, literally meaning 'bird's-cave', is the name given to the forest. In each case 'forest' should be read as 'forest area'; within each area non-forest vegetation may occur.

2 The Central Plateau

2.1 Physiography

Ethiopia consists of two major high plateau regions divided by the Rift Valley system. Regions of low-lying plains border the plateaux in the east, south and west. In the west, extending from the former province of Eritrea in the north to Kenya in the south, we find the larger Ethiopian Plateau, also known as the Northwestern Highlands. In the Southeast, a smaller plateau designated as the Southeastern Highlands occurs, also known as the Somalian Plateau. The Ethiopian plateau includes parts of the administrative regions of Tigray, Gondar, Gojam, Wello, Wellega, Illubabor, Kefa, Gamo-Gofa and Shewa. Apart from the major river valleys, the whole of this region lies above 1000 m and about half of the plateau lies above 2000 m a.s.l. (Mohr 1971). The Southeastern Plateau is situated to the east and southeast of the Rift system.

The Shewa plateau, mostly situated above 2000 m a.s.l., occupies the central portion of the Ethiopian Plateau and lies between the middle valleys of the rivers Abay (Blue Nile) and Awash, and the upper valley of the Omo. It extends westwards into eastern Wellega and forms a crescent-like region draining into the Abay. The surface consists of plateau basalts into which the important tributaries of the Abay have cut deep gorges, isolating smaller tablelands (Westphal 1975).

The Rift Valley, dividing the Ethiopian highland massif into two parts, is characterized by a chain of lakes throughout the greater part of the Valley. It extends generally SSW-NNE from Lake Rudolph in the south to Afar in the north. The Rift Valley passes through the administrative regions of Gamo-Gofa, Sidamo, Shewa, Harerge, Wello, and Tigray. Fig. 1 shows the geographical position of the country and the different regions.

2.2 Geology

2.2.1 Bedrock

The pre-Cambrian rocks which underlie the whole of Ethiopia consist mainly of a complex of metamorphic rocks of many different grades and types. Igneous rocks also constitute an important proportion of the pre-Cambrian rocks. The pre-Cambrian rocks might be found exposed in the peripheral regions of the country, and in many deep river valleys. However, for the most part, especially in the central and eastern parts, they are overlain by more recent rocks. Mesozoic rocks, mainly sandstones and limestones, cover the pre-Cambrian rocks; they appear in deep gorges in the Northwestern Highlands and in the highly eroded terrains of northern Ethiopia. Mesozoic rocks are also found on the southeastern slopes of the SE Highlands. Volcanic activities during the Tertiary period resulted in the extrusion of large quantities of flood lavas which now cover the Mesozoic rocks in most parts of the country. These lava flows occurred in a series of layers to form what is now known as the Trap Series.

Various rock types, including rhyolites, trachytes, tuffs, and ignimbrites, compose the Trap Series, but basalts are the most important components and they constitute the main rock type of the Central Plateau. The basalts are uniform in composition over the whole range of the high plateaux, both chemically and mineralogically. A detailed survey of the geology of Ethiopia is found in Mohr (1971). A survey of the chemical investigation of the rocks for the central eastern plateau, and the lithology of some selected land forms, are found in Zanettin et al. (1974) and Merla et al. (1979), respectively.

2.2.2 Soils

Detailed descriptions of Ethiopian soils are hardly available. Data on chemical properties and colours of the soil are found in the work of Murphy (1968), who surveyed soils, mainly along highways, throughout most of the country. Lundgren (1971) studied some soil properties of a montane forest on the Southeastern Plateau. The majority of the soils of Central Ethiopia are of volcanic origin (Logan 1946). Von Breitenbach (1963) characterized the lava plateaux by means of two principal soil types originating from the disintegration of volcanic substrates intermingled with sand and limestone: the black and compact clays ('Black soil') and the reddish-brown and heavy loams ('Red soil'). The former type appears on flat plateaux and in the bottom of valleys, and the latter on mountain and valley slopes and on better drained plateaux. The red and brown soils, and loams are the most common soils in the highlands; they probably make up over 60% of the plateau soils (Logan 1946) and are also the most common forest soils.

No classification of Ethiopian soils has yet been attempted, but d'Hoore (1964) presented some useful information. His elements and associations have been trans-

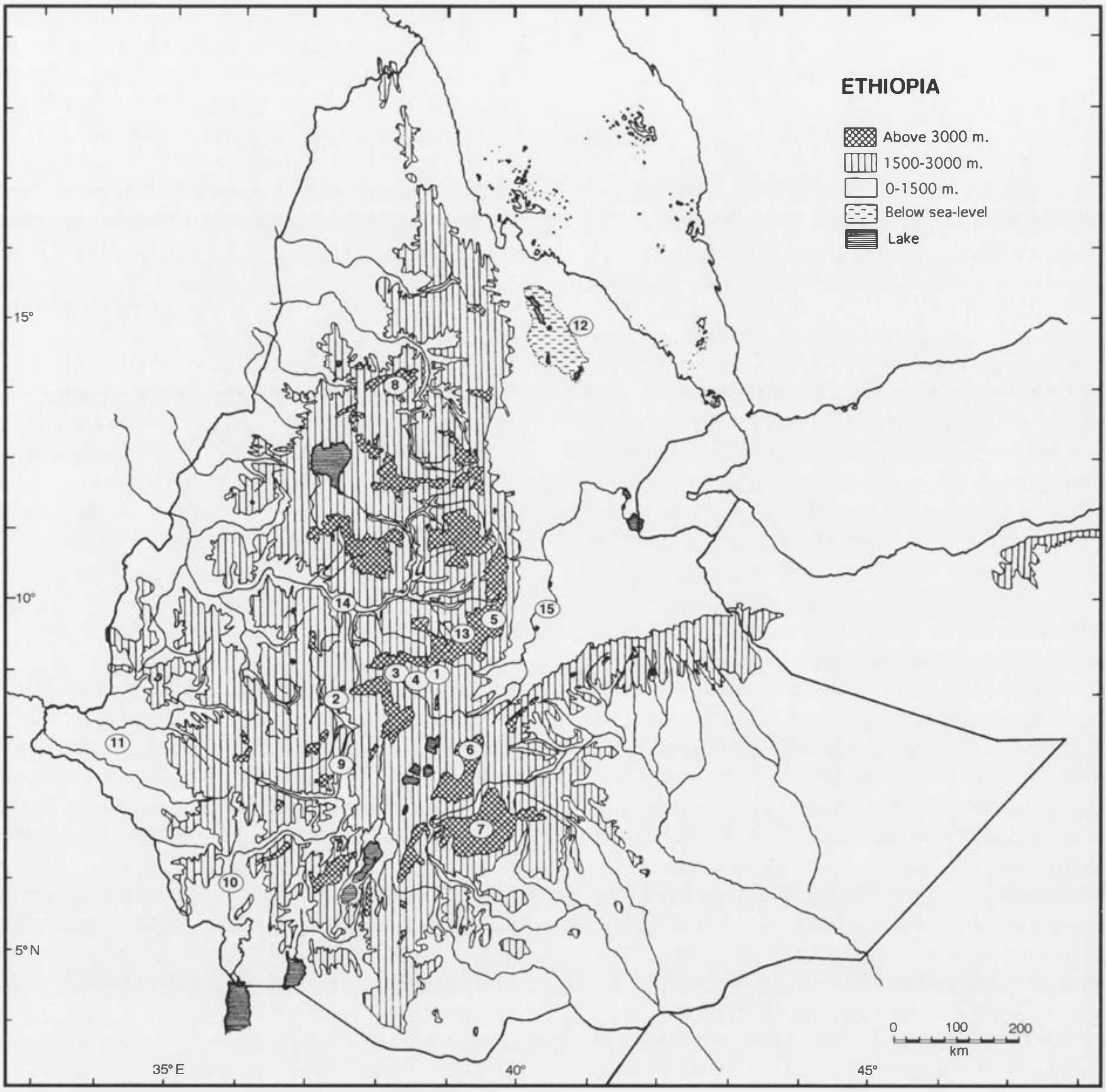

Fig. 1. Map of Ethiopia showing the major physiographic regions, study sites and important places mentioned in the study: 1 = Addis Abeba; 2 = Jibat forest; 3 = Chilimo forest; 4 = Menagesha Suba forest; 5 = Wof-Washa forest; 6 = Mt. Bada; 7 = Bale Mts.; 8 = Semien Mts.; 9 = Ghibe River; 10 = Omo River; 11= Baro Lowlands; 12 = Afar Depression; 13 = Debre Berhan; 14 = Abay (Blue Nile) River; 15 = Awash River. Note the extent of area above 3000 m.

lated into the names of the soil orders of the new soil classification system (FAO/UNESCO 1974). Westphal (1975) presented a survey of what he broadly defined as the soil regions of Ethiopia. According to this characterization, Alfisols (mainly belonging to the suborder Ustalfs), Vertisols and Inceptisols dominate the Central Plateau. In the National Atlas of Ethiopia (E.M.A. 1988) various types of Vertisols, Luvisols and Cambisols have been mapped as constituting the bulk of the soils of the Central Plateau of Ethiopia. A short definition of the soil groups is given by Buringh (1979).

As soils and soil-forming processes are influenced by environmental factors such as topography and climate, and because a nation-wide soil classification is lacking, it is still very difficult to indicate a clear demarcation of the boundaries between the soil types. Considering the great topographic and geological variability, the best one can say is that Ethiopia has a great variety of soil types, which often form mosaics.

2.3 Climate

2.3.1 Rainfall

The distribution of rainfall in East Africa is generally seasonal, depending on the convergence and alteration between the main air streams over this part of the continent (Lind & Morrison 1974). Four distribution patterns have been distinguished in Ethiopia (Daniel 1977). In the southwest, rainfall occurs all-year round (Type 1), while in the southeast, rain falls during spring and autumn (Type 2). Coastal regions along the Red Sea receive rainfall in winter (Type 3) whereas the remainder of the country has a pronounced summer maximum (Type 4). The three most important seasonal winds accounting for the seasonal distribution of rainfall are (1) the southeasterlies, prevailing from about May to October, (2) the northeasterlies, from about November to April, and (3) the Atlantic equatorial westerlies from March to November. The latter winds, which are more pronounced in the summer months, June-August (Daniel 1977), bring most of the rain (Liljequist 1986).

The amount of rainfall varies considerably. Regional variation in rainfall in Ethiopia is mainly determined by two factors, namely the direction of moisture-bearing seasonal air currents and the elevation (Kebede 1964; Daniel 1977). In addition, variation in topography is of influence (Kebede 1964; Lind & Morrison 1974; Liljequist 1986). Daniel (1977) recognized 14 rainfall regimes for Ethiopia which can be grouped into two main types. The difference between the two types is determined by the occurrence of rain throughout the year (Type 1) or whether there are two rainy seasons (Type 2). Both types are represented in the Central Plateau of Shewa. Type 1 prevails in the western and central parts of the Plateau while Type 2 is characteristic of the north and eastern half of the Plateau. Within Type 1 one can distinguish between so-called spring rains or 'small rains' falling in April and May, and the 'big rains' falling in June-September. The easterly and southeasterly moist air currents produce the former, while the warm, moist southwesterlies and southeasterlies account for the latter. These air currents are also responsible for the 'small rains' coming in March-April, and 'big rains' falling from July to September. A Type 2 area on the Central Plateau of Shewa near Addis Abeba, situated in the middle of the Central Plateau, at 2440 m a.s.l., receives an annual rainfall of 1270 mm.

2.3.2 Temperature

The seasonal variation in temperature in Ethiopia is small (Logan 1946; Westphal 1975; Friis et al. 1982; Liljequist 1986). Low temperatures are attained during the rainy months when there is a maximum of cloud cover. High temperatures occur during the dry and sunny season. Daily temperature variations, especially during dry periods with clear skies, can be high. The pattern of temperature distribution in Ethiopia varies from place to place, mainly in relation to the altitudinal variation.

Traditionally, Ethiopians divide the country into five climatic regions: 'wirch', 'dega', 'woina dega', 'qolla' and 'bereha'. These divisions are mainly based on elevation, and hence temperature as well. Daniel (1977) combined altitude, temperature and potential evapotranspiration, and arrived at the following comparison with the traditional classification scheme:

Type	Description	Altitude (m)	Potential evapo-transpiration (CM)
Wirch	cool	> 3000	< 80
Dega	cool temperate	2300-3000	80-100
Woina dega	temperate	1500-230	110-125
Qolla	warm temperate	800-1500	125-160
Bereha	hot	< 800	>160

According to Delliquadri (quoted by Westphal 1975), average January temperatures, representing 'winter', lie between 15 and 20 °C in the highlands with the 15 °C-isotherm possibly coinciding with the 2400-m contour line. Average April temperatures, representing 'spring', are the warmest throughout Ethiopia. The 25 °C-isotherm surrounds the Ethiopian highlands at this time. During the 'summer' season the Ethiopian highlands experience minimum temperatures, while 'autumn' patterns are similar to those of 'winter' and 'spring'. It should be mentioned here that there are only two main seasons in Ethiopia: a long dry season and a shorter wet season.

2.3.3 Climatic classification

The climate map of Ethiopia based on the Köppen system (E.M.A. 1988) divides Ethiopia into three broad climate types which are subdivided into nine classes. The three main climate types recognized in this system are: the Dry climate, the Tropical Rainy climate, and the Temperate Rainy climate. According to this classification, the Central Plateau of Ethiopia is characterized by a Warm Temperate Climate I (CWB) type and Warm Temperate Climate II (CFB) type. The former climate type prevails in regions with distinct dry winter months, covering most of the NW and SE Highlands and extending over an altitudinal range from 1750 m - 3200 m. The latter climate type prevails in regions with sufficient rainfall at all seasons, and occurs in the southwestern part of these Highlands.

2.4 Vegetation

2.4.1 General vegetation survey

Until early this century, general surveys or descriptions of Ethiopian vegetation were mostly presented by foreign travellers passing through the country on a mission other than floristic. Later, more elaborate attempts have been made towards a broader understanding of the country's vegetation and its classification. In some of these studies, vegetation classes have been subjectively assessed, based on similarities in geographical distribution with other East African countries (O. Hedberg 1951, 1978; Pratt et al. 1966; Coetzee 1978; White 1983a), while others, such as Hamilton (1982), based their vegetation units on altitudinal distribution and moisture availability.

More significant contributions to Ethiopian vegetation classification include those of Pichi-Sermolli (1957) and von Breitenbach (1961, 1963). The former recognized 24 vegetation units for the whole country, whereas the latter proposed seven broadly defined units which are further subdivided into smaller associations. More recently, authors have criticized these surveys. Gilbert (1986) argued that some vegetation types described by Pichi-Sermolli hardly differed from each other, while others have been oversimplified. Friis et al. (1982) pointed out that von Breitenbach's associations lack essential information on localities and distribution.

Descriptive and classificatory studies on a smaller scale, referring to local conditions and isolated vegetation types, were carried out by Logan (1946), Scott (1955), Sebald (1968), Beals (1969), Wilson (1977), Verfaillie (1978), Klötzli (1981), Hailu (1982), Weinert (1983), Friis et al. (1982), Isaac (1984), Zerihun (1985), Friis (1986, 1992), Lisanework (1987), Sebsebe (1988), Zerihun & Backéus (1991) and Miehe & Miehe (1993). In the National Atlas of Ethiopia (E.M.A. 1988), ten vegetation types have been identified and their general distribution mapped. However, this classification is based on the theory of climatic climax vegetation; therefore it can hardly be used for the present natural vegetation.

The following brief summary of Ethiopian vegetation has been taken from the survey by Friis (1992). The southwestern slopes of the NW Highlands are covered by extensive transitional rain forests. These forests occur at altitudes between 1500 and 2600 m, and characteristically contain a mixture of *Podocarpus* and broad-leaved species in the canopy, with *Aningeria adolfi-friedericii* as a predominant species. The vegetation at higher altitudes and under drier conditions, is dominated by the conifers *Podocarpus gracilior* and *Juniperus procera*. These latter forests occur in both the NW and SE Highlands at altitudes from ca. 1500 - 2700 m. The dry evergreen forests have been subjected to human interference during a very long period, and at present they are only found scattered and in very small patches. Deciduous woodland and wooded grasslands are the main vegetation types of the western lowlands of Ethiopia. Along a north-south gradient they show a considerable variation in both physiognomy and floristic composition.

The 'Ethiopian undifferentiated woodland' (*sensu* White 1983a) is related to a characteristic type of Sudanian woodland and occurs along the western escarpment of the NW Highlands. The dominant woodland trees include *Balanites aegyptiaca*, *Boswellia papyrifera*, *Combretum collinum*, *Steriospermum kunthianum* and *Terminalia* spp. Sudanian wooded grassland with *Terminalia* spp. is found in the Baro lowlands. In addition, small patches of natural dry semi-evergreen forest and riverine forests occur here.

The plant cover of the Ghibe-Omo Basin is poorly known; wooded grasslands and bush land of the Somalia-Masai type are considered as parts of the natural vegetation.

Arundinaria alpina occurs in patches on the wet side of the mountain massifs. Above 3300 m a.s.l., Afro-Alpine vegetation dominates the landscape. This type is poor in species; it is only found on the highest mountains, such as the Semien mountains in the north, and the Bale mountains in the southeast.

The Rift Valley, especially in the Lake Region, is covered by *Acacia* woodland (mainly *Acacia tortilis*). This vegetation type is also found in the Lower Awash Valley, and along the foothills of the eastern escarpment of the NW Highlands. Along the Afar Depression in the northeast, the Somalia-Masai semi-desert grassland and bushland forms the major vegetation type.

The southeastern lowlands of Ethiopia are mainly covered by the Somalia-Masai type *Commiphora* deciduous bushland and thickets. Along water courses in almost all the vegetation types mentioned above, riverine vegetation, including riverine forest, prevails.

2.4.2 Forest vegetation of Ethiopia

Among the general vegetation studies mentioned above, some are of particular importance for a forest typology. Both Logan (1946) and Pichi-Sermolli (1957) provided a general outline of Ethiopian forest vegetation, comprising three distinct forest types: Montane Dry Evergreen Forest, Montane Moist Evergreen Forest, and Arundinaria Bamboo Forest. Von Breitenbach (1963) recognized more forest types according to their dominant species, and grouped them into two very broad categories: Lower and Upper-Highland Forests. The most recent surveys of Ethiopian forests are those by Friis et al. (1982), and Friis (1986, 1992); the monograph by Friis (1992) presents a description of the forests and forest trees of North-East Africa, which includes the following types occurring in Ethiopia:

Fig. 2. Remains of isolated *Juniperus procera* trees in a farmland near the Chilimo forest.

a. Dry peripheral semi-deciduous Guineo-Congolian forest; it is restricted to the Baro Lowlands of western Illubabor, western Ethiopia.
b. Transitional rain forest; occurring scattered on the SW Escarpment of the NW Highlands.
c. Afromontane rain forest; in the southwestern parts of the NW and SE Highlands.
d. Undifferentiated Afromontane forest; in both the NW and SE Highlands, especially on the plateaux of Shewa, Wello, Sidamo, Bale and Hararghe.
e. Dry single-dominant Afromontane forest of the Ethiopian Highlands; in the northern half of the NW Highlands, especially in parts of Gojam, Gonder and Tigray.
f. Dry single-dominant Afromontane forest of the escarpments, including transitions between single-dominant Afromontane forest and East African evergreen and semi-evergreen bushland; a physiognomically heterogeneous but floristically more homogeneous vegetation ranging from forest to evergreen scrub with scattered trees.
g. Riverine forest; exhibiting a floristic composition that varies depending on altitude and geographical location.

2.4.3 Human impact

The estimates of the extension of various forest types in Ethiopia today, and in the past, are numerous and vary widely. Logan (1946) estimated that what he called 'high forest' covered about 5% of the area of the highlands whereas von Breitenbach (1963) estimated the extent of 'highland forests' to be 4% of the total land area. Mesfin (1972) reported that ca. 85% of the original forest had disappeared and that only ca. 5% of the country was still covered by forests. The National Mapping Agency of Ethiopia (E.M.A. 1988) estimated that once 30% of the entire country was covered with forest and that only 3% is left nowadays. However, it is very difficult to establish the past and present extent of forest vegetation in Ethiopia for two reasons (Friis 1986). First, the estimates do not distinguish between natural high forest, secondary forest, and other seral stages in forest regrowth. Therefore, it is not possible to make comparisons because it is difficult to infer exactly what type of vegetation is implied. Second, estimates of past forest cover were speculative, while being mainly based on the combination of distribution of rainfall and remnant forest patches.

Despite the uncertainties mentioned, we may assume that once the extent of forests in Ethiopia was much larger than at present. Isolated forest trees occur scattered throughout most of the highlands (Fig. 2), suggesting the former presence of forest there. Patches of forest and woodland, with a species composition similar to that of the remaining natural forests, are very common around churchyards and religious burial grounds (Fig. 3) which are abundant in the highlands. According to Wilson (1977), the density of churches in Central Tigray (north of the Central Plateau) is one/ 19.1 km^2. Forest patches which are remains of a formerly much more extensive area are present both in the NW and SE Highlands. In the north, these patches are found scattered along the eastern escarpment of the NW Highlands.

Fig. 3. A forest patch on religious burial ground in the Wello administrative region. Trees on the hill top (arrow) are *Olea europaea*; *Euphorbia* sp. is visible as isolated trees to the right on the lower slopes. Note the contrast with the eroded slopes in the background.

The obvious assumption (e.g. Logan 1946; Friis 1986) that much of the forested area was turned into fields and grassland, has to be substantiated with evidence from other studies. For instance, in the northeastern part of the Central Plateau, houses are built of stone, which is a different system compared to the tradition in the rest of the plateau, suggesting scarcity of local timber for at least a few hundred years. Tewolde (1989) suggested that highland forests did not have a continuous distribution, but were interrupted by a mosaic of highland grasslands and swamps, where impeded drainage in the valleys and other edaphic factors limited the growth of trees. To obtain more evidence as regards the past extent of forest vegetation in Ethiopia, relevant information has to be obtained from palynological studies, which are crucial for the reconstruction of the past climate and vegetation history of the region.

Whatever the extent of the land surface that might have been covered by forests, most of the forested land has disappeared due to climatic change and particularly human activities (Hamilton 1974). A historical account of environmental degradation was presented by Tewolde (1989). Of special importance are the changes in the social organization and land tenure that started in the 17th century and resulted in a land-holding system that put all land other than that under cultivation, available for common use by the local population. The consequence was, that the land came to be used virtually as a source for food, feed and wood. Since the peasants were not allowed to organize themselves, the local resources were exploited chaotically without any co-operative responsibility (Tewolde 1989). Uncontrolled exploitation is still going on, especially to satisfy domestic needs for firewood and construction materials.

The very high annual rate of population growth, 2.5% between the years 1980 and 1985 (Sayer et al. 1992), has also led to further replacement of forests by agricultural land. Despite the long history of agriculture in Ethiopia (Mesfin 1972; Tewolde 1989), tree planting was either unknown or not considered necessary (Mesfin 1972), so that hardly any new wood resources were developed until the end of the 19th century. By this time, wood scarcity, at least on the Central Plateau, was so acute that exotic species (e.g. *Eucalyptus globulus*, Pohjonen & Pukkala 1990) had to be imported to establish plantations.

To summarize the trends in vegetation change, some further figures are presented. Already 50 years ago, Logan (1946) noted that the forest extending from Addis Alem to Jumjum (ca. 15 km) had been reduced to scattered mature trees with sporadic patches of scrub over a period of 45 years. This process has continued further to the west to the same extent in the last 15-20 years. Of the estimated 87 % of forest and woodland cover in the Ethiopian highlands, only 40% was left by 1950 and as little as 5.6 % by 1980 (Sayer et al. 1992). For the country as a whole, the figures are as follows: of the original 35% forest cover, 16% was left by 1952, 3.6 % by 1980, 2.7% by 1987 and about 2.4% by 1990 (Sayer et al. 1992). The few scattered and relatively small areas of forest that survive today are largely confined to inaccessible steep hill slopes, escarpments and mountains far from motorways.

2.5 History of climate and vegetation

There is ample evidence of long-term changes in the climate and vegetation of Africa (O. Hedberg 1954; Moreau 1938, 1951, 1963; Coetzee 1964, 1967; van Zinderen Bakker & Coetzee 1972; Livingstone 1975; Potter 1976; Hastenrath 1977; Axelrod & Raven 1978; Hamilton 1981, 1982; Bonnefille & Hamilton 1986). The highlands of Ethiopia and East Africa provide some of the clearest and most convincing pieces of evidence for these changes (Livingstone 1975), although palynological evidence for long-term changes in Ethiopia is still scanty. Fossil pollen and spore assemblages in Upper-Neogene lignitified lacustrine deposits have been recorded from the northwestern Ethiopian highlands (Kedamawit 1986). They show the following features:

- presence of species belonging to genera such as *Afrocrania*, *Anthonota*, *Brachystegia*, *Holoptelea*, *Iodes*, *Isoberlinia*, *Isomacrolobium*, *Oligocodon* and *Rauvolfia*, which are completely lacking in the present Ethiopian flora;
- absence of a gymnosperm flora, which is now the predominant highland flora, with particularly *Podocarpus* and *Juniperus*;
- much higher abundance of pteridophytes;
- poor non-arboreal flora, with low representation of i.a. Poaceae and Cyperaceae.

All these features suggest a warm and humid climate with a richer flora than nowadays (Friis et al. 1992).

Pollen spectra from Holocene sediments around Lake Rudolph [(Lake Turkana), (northern Kenya and Ethiopia)], contain relatively high quantities of tree pollen assigned to the genera *Euclea*, *Ekebergia*, *Podocarpus*, *Juniperus* and *Olea*. This suggests a wet period during the early Holocene. Later, the trees declined while grasses became much more common, suggesting drier conditions (Bonnefille & Hamilton 1986).

From a pollen diagram from Mt. Badda (4040 m a.s.l., Arsi province) presented by Hamilton (1982), four pollen zones were recognized:

- Zone D, before ca. 10 000 B.P., with a much higher value for Chenopodiaceae-type pollen than known from elsewhere in montane Eastern Africa. The high abundance of *Suaeda* pollen suggests the occurrence of semi-desert or salt pans in a much drier climate. The presence of a dry montane forest on the Arsi mountains is indicated by the abundance of pollen types assigned to montane forest genera, such as *Podocarpus*, *Juniperus*, *Olea* and *Myrica*. The scarcity of pollen types suggesting wetter environments, e.g. *Alchemilla*, *Ericaceae*, *Hagenia*, *Macaranga kilimandscharica*, and Urticaceae, is further evidence of arid conditions.
- Zone C, max. 50 cm, based on a thin pollen deposition, covering a period of 6000-7000 years, has not been treated in detail.
- Zone B, ca. 3700 - 1850 B.P., is characterized by pollen of *Podocarpus*, *Juniperus* and *Olea*, indicative of dry montane forest.
- Zone A, ca. 1850 B.P., shows a major change in vegetation, primarily due to human influence. A widespread decline of *Podocarpus* pollen and the increase in *Celtis* (secondary forest), *Dodonaea*, *Hagenia* and *Myrica* (forest at high altitude), and Chenopodiaceae, *Plantago* and *Rumex* (grazed and cultivated land), suggests a devastation of *Podocarpus* forest and a replacement by secondary forest, montane woodland, and agricultural land. As compared with other East African mountains, where human influence is supposed to be of very recent origin, vegetation degradation and soil erosion in the Ethiopian highlands have a longer history.

A second peat core studied by Hamilton (1982) from the Bale Mountains (3830 m a.s.l., Bale province) was dated at 7920 ± 80 BP., and comprises three pollen zones (A - C). There seems to be a correlation between the A and B pollen zones of both the Bale Mts. and the Badda Mts., indicated by (a) persistent *Podocarpus* and *Juniperus* presence, indicative of a dry montane forest; (b) relatively high amounts of *Celtis*, *Dodonaea* and *Hagenia* pollen; (c) decrease in Ericaceae over the Zone B/A (1850 B.P.) boundary, indicating human disturbance; and (d) increase of Urticaceae suggesting the opening up of the forests. A switch to drier climates at the Zone C/B boundary is indicated by the rise in *Podocarpus* pollen, a phenomenon observed in other East African pollen diagrams too. Moister conditions than in Zone B are indicated for Zone C by higher values of *Macaranga kilimandscharica* and *Rapanea*-type pollen. Palynological studies on the vegetation history of the Lake Wenchi area, western Shewa, by Bonnefille & Buchet (1987) indicate a rather unaltered situation over the last 1000 years. The present-day vegetation around the lake comprises i.a. *Juniperus*, *Hagenia* and *Olea* species.

2.6 Phytogeographical description

2.6.1 Africa

The following short characterization is based on descriptions by Wickens (1976), Brenan (1978), Friis (1986) and Iversen (1991). Most of these descriptions are in agreement with the classifications of Chapman & White (1970) and White (1976, 1983a). Here, we adopt the system of White (1979, 1983a) with four phytochoria types at the rank of a region: (a) regional centres of endemism, (b) an archipelago-like centre of endemism, (c) an archipelago-like centre of extreme floristic impoverishment, and (d) regional transition zones and mosaics. The phytogeographical regions of Africa are shown in Fig. 4. Each regional centre of endemism is characterized as a phytochorion with > 50% of its species confined to it with a total of more than 1000 endemic species. The phytochoria constituting regional centres of endemism are: Guineo-Congolian, Zambezian, Sudanian, Somalia-Masai, Cape, Karoo-Namib and Mediterranean; two additional regional centres of endemism are recognized for Madagascar; East Malagasy and West Malagasy.

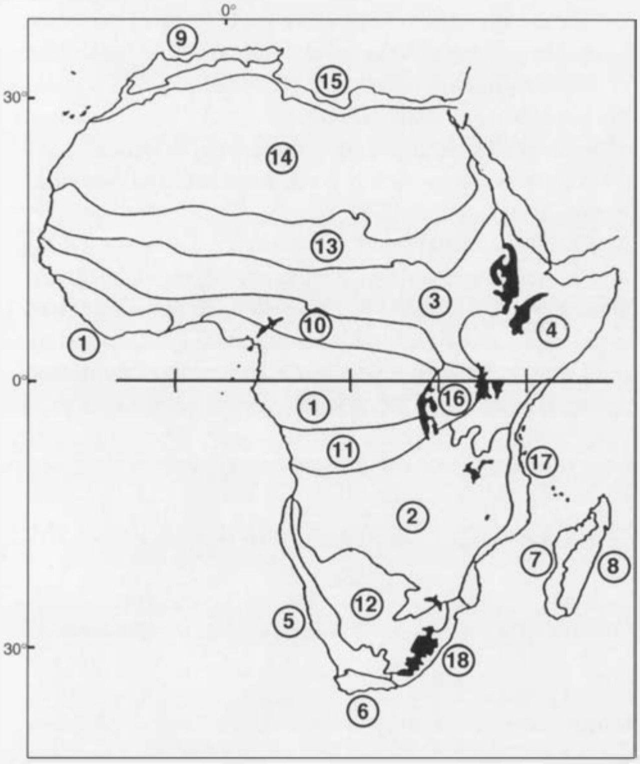

Fig. 4. Phytogeographical map of Africa according to White (1983a) taken from Iversen (1991). Regional centers of endemism: 1 = Guineo-Congolian; 2 = Zambezian; 3 = Sudanian; 4 = Somalia-Masai; 5 = Karoo-Namib; 6 = Cape; 7 = West Malagasy; 8 = East Malagasy; 9 = Mediterranean; Regional transition zones: 10 = Guineo-Congolian/Sudanian; 11 = Guineo-Congolian/Zambezian; 12 = Kalahari-Highveld; 13 = Sahel; 14 = Sahara; 15 = Mediterranean/Sahara; Regional mosaics: 16. Lake Victoria; 17. Zanzibar-Inhambane; 18. Tongaland-Pondoland. Black: Afromontane and Afroalpine areas.

Since the boundaries between these regional centres of endemism are not sharp, and because there is some overlap between adjacent phytochoria, a phytogeographical category named 'transitional zone' is employed to characterize overlapping zones. These are: Guineo-Congolian/Zambezian, Guineo-Congolian/Sudanian, Lake Victoria, Zanzibar-Inhambane, Kalahari-Highveld, Tongaland-Pondoland, Sahel, Sahara, and Mediterranean/Sahara.

The archipelago-like regional centre of endemism corresponds to the disjunct Afromontane regions with floristic similarities to each other that are greater than those to adjoining areas. This centre comprises all the montane forests and extends discontinuously from Ethiopia in the north to the Cape Province in the south and the Cameroon mountains in the west.

The archipelago-like centre of extreme floristic impoverishment refers to the Afroalpine zone, situated at higher altitudes than the Afromontane Region.

2.6.2 The Afromontane Region

The Afromontane Region comprises two of the three belts of highland vegetation distinguished by Hedberg (1951), the Montane forest belt and the Ericaceous belt; the Alpine belt characterizes the Afroalpine Region (Wickens 1976). The Afromontane Region is an archipelago-like centre of endemism mostly found above 2000 m a.s.l. in the Tropics (White 1983a,b). This region extends from Ethiopia in the north to the Cape Province in the south and to the Cameroon mountains in the west, but it is most prominent in East Africa. The altitudinal demarcation between lowland forest and highland vegetation varies: 900 m (Dowsett-Lemaire 1989), 1300-1500 m (Chapman & White 1970; Hamilton 1974), and 1500 m (Friis 1992). According to White (1983a), most Afromontane communities are found above 2000 m a.s.l. but may extend as far down as 1200 m under more oceanic conditions, as in the western Usambara mountains in Tanzania. In the Cape Region, exclaves of Afromontane forests can even be found only a few hundred metres above sea level (White 1983a). The delimitation of the boundary between lowland and upland forest is thus somewhat arbitrary (Lind & Morrison 1974).

A general analysis of the tropical African montane flora is lacking, but according to White (1983a) it comprises at least 4000 species, of which ca. 3000 are endemic to the Afromontane region or almost so; an endemic species being a taxon limited to a stated area. The Afromontane endemics are classified into the following three categories (Chapman & White 1970). These categories were initially based on observations of Malawi forest tree species, but they can also be applied to the montane vegetation elsewhere in Africa (Wickens 1976; Coetzee 1978):

1. Afromontane 'nephews', with a close relationship with the lowland forests of the Guineo-Congolian Region;
2. Afromontane 'orphans', without a close relationship with the humid tropics of Africa;
3. Afromontane flora *sensu stricto*, which never had relatives in the humid tropics of Africa or elsewhere.

In addition to the endemic categories, a few other groups of species are recognized in the description of the Afromontane flora. These are listed and defined as follows:

1. Linking species – species occurring in the Afromontane region and in one or more other phytochoria as well;
2. Marginal intruders – species widely distributed in one phytochorion, but they extend a short distance into one or more adjacent phytochoria;
3. Transgressors (chorological or ecological) – species which occur in two or more major phytochoria and are characteristic members of two or more vegetation types.

At present, the montane forest belt is reduced to insular entities separated by a wide variety of drier vegetation types below their altitudinal limits (Coetzee 1978). The forests of the montane belt have suffered from human impact and have been reduced in extent. Although many forest tree species are endemic to the Afromontane region as a whole, only very few are endemic to a single mountain; neither are there many vicariant species known (Chapman & White 1970). The large variability of Afromontane tree species regarding geographical distribution, ecological amplitude, and growth form makes the classification of the forests very difficult (White 1983a). The following pragmatic forest typology can be adopted: Afromontane rain forest, Undifferentiated Afromontane forest, Dry transitional montane forest, and Single-dominant Afromontane forests, such as *Juniperus procera* forest and *Hagenia abyssinica* forest.

2.6.3 Ethiopia

The principal physical characteristic of Ethiopia is the extension of high altitude areas. Yalden (1983) estimated that of the 371 432 km^2 of land above 2000 m a.s.l., 187 100 km^2, or 50.4%, is found in Ethiopia; for land above 3000 m a.s.l. the corresponding figures are 28 545 km^2, of which 22 750 km^2, or 79.7% is Ethiopian. Within Ethiopia, ca. 15% of the total land area of 1.12 million km^2 is above 2000 m a.s.l. and 2% is above 3000 m a.s.l. Due to the diverse climatic conditions and the high physiographic variability in Ethiopia, an important endemic element in its flora may be expected. Brenan (1978), referring to Cufodontis (1953-1972), concluded that approximately 21% of the 2638 species distinguished are endemic to Ethiopia. An IUCN report from 1986 estimates the size of Ethiopia's flora to be ca. 5750 species. The floristic endemism is paralleled by a faunistic endemism: 3.6% of the birds, and 12.8% of the mammals known in Ethiopia are endemic. There are 242 species of mammals, 847 species of birds and 30 endemic amphibian species found in the country (Sayer et al. 1992). Indeed, most endemics are associated with montane grassland and forest habitats.

As to Ethiopia as a whole, Friis (1986) distinguished three centres of local endemism for both the mountains of Ethiopia and adjoining Somalia, based on topography, rainfall regime, and physiognomy of the vegetation. In a later, more elaborate description (Friis 1992), six local phytochoria were recognized, mainly based on the presence of particular forest types:

1. Lowland dry peripheral Guineo-Congolian forest area, LGC, including the exclave of lowland dry peripheral semi-deciduous Guineo-Congolian forest vegetation in the Nile Valley plains and in the Baro Lowlands.
2. Transitional area between Lowland Guineo-Congolian and Afromontane vegetation, TGC, on the slopes of the SW Escarpment of the NW Highlands.
3. Humid Afromontane area, HUA.
4. Widespread, Afromontane forest area, WIA.
5. Transitional area between Afromontane and Somalia-Masai vegetation, TSM.
6. Riverine forest area, RIV.

A maximum of Afromontane taxa is reached in the phytochoria TGC, HUA, WIA, and TSM. Guineo-Congolian taxa are almost completely restricted to LGC. Overlapping taxa occur in all phytochoria, but are most numerous in the humid types TGC and HUA.

3 Study area: location and description

3.1 Introduction:
Dry and humid Afromontane forests

The four forest sites (Fig. 1) included in this study are different from each other with respect to climate, topography, environment, history of land use and human impact. The characterization of forests as 'moist' or 'dry', and the criteria followed to define the limits are loose. Logan (1946) used altitudinal variation to distinguish between what he calls 'climatic moist woodland' and 'climatic dry woodland' on the Ethiopian Plateau. Trapnell & Langdale-Brown (1962) characterized wet montane forests as those vegetation types with a high proportion of large-leaved and soft-leaved species. The dry montane forests, on the other hand, are described as being dominated by hard-leaved evergreens. Coetzee (1978) considers temperature and moisture to be the important variables that help delimit moist and dry evergreen forests in East Africa. Swaine (1992) described dry forests in West Africa as having two-peak annual rainfall between 850 and 1350 mm, with 6 - 10 dry months of less than 100 mm rain per year.

In the present study, forests are delimited as moist or dry following Gerhardt & Hytteborn (1992), who set the climatic limits for the dry forests to be a drought period of about half the year in one or two periods and an annual precipitation of between 400 - 1700 mm. The moist forests can be climatically delimited as having a period of at least six months of rainfall in one period and an annual precipitation of at least 1700 mm.

Three of the forests in the present study can be considered as dry Afromontane forests, while one is a humid Afromontane forest. The three dry forests are the Chilimo forest, the Menagesha Suba forest and the Wof-Washa forest; the humid forest is the Jibat forest. The mountains and escarpments covered by the forests differ from each other in geographical location, altitudinal variation, exposure and slope. The escarpments containing the Wof-Washa forest extend north-south, and the forest is situated on an eastern slope. The Menagesha forest is situated on the western slope of the mountain which has a north-south alignment. On the other hand, the hill chains bearing the Chilimo forest run from east to west, and the forest is situated on a southern slope.

The only forest among the dry forests that escaped selective cutting for commercial use is the Wof-Washa forest. Considerable exploitation occurred in the Menagesha forest, but there still remains a small patch of the original primary forest. The Chilimo forest is the most severely influenced and this was partly due to its proximity to a town and a motor road. Although there had been some selective cutting in the Jibat forest, the effects are minor also because of its large size.

3.2 The Jibat forest

The Jibat forest is located in western Shewa about 200 km west of Addis Abeba. The forest is situated on the western slope of a mountain range with approximately a north-south alignment (see Fig. 1 in Tamrat 1994). The forest extends between ca. 2000 m and 2950 m a.s.l. (Fig. 5). The soils of this area have not yet been systematically described. However, most of the plateau soils on hillsides and steeper slopes are red to reddish-brown.

At the peak of the mountain, where there is at present an extensive bamboo cover, there are signs of what is believed to be the ruins of a palace from the 15th century. Charcoal pieces and fragments of pottery have been found in soil pits. This indicates that once there was a settled population at the site and that the existing forest includes secondary vegetation. There is one defunct sawmill in the forest; selective cutting and charcoal production (Fig. 6), however, is still in progress. For a more detailed description of the forest area, see Tamrat (1994).

Meteorological data from Shenen at 2550 m a.s.l. (8° 48' N, 37°33' E), a small town at the edge of the forest, are presented here. The mean annual rainfall is 1800 mm, with a high concentration in the months May to October (Fig. 7a). The mean monthly daily temperature maxima range from 21.3 to 23.5 °C, while the means of the daily minima range from 8.8 to 10.1 °C. The mean monthly temperatures range from 15.4 to 16.5 °C, and show little variation. The nights may be cold, especially in winter; hail and frost are not uncommon in the area, as could be observed during the field work. The months November to January are relatively dry.

3.3 The Chilimo forest

The Chilimo forest is situated 90 km west of Addis Abeba, very near to the small town of Ghinchi, and close to the

Fig. 5. A view of part of the Jibat forest at 2400 m a.s.l. Note the variation in tree species of which *Albizia* sp., *Ficus sur* and *Olea welwitschii* are the most abundant at this altitude.

main road running from the capital to western Ethiopia. Its geographical location is 38°10' E, and 9°05' N (Fig. 8). It is situated between ca. 2400 and 2900 m a.s.l. The forest is a small enclave in the western section of a chain of hills and ridges that stretch 200 km from north of Addis Abeba westwards up to the Ghedo Highlands; locally river valleys and gorges cut through the chain. This entire upland is believed to have been covered once by *Juniperus-Podocarpus* forest. Most of this forest has been cleared in order to obtain more agricultural land; at present shrublands of various types (Zerihun & Backéus 1991) dominate most of the landscape. The remaining forests cover an

Fig. 6. Charcoal production in the Jibat forest.

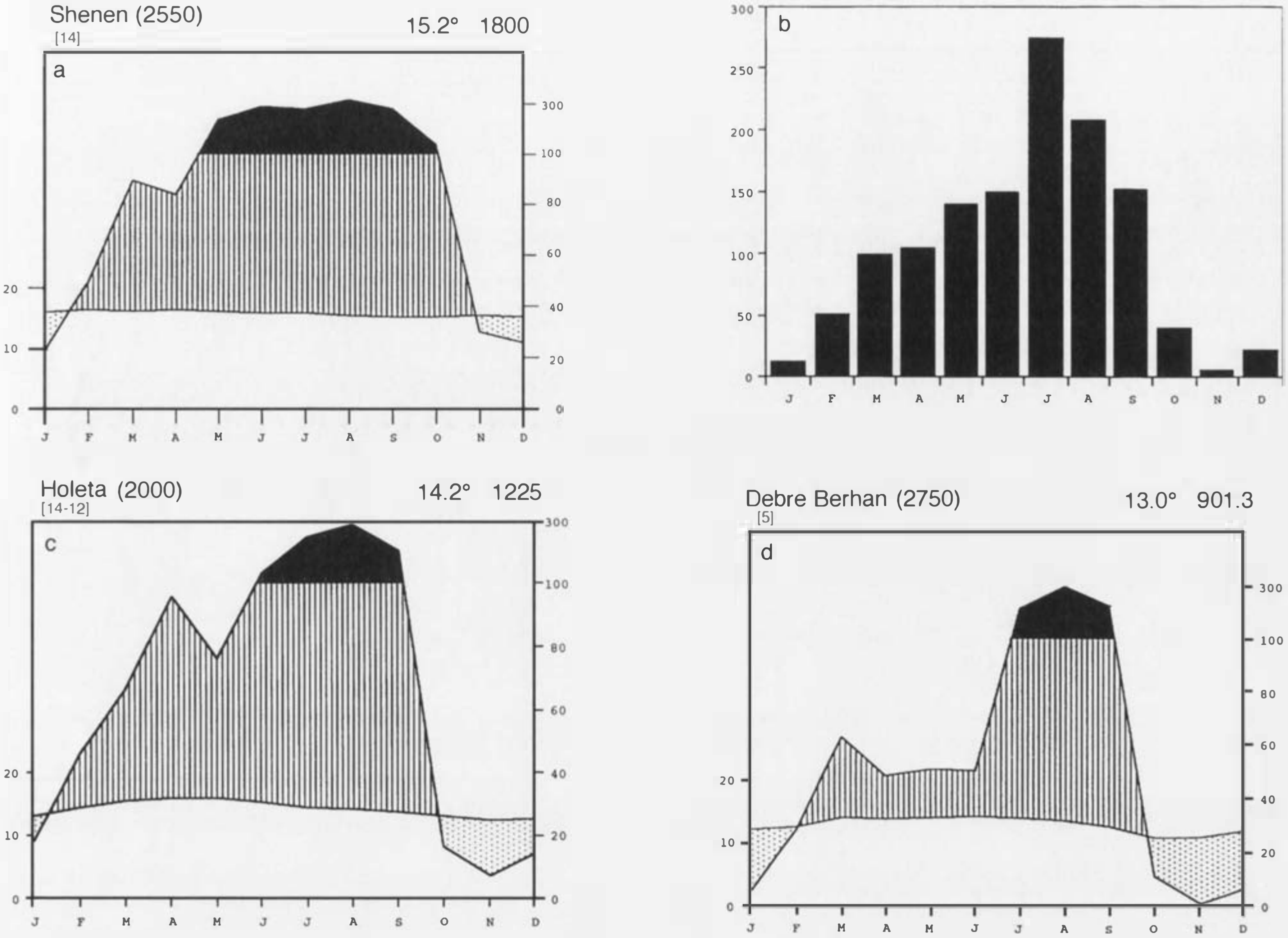

Fig. 7a. Climate diagram for the Jibat forest - town of Shenen, 2550 m a.s.l. (after Walter 1979).
b. Rainfall distribution for the Chilimo forest - town of Ghinchi at 2290 m a.s.l.; monthly values are averages over the years 1983-1989.
c. Climate diagram for the Menagesha forest - town of Holeta, 2000 m a.s.l. (after Walter 1979).
d. Climate diagram for the Wof-Washa forest - town of Debre Berhan, 2750 m a.s.l. (after Walter 1979).

area of ca. 2400 ha. Selective cutting of trees for commercial use has continued until about 1973 (Fig. 9).

Saw mills were established at Jumjum, Gaji, Bejiro and Chilimo, forest sites along the stretch of hills mentioned above. There is virtually no forest remaining at Jumjum, 70 km west of Addis Abeba. A saw mill, supposed to be the oldest in the country (Logan 1946), was in operation for a long time with a production capacity of 100 m^3 of wood per month. Further west along the chain of hills, at Gaji, 80 km west of Addis Abeba, there were three small mills with an estimated output of 350 m^3. Still further west at Bejiro, about 100 km from Addis, there was one mill, producing about 100 m^3 per month. Both these forests have been reduced to small patches of secondary forest vegetation. The saw mill at Chilimo produced an estimated 300 m^3 of wood per month.

The soils are reddish brown, gravelly and shallow at higher altitudes, while at lower sites they tend to become dark-grey and deep. The soils in the surrounding low plains are vertisols, black soils with a characteristic high clay content.

Rainfall data for the period 1983-1989 are shown in Fig. 7b; there are no temperature data available for this site and a climate diagram could not be constructed. The mean annual rainfall is 1264 mm, and there are five rainy months, May-September, with a peak in July.

3.4 The Menagesha Suba forest

The Menagesha Suba forest is located about 15 km to the west of the outer boundaries of the capital city, Addis Abeba. Its geographical location is 38° 35' E, and 9° 00' N (Fig. 10).

The area consists of an almost isolated massif, sur-

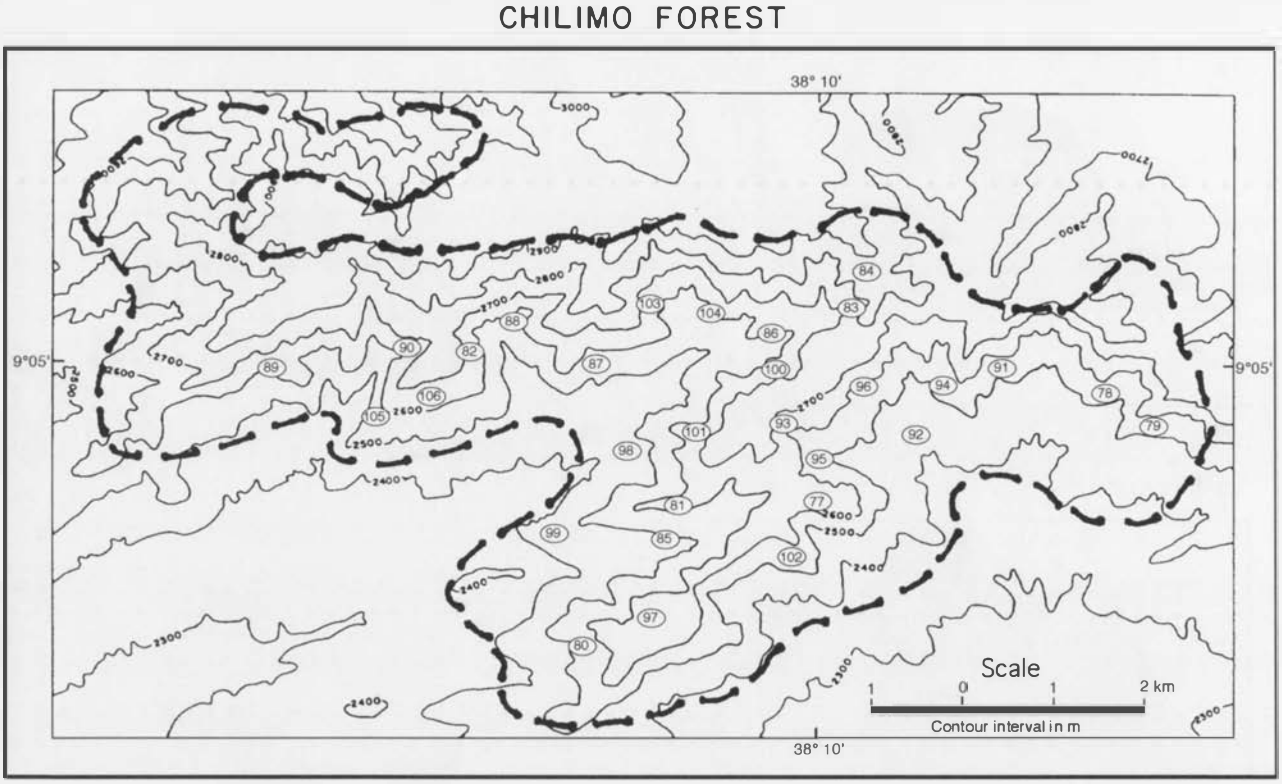

Fig. 8. Topographic map of the Chilimo forest area showing approximate boundaries of the Chilimo forest and the location of the sample plots.

rounded by low-lying plains. The forest is situated on Mt. Wachacha, a denuded silicious volcanic cone (Mohr 1971), which culminates in two prominent peaks, locally known as 'Amota' (3385 m) and 'Mogle' (3220 m a.s.l.). The topography of the area is extremely dissected, with alternating ridges and valleys dominating the landscape. The forest covers the western half of the mountain, while the eastern slope has been turned into farmland. Above 3000 m a.s.l. barley is commonly grown.

The soils at higher altitudes are light brown and shallow; the substrate is locally rocky. At lower altitudes the soils are reddish-brown, deep and less gravelly. The forest has its lower boundary at ca. 2300 m a.s.l. and extends up to ca. 3000 m a.s.l.

Fig. 9. Boundary between the closed forest of Chilimo and grazing land. *Juniperus procera* is the most abundant species here. Note the saw-dust heap in the center of the picture.

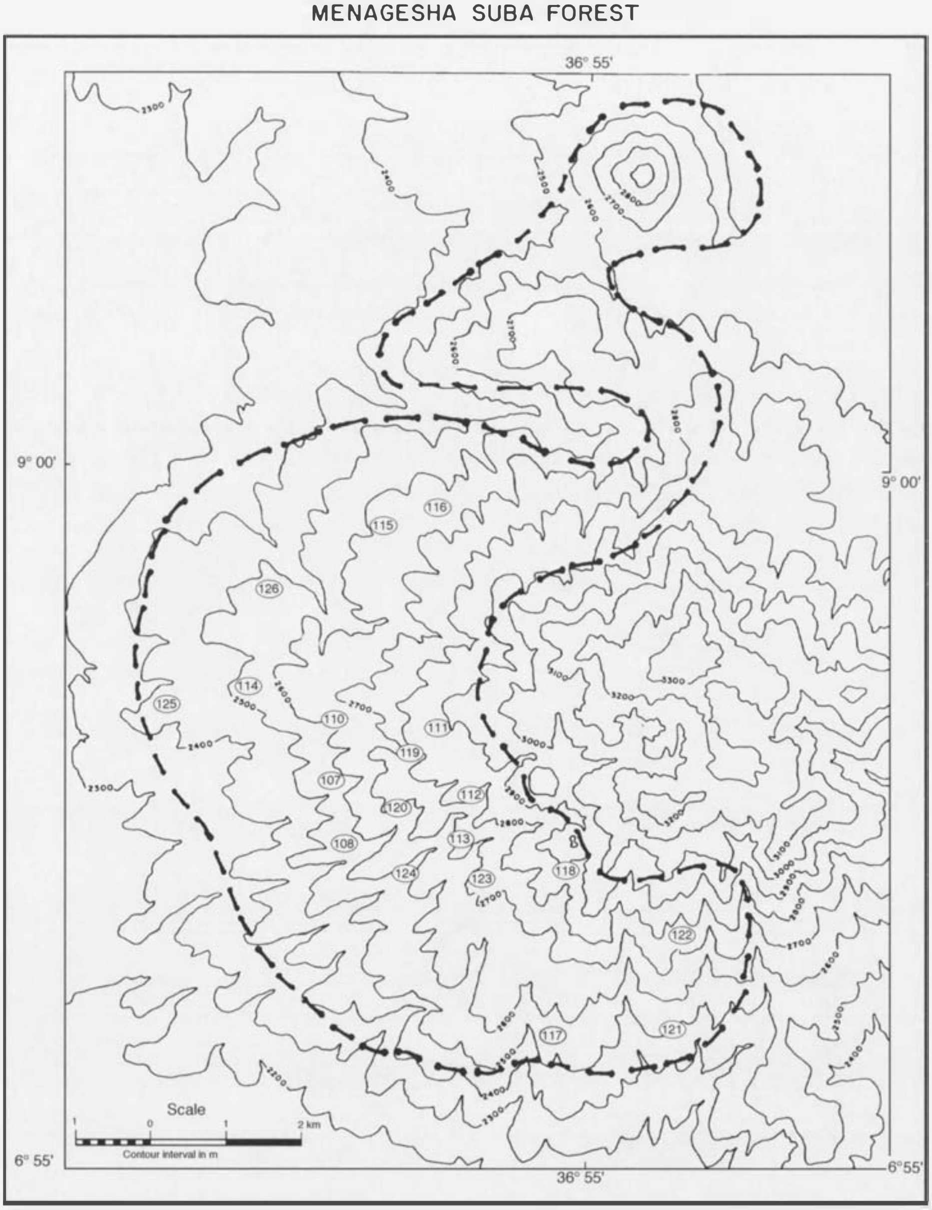

Fig. 10. Topographic map of the Menagesha Suba forest area showing the boundaries of the Menagesha forest and the location of the sample plots.

There are no meteorological data available for the forest. The mean annual rainfall recorded at Holeta at 2380 m a.s.l.; 9° 05' N, 38° 32' E, a town 5 - 7 km west of the forest, is 1225 mm (Fig. 7c). There are six rainy months, April-September, with most rain falling in July-September. The period October-January is relatively dry. The mean monthly daily temperature maxima range from 19.1 to 23.8 °C, and the corresponding minima from 2.4 to 9.2 °C. The mean monthly temperatures range from 12.4 to 15.9 °C. May is the warmest month and November the coldest.

The Menagesha forest is believed to have been planted under King Zera Yakob (1434-1468), who ordered the collection of seeds from the Wof-Washa forest (Sebsebe 1988). The total area covered by natural forests is about 2720 ha; at present only a very small part hereof, ca. 100 - 150 ha, is in a primary state. Because of its proximity to the capital and three other small towns, the forest has been more intensively exploited than the other forests included in this study. The forest became protected for the first time by a Royal Decree in 1888. Soon thereafter, however, exploitation recommenced, and a steam-powered sawmill was established, which produced ca. 150 - 200 m^3 of wood per month (Logan 1946). This plant was abandoned in 1955 in order to preserve the small remains of natural forest.

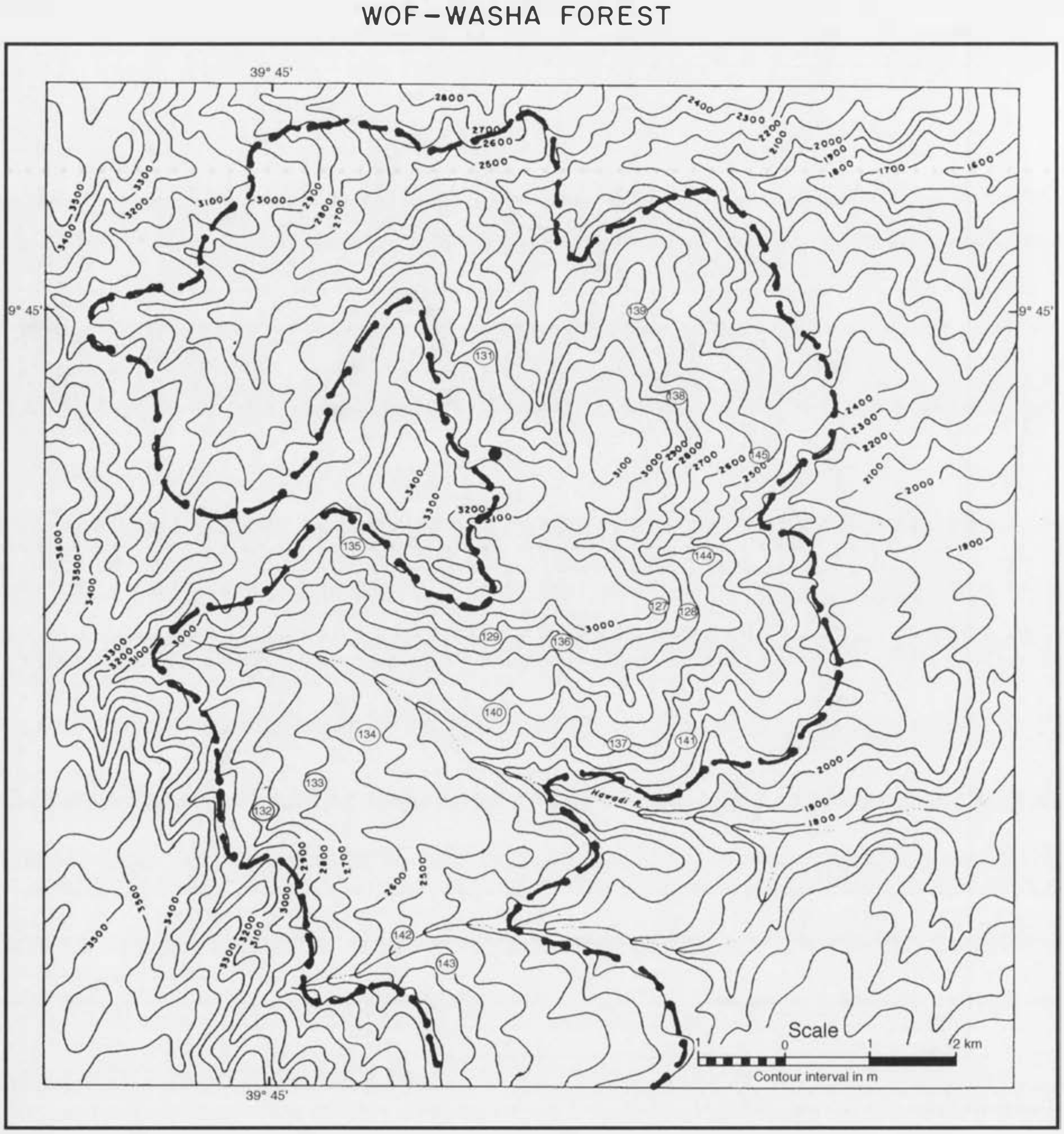

Fig. 11. Topographic map of the Wof-Washa forest area showing the boundaries of the Wof-Washa forest and the location of the sample plots.

3.5 The Wof-Washa forest

The Wof-Washa forest is situated on the slopes of the eastern escarpment of the NW Highlands. The escarpment forms part of the catchment of the Awash river system which drains into the Danakil Plains in the northern section of the Rift Valley. The forest is located between 39° 45' E and 9° 35' N; it covers an area of ca. 3600 ha (Fig. 11). The topography is highly dissected. The slopes of the escarpment are steep and they rise almost abruptly from the lowlands at 2100 m up to about 3600 m a.s.l. (Fig. 12). Outside the northern boundary of the forest the escarpment stretches for 4 - 5 km forming a cliff that falls ca. 100 - 200 m.

The bedrock consists of Termaber basalts, which constitute the major rock type of the region; they are named after the Termaber Pass near Debre Sina (ca. 20 km north

Fig. 12. View towards the southern edge of the Wof-Washa forest. *Juniperus procera* and *Podocarpus gracilior* are the most abundant species here. Note the eroded slopes of the escarpment in the background.

of the forest). The lithology of the area is very heterogeneous (Zanettin et al. 1974). It comprises ferric basalts, fine grained basalts, zeolitised basalts, phonolites, alkali-trachytes, trachyphonolites and subordinate alkaline and peralkaline rhyolites. The basaltic assemblage is reported to be alkaline. The Termaber basalts differ from the typically fissured ones of the plateau, owing to markedly lower SiO_2 and much higher Al_2O_3 and alkali contents. It is worth noting that the alkaline character of the Termaber rocks is essentially due to the high level of Na_2O (Merla et al. 1979). Reddish-brown soils are predominant on slopes, while black soils are prevalent in valley bottoms and on the surrounding highland plains. The soils are very shallow and mostly rocky, especially on the slopes. Soil erosion is a very serious problem in these highlands.

There are no climate data available for the forest area itself. There are two rainy seasons in this region; March-May and July-September (Daniel 1977). The first season includes the so-called 'small rains' which have a peak in April, while the latter season includes the 'big rains' with high concentrations in July and August.

It is worth mentioning here, that cloud persistence is not uncommon in this forest; a phenomenon not observed elsewhere on the Central Plateau. A cloud belt is formed at the altitude of the forest belt and stays for the most part of the day. Hedberg (1964) mentioned that low clouds and mist occur frequently on the upper parts of the mountains of East Africa. Such cloud formation is the result of orographic condensation and forced convective raising. Vascular plants probably can not benefit much from it, but the condensation of fog on foliage can be so great that water drips to the ground and thereby augments the supply of soil moisture (Daubenmire 1947; Kerfoot 1968). It is thought that this cloud formation causes most of the precipitation to occur at the level of the forest belt (Lind & Morrison 1974). Cloud forests, montane forests frequently enshrined by clouds and fog, and benefiting from cloud interception have been described from Colombia by Sugden (1982).

The climate data from Debre Berhan, at 2750 m a.s.l. (9° 40' N, 39 °30' E) and 30 - 35 km west of the forest, can be presented for comparison (Fig. 7d). The mean annual rainfall at Debre Berhan is 901 mm. The small rains come in March and the big rains last from late June to September, with a peak in August. The mean monthly temperatures of the daily maxima in Debre Berhan range from 18.5 to 20.6 °C, and the corresponding minima from 3.2 to 9.2 °C. The mean monthly temperatures range from 11.0 to 14.3 °C.

The Wof-Washa forest is located in a remote area far from roads and towns. Forest products are mainly used by local people, and Wof-Washa is perhaps the only forest on the Central Plateau where commercial exploitation has not taken place.

4 Floristic, environmental and statistical analysis

4.1 Sampling procedure

4.1.1 Vegetation analysis

A reconnaissance survey of the Central Plateau of Shewa was made in October-November 1988. Boundaries of the four forests selected were established on the basis of recent topographic maps, scale 1:50 000. Field data were collected in different periods, as follows:

- Jibat forest, November 1988 to January 1989 and December 1990 to February 1991;
- Chilimo forest, December 1989 to January 1990;
- Menagesha forest, February to March 1990;
- Wof-Washa forest, January to February 1991;

The selection of sample plots and the methods of vegetation and environmental analysis are briefly described here (see further Tamrat 1994).

First a reconnaissance was made across the entire forest in order to obtain an impression about the internal variation in site conditions and physiognomy of the vegetation. Then, sample plots were selected in such a way that the various conditions encountered were represented by at least one sample and the sample plots were more or less evenly distributed throughout the forest. Due to the rough topography and inaccessibility of parts of the forest areas, this latter guideline could not always be followed.

In each plot, the vegetation was described according to the Braun-Blanquet approach (Braun-Blanquet 1964; see Westhoff & van der Maarel 1978). Plots were usually 900 m^2 (30 m × 30 m) in size. Cover-abundance values were estimated for all tree and shrub species following the modified 1 - 9 Braun-Blanquet scale (Westhoff & van der Maarel 1978; van der Maarel 1979), as follows:

r ⇒ 1 (rare)
+ ⇒ 2 (occasional)
1 ⇒ 3 (abundant)
2m ⇒ 4 (very abundant)
2a ⇒ 5 (cover 5 - 12.5%)
2b ⇒ 6 (cover 12.5 - 25%)
3 ⇒ 7 (cover 25 - 50%)
4 ⇒ 8 (cover 50 - 75%)
5 ⇒ 9 (cover > 75%)

Additional tree and shrub species within 10 m distance from the plot's boundaries were recorded as 'present'. Inside the sample plot a 2 m × 2 m subplot was laid out for the analysis of the field layer. Here, cover-abundance values for all herb and graminoid species and the cover of litter were estimated using the same scale. Additional field layer species occurring outside the subplot, but within the sample plot, were noted as 'present'. In this way, the analyses can be considered as relevés in the Braun-Blanquet sense of the word.

The total number and distribution of relevés taken from each forest varied with accessibility but a relevé density of at least one relevé/ 400 ha could be reached:

Forest	Area (ha)	No. of relevés	Running no.	Relevé density (per ha)
Jibat	32 000	77	1 - 77	1/400 ha
Chilimo	2400	30	78 - 107	1/80 ha
Menagesha	2720	20	108 - 127	1/140 ha
Wof-Washa	3600	19	128 - 146	ca. 1/190 ha

Due to an all-weather road passing through the Chilimo forest it was possible to make relatively more relevés in this forest. The 146 relevés included are considered to give a fair representation of the total within- and between-variation of the forests studied. In addition to the floristic analysis, the following notes were made: the total number of dead standing trees was counted, and the occurrence of logs and stumps within the plot were noted. Occurrence of epiphytic bryophytes and lichens were noted.

Plant species were identified and checked at the National Herbarium, Addis Abeba University. Voucher specimens are kept at the National Herbarium. Nomenclature follows Cufodontis (1953-1972). The nomenclature of species belonging to the following families follows I. Hedberg & Edwards (1989): Anacardiaceae, Aquifoliaceae, Celastraceae, Crassulaceae, Fabaceae, Icacinaceae, Meliaceae, Melianthaceae, Moraceae, Pittosporaceae, Rhamnaceae, Rosaceae, Rutaceae, Sapindaceae, Simaroubiaceae, Ulmaceae and Urticaceae. The nomenclature of grasses follows Fröman & Persson (1974) and that of Pteridophyta follows Johns (1991).

Information on the exact location and site conditions is available from the author (at his permanent address) upon request.

4.1.2 Site description and soil analysis

For each plot, altitude (m a.s.l.), slope (°) and aspect were determined. Aspect was indicated with a modified scale, referring to the total amount of solar energy received, based on Zerihun et al. (1989): N = 0, NE = 1, E = 2, SE = 3, S = 4, SW = 3.3, W = 2.5, NW = 1.3, Ridge top = 4.

A composite soil sample of 1 - 1.5 kg was obtained by mixing samples from five different points in the plot, four located in the corners and one in the middle. Separate samples were taken per 10 cm depth until 60 cm depth, or until the bedrock was reached. Soil samples were analysed at the Soil Laboratory of the Ministry of Agriculture, Addis Abeba, following standard procedures (Allen 1989). The following physical and chemical properties were included:

- texture (hydrometer method), with the categories sand, silt and clay, expressed as % weight;
- Organic matter (Walkely-Black wet oxidation) as % dry weight;
- pH and electrical conductivity (mmhos/l) (1:1 soil-water suspension);
- P, as available phosphorus (Bray No. II method) (ppm);
- N, as total nitrogen (Kjeldahl method) (meq./100 g);
- Ca and Mg (atomic absorption method) (meq./100 g);
- Na and K (flame photometry) (meq./100 g);
- Cation exchange capacity (extraction with ammonium acetate at pH 7) (meq./100 g).

4.2 Multivariate analysis

Various multivariate methods were used to describe the floristic composition of the vegetation and to examine the relation between vegetational variation and the variation of the environmental factors involved, particularly the gradient structure.

4.2.1 Classification

Relevés were grouped into clusters with the aid of the programs TABORD (van der Maarel et al. 1978) and TWINSPAN (Hill 1979). First, the Jibat material was treated separately (Tamrat 1994); then the three dry forests were treated separately and subsequently they were treated together.

The following options were chosen in the TABORD program:

- Weighted-Pair-Group Agglomerative clustering with the Similarity Ratio as a measure of resemblance;
- Fusion limit of 0.50;
- Allocation threshold of 0.50 (Jibat), 0.20 (Wof-Washa and Chilimo forests) and 0.25 (Menagesha forest). For the TABORD classification of the three dry forests together, an allocation threshold of 0.25 was used. The resulting cluster structure was then arranged in an ordered phytosociological table (subprogram TABOP) using a frequency limit of 0.60 for characterizing species.

The following options were chosen in TWINSPAN:

- Number of cut levels: 9;
- Minimum group size for division: 2;
- Maximum number of indicators per division: 7;
- Maximum division level: 6;
- Different weights at different cut levels: all set to 1;
- Indicators at different cut levels: all values set to 1.

The final classification was based on a combination of the results from TABORD and TWINSPAN. Generally, the clusters obtained with TABORD at a fusion level of 0.50 (Similarity Ratio) and TWINSPAN at the 5th hierarchical level, were similar, meaning that largely the same relevés were assigned to the same clusters in both procedures. However, the TWINSPAN groups were less homogeneous because some relevés were assigned to a cluster on the basis of the occurrence of certain species which were recognized by TWINSPAN as good indicator species, but which occurred with a low frequency in the cluster under consideration.

Another drawback, related to the previous problem, is that the blocks of species considered characteristic of a certain cluster, are rather loose; many species have a low frequency and occur also in subclusters of another cluster. Thanks to the relocation procedure and the diagonal structuring option in TABORD, the clusters obtained with this program are more homogeneous and can more easily be inspected in the resulting table. In the combined approach followed here, TWINSPAN results were used to start TABORD with a well-prepared initial clustering array.

After seven provisional clusters were obtained for the Jibat humid forest relevés, and ten clusters for the relevés from the three dry forests respectively, the TABORD program was run on the entire material with the same options as mentioned above (except for the allocation threshold, which was 0.20) and with 17 clusters as the optimal solution. This did not alter the composition of the clusters, although some minor differences in the allocation of single relevés occurred. The clusters thus obtained with the program TABORD were characterized as local plant community types, and described as ‘types’, which were provisionally characterized by dominating and/or characteristic species, mainly trees and shrubs, a dominating species having an average cover-abundance value of at least 7, a characteristic species having a high frequency in the type and a lower frequency in most other types.

The community types identified were further characterized by means of environmental factors which appeared to be correlated to the floristic composition of the types. This was achieved with the program DISCRIM (ter Braak 1982, 1986), a program that uses simple discriminant functions based on a set of environmental variables to test for significant separation between groups. DISCRIM is linked to the TWINSPAN program and selects the most discriminating variables at each level of classification; it is helpful in identifying environmental variables that optimally predict the floristic classification.

The community types distinguished were further refined in a synoptic table where each column represents a community type and species occurrences are summarized as synoptic cover-abundance values. These synoptic values are the product of the species' frequency and average cover-abundance values (van der Maarel et al. 1987). Here, the types from both the moist and the dry Afromontane forests will be documented in one table (Table 1).

Finally, the types were named after two (in some cases one or three) of the dominant and/or characteristic species; the first species being one of the canopy or subcanopy species.

4.2.2 Ordination

The main ordination program used was CCA, Canonical Correspondence Analysis (ter Braak 1986, 1987), a technique which reveals linear combinations of environmental variables explaining most of the variation in the species scores along the ordination axes. All species and environmental data were included in this analysis. CCA is sometimes considered as a direct gradient analysis because it is based on the variation in the environmental data included. However, it is at the same time an indirect method because the variation in species occurrences is used. CCA was performed with procedures in the program-package CANOCO (ter Braak 1988).

An analysis of variance (ANOVA) was carried out to find significant differences between the derived community types in terms of the environmental variables. Quantitative relationships between the environmental variables were analysed by calculating a matrix of Pearson's correlation coefficients. Both the ANOVA and Pearson's correlation coefficients were calculated with the General Linear Models (GLM) procedures available in the SAS (Statistical Analysis Systems) program package (Anon. 1990).

As in the clustering procedure, the CCA ordination was first applied to the humid forest and dry forest relevés separately, and then to the entire material. Since the result of this run was overruled by the contrast between one deviating high-altitude type in the moist Jibat forest, a new CCA was run on the entire material after removing the relevés of this 'type'.

4.3 Results

4.3.1 Classification: humid forest types

The 77 relevés from the Jibat forest showed a large variation, with a total of 131 species identified. The results of the programs TWINSPAN and TABORD were largely the same. Because the tabular output of TABORD shows a clearer structure, this output was taken as the basis for the description of the types obtained.

A division of the material into seven clusters was considered optimal; more clusters would give more homogeneous groups, but their ecological interpretation would become more difficult; a smaller number of groups would mean that some groups would become too heterogeneous in terms of floristic composition and environmental characterization. However, one relevé did not show a sufficient similarity with any of the seven clusters and was separated as a cluster of its own (number 8). One other relevé, which did not fit any cluster was considered to represent a fragmentary development and was neglected in all further analyses.

The eight community types obtained in this way were named after one or two of the dominant and/or characteristic tree and shrub species. They are indicated by a running number following the letter 'H' for humid. Here, they will be briefly described under reference to Table 1. A detailed description of the types is given in Tamrat (1994).

H1. *Arundinaria alpina* type

The dominant species in this type is *Arundinaria alpina*, the mountain bamboo. The main associated characteristic species are *Hagenia abyssinica* and *Rapanea simensis* in the tree layer, and *Carex spicato-paniculata* and the grass *Oplismenus compositus* in the field layer.

H2. *Ilex mitis-Rapanea simensis* type

Characteristic tree species in this community type, in addition to the two occurring in the type's name, include *Galiniera coffeoides* and *Olinia aequipetala. Oplismenus compositus* reaches a high abundance in the field layer.

One relevé from the Chilimo forest showed about equal similarity to this type as to the typical Chilimo type D-5, to be described below. It was considered as a transitional relevé and excluded from synoptic community calculations.

H3. *Syzygium guineense-Psychotria orophila* type

The main characteristic species in this type are the dominant tree *Syzygium guineense* and the characteristic shrub *Psychotria orophila.* Further characteristic species are the trees *Apodytes dimidiata*, *Galiniera coffeoides* and *Ilex mitis*, and the shrub *Dracaena afromontana.*

H4. *Olea hochstetteri-Olinia aequipetala* type

This type is characterized by the abundant trees *Olea* and *Olinia*, which are associated with *Lepidotrichilia volkensii* and *Apodytes dimidiata*; *Oplismenus compositus* is the dominant species in the field layer.

H5. *Croton macrostachyus-Ficus sur* type

The most abundant tree species in this type other than the

Table 1. Synoptic phytosociological table of all moist and dry Afromontane forest types. Values are the product of average cover-abundance value and frequency in the type. Only species with at least one value ≥ 1.0 are included, as well as *Aningeria adolfi-frederici*, an important montane tree elsewhere in Ethiopia. Values in bold italics refer to occurrences as characteristic species, as mentioned in the description in Ch. 4.3. The sequence of types follows roughly the arrangement in the ordination diagram of humid and dry forests (Fig. 14b).

Vegetation type	H1	H7	H6	H5	H4	H3	H2	D5	D7	D3	D8	D6	D4	D1	D2	D10	D9	H8
Size	7	2	2	4	16	22	22	20	9	3	4	3	8	9	5	3	4	1
Arundinaria alpina	***9.0***	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hagenia abyssinica	***1.1***	0.0	0.0	0.0	0.1	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0
Impatiens aethiopica	0.0	***9.0***	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Vepris dainellii	0.0	***1.5***	0.0	0.0	0.1	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Syzygium guineense	0.0	***8.0***	0.0	***3.2***	3.2	***6.9***	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Galiniera coffeoides	0.0	***6.5***	0.0	0.1	0.6	***4.3***	***3.8***	0.0	0.1	0.0	0.0	0.0	0.0	0.3	0.1	***3.3***	0.1	0.0
Prunus africana	0.0	***4.0***	1.3	0.1	1.5	0.0	1.0	0.0	1.2	0.0	0.9	0.1	0.1	0.0	0.0	0.0	0.0	0.0
Hippocratea sp.	0.0	0.0	***1.3***	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cassipourea malosana	0.0	0.0	***1.5***	0.4	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
Carex spicato-paniculata	***4.8***	0.0	***8.0***	2.1	0.1	0.0	1.6	0.0	0.0	0.0	***7.0***	***6.3***	1.7	0.0	0.0	0.0	0.0	0.0
Olea welwitschii	0.0	1.0	***7.0***	0.8	0.2	0.0	0.0	3.7	2.1	1.3	3.5	0.8	***4.5***	0.5	0.0	0.0	0.0	0.0
Carissa edulis	0.0	0.0	***4.0***	0.0	0.0	0.0	0.0	1.0	0.4	0.0	0.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0
Millettia ferrruginea	0.0	2.0	***4.0***	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Calpurnea aurea	0.0	0.0	***4.0***	1.7	0.1	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rytigynia neglecta	0.0	0.0	***3.5***	1.3	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Oplismenus compositus	***4.8***	0.5	***4.5***	3.4	***7.1***	1.7	***5.3***	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0
Maytenus addat	0.0	0.0	***4.0***	0.5	0.2	0.2	1.4	***3.7***	***3.6***	0.2	0.4	***4.3***	0.4	0.0	0.0	0.0	0.0	0.0
Hypoestes triflora	0.0	0.0	***5.0***	***5.5***	0.4	0.9	0.5	0.9	***5.8***	0.0	***7.3***	0.2	0.1	0.0	0.0	0.0	0.0	0.0
Teclea nobilis	0.0	0.0	***1.3***	***1.7***	0.3	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Croton macrostachyus	0.0	0.3	0.3	***4.3***	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0
Ficus sur	0.0	0.0	0.0	***3.0***	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0
Ehretia cymosa	0.0	0.0	0.0	***1.5***	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Albizia sp.	0.0	***3.5***	1.0	***4.5***	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Olea hochstetteri	0.0	1.5	***8.0***	***3.6***	***6.0***	2.9	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Olinia aequipetala	0.0	0.0	0.0	0.1	***2.9***	0.7	***3.3***	***4.0***	***4.0***	0.2	2.6	***5.3***	0.1	0.8	0.0	0.1	0.0	0.0
Lepidotrichilia volkensii	0.0	1.3	0.0	0.4	***1.7***	0.7	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Apodytes dimidiata	0.0	0.3	***4.0***	0.3	***4.0***	***2.7***	0.5	0.1	0.1	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Psychotria orophila	0.0	1.3	0.0	0.8	1.2	***5.9***	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Dracaena afromontana	0.0	0.3	0.0	0.0	0.9	***2.3***	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ilex mitis	0.0	0.0	0.0	0.0	0.1	***5.6***	***6.0***	0.0	0.1	0.4	0.0	0.0	0.0	***3.9***	***3.2***	2.2	0.1	0.0
Rapanea simensis	***2.7***	0.0	0.0	0.0	0.2	0.0	***5.7***	0.0	0.3	0.1	0.1	1.6	0.0	0.0	0.0	0.0	0.0	0.0
Hypoestes forskali	0.0	0.0	0.0	0.0	0.1	0.2	0.0	***5.0***	0.0	0.0	0.0	***3.8***	1.2	0.0	0.0	0.0	0.0	0.0
Rhus glutinosa	0.0	0.0	0.0	0.0	0.0	0.0	0.0	***2.2***	1.0	0.0	0.1	0.1	0.8	0.0	0.0	0.0	0.0	0.0
Scolopia theifolia	0.0	0.0	0.0	0.0	0.0	0.0	0.0	***5.6***	1.3	0.0	0.0	0.0	***5.5***	0.2	0.0	0.0	0.0	0.0
Podocarpus gracilior	0.0	0.3	0.0	0.0	0.0	0.0	0.0	***4.5***	***6.6***	0.0	0.1	***6.0***	0.7	0.0	0.0	***6.3***	***7.8***	0.0
Allophylus abyssinicus	0.0	0.3	0.0	0.0	0.1	0.0	0.3	0.5	***3.9***	0.0	***3.8***	0.7	0.4	0.0	0.0	***1.7***	0.6	0.0
Bersama abyssinica	0.0	0.5	0.3	1.3	0.3	0.4	0.2	0.5	***2.1***	0.0	1.0	0.4	0.7	0.0	0.0	0.9	0.8	0.0
Ekebergia capensis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	***1.8***	0.0	0.1	0.7	0.0	0.0	0.0	0.0	0.5	0.0
Thymus sp	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	***1.6***	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Osyris lanceolata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.3	***2.7***	0.1	0.0	0.0	0.4	0.0	0.0	0.0	0.0
Erica arborea	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	***8.7***	0.1	0.0	0.0	0.7	0.0	0.0	0.0	***9.0***
Myrica salicifolia	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	***1.7***	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
Tolpis virgata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	***2.2***	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nuxia congesta	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.6	0.6	***1.3***	0.4	0.4	0.2	0.2	0.0	0.0	0.1	0.0
Juniperus procera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.1	0.1	***6.7***	***8.5***	0.4	***5.0***	***7.1***	***7.8***	1.0	1.8	0.0
Dovyalis abyssinica	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	1.1	0.1	***4.0***	2.0	1.0	0.4	0.2	1.3	0.6	0.0
Sideroxylon gillettii	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	***3.2***	0.0	1.1	0.0	0.0	0.0	0.0	0.0
Myrsine africana	0.0	0.0	0.0	0.0	0.0	0.0	0.1	1.8	0.4	1.3	***4.8***	***4.0***	1.4	***3.3***	***3.6***	0.0	0.1	1.0
Olea europaea	0.0	0.0	0.0	0.0	0.0	0.0	0.0	***3.7***	2.1	1.3	***3.5***	***8.0***	***4.5***	0.5	0.0	0.0	0.0	0.0
Spiniluma oxyacantha	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.3	0.0	0.9	0.1	***6.4***	0.0	0.0	0.0	0.0	0.0
Pittosporum viridiflorum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.3	0.0	***2.7***	0.0	0.0	0.0	0.0	0.0
Ehrharta erecta	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.3	1.1	0.3	0.0	0.2	0.9	***7.7***	0.0	***6.7***	0.1	0.0
Maytenus arbutifolia	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	***2.0***	0.4	1.8	***2.3***	***3.2***	0.9	2.0	0.0
Cynoglossum amplifolium	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.2	***2.6***	0.0	0.0	0.0
Peucedanum winkleri	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	***2.1***	0.0	0.0	0.0
Euphorbia obovalifolia	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	***4.0***	0.0	0.0
Maesa lanceolata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.4	0.0	***2.2***	0.1	0.0
Pavetta abyssinica	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	***1.3***	***1.5***	0.0
Pteris cretica	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	***4.7***	***4.1***	0.0
Geranium arabicum	0.0	0.0	0.0	0.0	0.6	0.1	1.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.6	0.6	1.3	0.0
Aningeria adolfi-frederici	0.0	0.3	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

species occurring in the name, are *Albizia* sp., *Olea hochstetteri* and *Syzygium guineense. Teclea nobilis* is a characteristic shrub. The field layer is heterogeneous and consists mainly of species of *Carex spicato-paniculata* and *Hypoestes triflora*.

H6. *Olea welwitschii-Carissa edulis* type

In this community type, *Olea welwitschii* is the dominant tree while *Carissa edulis* is the dominant shrub. Other characteristic species include *Apodytes dimidiata, Calpurnea aurea, Maytenus addat, Millettia ferruginea, Olea hochstetteri* and *Rytiginia neglecta. Teclea nobilis* is a characteristic shrub. The most important field layer species are *Carex spicato-paniculata, Hypoestes triflora* and *Oplismenus compositus.*

H7. *Syzygium guineense-Vepris dainelli* type

The tree layer in this community comprises the two characteristic species, of which *Syzygium* is dominant, and *Albizia* sp., *Galiniera coffeoides, Millettia ferruginea, Prunus africana, Vepris dainellii.* The field layer consists mainly of the dominant herb *Impatiens aethiopica.*

H8. *Erica arborea* type

This community type is based on a one-relevé cluster; it occurs on a site where the vegetation was burned down 25 years ago. The community is almost entirely composed of *Erica arborea* individuals, 5 - 6 m tall. *Oplismenus compositus* and seedlings of *Myrsine africana* are abundant in the field layer.

4.3.2 Classification: dry forest types

The results obtained with the total set of 69 dry forest relevés, including 102 species, were taken as a basis. In this analysis the results of TWINSPAN and TABORD were not always similar. Again, because of the clearer structure in the output table, the final TABORD results were taken as a basis. The results are included in Table 1.

One relevé, no. 7 from the Chilimo forest, appeared to be insufficiently similar to any other cluster. There are a number of *Juniperus* stumps in this stand. Due to the steep slope, the plot size had to be limited to 750 m^2 in stead of the standard size (900 m^2). This plot was omitted from further analysis. Relevé no. 57 from the Wof-Washa forest, originally assigned to cluster no. 10, was relocated to cluster no. 9 because it was more similar to this cluster as regards the characteristic species. Ten community types were derived from the combined analysis of the three dry forests, and these are indicated with a running number following the letter ‘D’ for dry. They will now be described briefly. It is clear from this description that the dry forest types are more similar to each other than the humid types. *Juniperus procera, Podocarpus gracilior, Maytenus arbutifolia* and *Myrsine africana* occur in most of the types.

The cluster structure of the dry forest relevés showed some changes in the joint treatment of the moist and dry forest material. Types D5 and D6 were now united into one cluster, and so were D9 and D10. The similarity between the relevés of D5 and D6 was considered relatively more important in relation to their joint dissimilarity to the H-types. The same holds for the relevés of D9 and D10. However, the differences between the respective types, which concern some locally differentiating species, were considered large enough to maintain the types.

D1. *Juniperus procera-Myrsine africana-Ehrharta erecta* type

This type has a well-developed tree and shrub layer with old emergent *Juniperus* trees, associated with *Ilex mitis*, which has its optimum in the humid forest. *Maytenus arbutifolia* and *Myrsine africana* are both characteristic in the shrub layer, like in the next type, but *Myrsine* is more abundant. The dominant species in the field layer is the grass *Ehrharta erecta.*

D2. *Juniperus procera-Maytenus arbutifolia-Peucedanum winkleri* type

Juniperus procera is dominant in the tree layer; the associated species include *Ilex mitis* in the tree layer, and *Maytenus arbutifolia* and *Myrsine africana* in the shrub layer. The herbs *Cynoglossum amplifolium* and *Peucedanum winkleri* are abundant in the field layer.

D3. *Erica arborea-Myrica salicifolia* type

Erica arborea forms a well-defined layer in this type. The canopy of the *Juniperus procera* trees is rather discontinuous. Other associated trees and shrubs in this community include *Myrica salicifolia, Myrsine africana, Nuxia congesta, Osyris lanceolata, Olea europaea, O. welwitschii* and *Tolpis virgata. Thymus* sp. is a characteristic component of the field layer.

D4. *Spiniluma oxyacantha-Scolopia theifolia* type

The dominant species in this community type is the tree *Spiniluma oxyacantha,* which forms a canopy at a height of 5 - 7 m. Other tree and shrub species include *Scolopia theifolia, Juniperus procera, Maytenus arbutifolia, Olea europaea, O. welwitschii, Pittosporum viridiflorum and Sideroxylon gilletti.* The most abundant field layer species are *Carex spicato-paniculata* and *Hypoestes forskali.*

D5. *Scolopia theifolia-Podocarpus gracilior* type

Additional associated tree and shrub species in this community type include *Juniperus procera, Olea europaea, O. welwitschii, Olinia aequipetala, Maytenus addat, Myrsine africana* and *Rhus glutinosa.* The grass *Ehrharta erecta* is a characteristic field layer species.

D6. *Podocarpus gracilior-Olea europaea* type
This community type is characterized by *Podocarpus gracilior* and *Olea europaea* as the dominant trees. Other associated species in this group include *Maytenus addat*, *Myrsine africana*, *Olinia aequipetala* and *Rapanea simensis*. *Carex spicato-paniculata* is dominant and *Hypoestes forskali* is abundant the field layer.

D7. *Podocarpus gracilior-Allophylus abyssinicus* type
This community type is found at the lower end of hill slopes and valley bottoms. Characteristic species in this group also include *Bersama abyssinica*, *Ekebergia capensis*, *Maytenus addat*, *Olea europaea*, *O. welwitschii* and *Olinia aequipetala*. The field layer is dominated by *Hypoestes triflora*.

D8. *Juniperus procera-Sideroxylon gillettii* type
Juniperus procera constitutes the dominant tree layer. There is a prominent cover of tree lichens, *Usnea* spp., on the *Juniperus* trees. *Dovyalis abyssinica* is also characteristic for this type. Other tree and shrub species include *Maytenus arbutifolia*, *Myrsine africana*, *Olea europaea*, *O. welwitschii* and *Olinia aequipetala*. The field layer is mainly composed of *Carex spicato-paniculata* and *Hypoestes triflora*.

D9. *Podocarpus gracilior-Maytenus arbutifolia* type
This community type is mainly dominated by *Podocarpus gracilior* in the tree layer. Other important but less abundant species in this type include the tree species *Juniperus procera*, and the shrubs *Maytenus arbutifolia* and *Pavetta abyssinica*. The fern *Pteris cretica* is a characteristic field layer species.

D10. *Euphorbia obovalifolia-Podocarpus gracilior* type
Euphorbia obovalifolia is the most characteristic species of the tree layer. Regenerating *Podocarpus gracilior* trees form a conspicuous subcanopy. Other trees and shrubs in this type include *Allophylus abyssinicus*, *Dovyalis abyssinica*, *Galiniera coffeoides*, *Ilex mitis*, *Maesa lanceolata* and *Pavetta abyssinica*. The ground cover is dominated by *Ehrharta erecta* and *Pteris cretica*.

4.3.3 Community-environment relations

Ordination of the humid forest relevés. Ordination with Canonical Correspondence Analysis of the Jibat relevés (see Fig. 2a in Tamrat 1994) revealed the following relationships between community types and environmental factors. Axis 1 of the ordination diagram reflects mainly a gradient in altitude, organic matter, phosphorus and cation exchange. Axis 2 reflects a gradient in calcium, pH and sand. The *Arundinaria alpina* type (H1) is clearly differentiated from the other community types H2 - H7, both along the first and the second axis. It is an outspoken high altitude type. Fig. 2b in Tamrat (1994), presenting the CCA ordination of all relevés except those of type H1, shows more clearly than Fig. 2a that altitude is the main differentiating factor for the other types, with type H2, *Ilex mitis-Rapanea simensis*, at the relative higher altitudes and type H5, *Croton macrostachyus-Ficus sur* at lower altitudes. Along axis 2 the differentiation is according to general nutrient status with types H2 and H5 on the richer soils and types H3, *Syzygium guineense-Psychotria orophila* and H7, *Syzygium guineense-Vepris dainelli* on the poorer soils.

Examination of the relationships between environmental variables revealed a strong correlation between altitude, organic matter, silt, cation exchange, nitrogen and phosphorus. The correlation between altitude and soil development has been further discussed by Tamrat (1994). There is also a correlation between altitude and slope steepness, which means that steep slopes are more common at higher altitudes. Clay content showed a negative correlation with silt and altitude. Further attempts were made to describe the community types in relation to those environmental factors that optimally predict the classification. This can be achieved with the program DISCRIM. Altitude is identified as the variable differentiating between the TWINSPAN clusters at the first and second levels of division. At lower levels in the hierarchic classification, it was possible to arrive at a more meaningful interpretation by using both species composition and environmental variables.

Ordination of the dry forest relevés. The results of the ordination with Canonical Correspondence Analysis of the relevés of the dry Afromontane forests of Chilimo, Menagesha and Wof-Washa is shown in Fig. 13a. The eigenvalues for axis 1 and axis 2 are 0.36 and 0.29 respectively.

Axis 1 reflects an altitudinal gradient; communities at high altitudes, particularly D2, *Juniperus procera-Maytenus arbutifolia-Peucedanum winkleri* and D3, *Erica arborea-Myrica salicifolia*, are shown to the right of the axis, while those occurring at lower altitudes are found to left. Axis 2 reflects a soil fertility gradient, with phosphorus as the most significant factor. The community types D9, *Podocarpus gracilior-Maytenus arbutifolia* and D10, *Euphorbia obovalifolia-Podocarpus gracilior*, occurring on soils with a high content of phosphorus, have high positive scores on axis 2. Community types on soils with a low phosphorus status, including D3, have negative scores. In terms of individual species one may conclude that *Podocarpus* is indifferent regarding the soil fertility gradient, and that *Maytenus arbutifolia* is indicative of the richer part, while *Scolopia theifolia* is indicative of the poorer part.

Some environmental variables are related to both axes. Phosphorus, having its clearest expression along axis 2, is also related to axis 1. Soil texture and organic matter also show this diagonal trend.

Table 2 presents information on the canonical coefficients and *t*-values of the regression coefficients of the various environmental variables on the two axes, as produced by the CANOCO program (ter Braak 1988). Since this Canonical Correspondence Analysis is used here as an exploratory technique one should not claim statistical significance for these coefficients. Still, the combined figures for altitude and phosphorus clearly indicate that these are the main environmental variables.

The results of the classification are generally in agreement with the configuration of the corresponding relevé positions in the ordination diagram (Fig. 13a). Generally, the types D1, D2, D3, D9 and D10, which are found towards the positive ends of axes 1 and 2, are well-separated, whereas the points representing types D4-D8 and most of the relevés of type D5, form a cloud in the left-central part of the diagram. This is due to the masking effect of either altitude or phosphorus, i.e. the relevés of these types are similar in their altitude or phosphorus status.

Table 2. Canonical coefficients (cc) of environmental variables on axes 1 and 2 of the Canonical Correspondence Analysis of (a) all Dry forest relevés; (b) Dry forest types D4-D8 only. *t*-values of the regression coefficients (ter Braak 1988) are added; critical value (df ≥ 18, $\alpha = 0.05$) = 2.1.

	a				b			
Axis	1		2		1		2	
Eigenvalue	0.36		0.29		0.26		0.18	
	cc	*t*	cc	*t*	cc	*t*	cc	*t*
Altitude	0.6	6.1	–0.4	–3.5	0.0	–0.1	0.4	2.1
Slope	0.0	–0.1	0.2	1.7	0.0	–0.4	–0.3	–1.9
Exposure	–0.1	–1.2	–0.1	–1.3	0.0	–0.4	0.1	0.4
Sand	–0.1	–0.3	–0.1	–0.2	0.1	2.1	–3.5	– 4.1
Silt	–0.9	–0.7	–1.2	–0.8	2.9	2.1	–1.0	– 4.3
Clay	–0.7	–0.5	–1.4	–0.9	3.2	2.1	–1.1	– 4.4
pH	–0.1	–1.3	0.2	1.8	0.2	2.2	0.5	2.2
Electrical conductivity	–0.1	–0.6	0.1	1.1	0.0	0.1	–0.1	–0.5
Na	0.0	0.0	0.1	0.7	0.3	1.8	–0.4	– 1.4
K	–0.1	–1.3	0.0	–0.2	–0.1	–0.6	0.0	0.1
Ca	–0.2	–1.2	0.1	0.6	–0.2	–1.2	–0.2	– 0.6
Mg	–0.1	–0.6	0.0	0.4	–0.1	–0.5	0.1	0.8
Cation exchange capacity	0.0	–0.3	0.3	2.1	–0.4	–2.4	0.0	0.1
Organic matter	0.2	0.8	0.2	1.0	0.3	1.0	–0.8	–1.8
N	0.1	0.7	–0.3	–1.5	–0.2	–1.0	0.6	1.3
P	0.2	2.3	0.6	4.6	0.2	2.0	0.0	–0.1

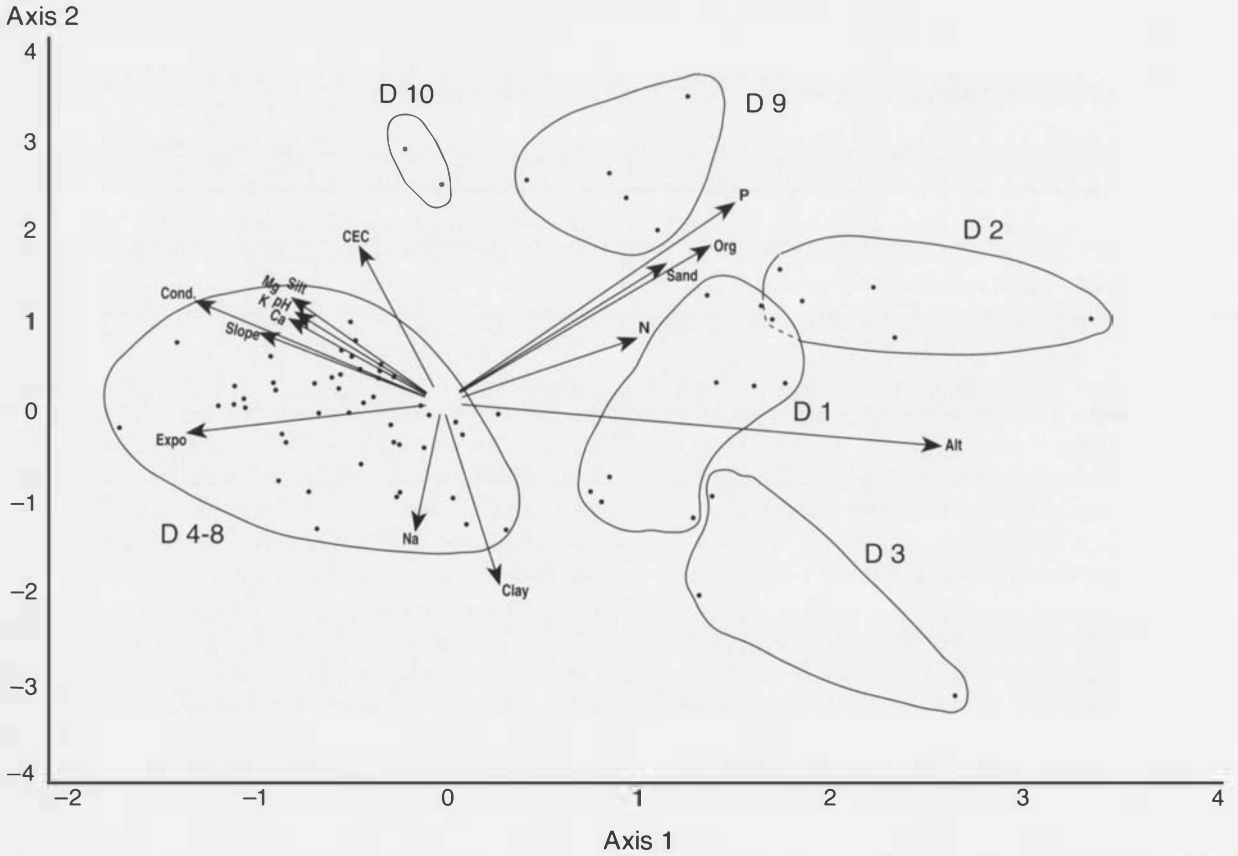

Fig. 13. a. Ordination diagram with axes 1 and 2 of a Canonical Correspondence Analysis of all relevés and environmental data of the dry forests of Chilimo, Menagesha and Wof-Washa. The position of the types D1 - D10 is indicated. Note the dense cloud of points representing clusters D4 - D8. Environmental vectors (for abbreviations, see Table 4) enlarged with a factor 3.

To find out whether there are any environmental gradients which may be correlated with floristic variation within these groups, a separate ordination was performed only for the relevés of community types D4 - D8. The eigenvalues for this CCA for axis 1 and axis 2 are 0.26 and 0.18 respectively (Table 2). The diagram for this ordination is shown in Fig. 13b. In this diagram, it appears more clearly that the community types D4 - D8 are arranged more or less along the same soil fertility gradient as detected in the entire material (Fig. 13a). Now, it is particularly the contrast between a high soil sodium content and high potassium and magnesium contents. Community types D4, *Spiniluma oxyacantha-Scolopia theifolia*, and D8, *Juniperus procera -Sideroxylon gilletti,* at the right-hand side of the diagram, are correlated with high values for sodium and phosphorus, while community types D5, *Scolopia theifolia-Podocarpus gracilior*, and D7, *Podocarpus gracilior-Allophylus abyssinicus*, at the left-hand side of the diagram, have high values of calcium, magnesium, nitrogen, organic matter and cation exchange capacity.

Axis 2 of the restricted ordination reflects to some extent the altitudinal variation (which is reflected more clearly in Fig. 13a). Type D8 is the higher-altitude type within the group D4-D8. Soil texture, particularly the amount of sand, which was shown to form an additional gradient along axis 1 of Fig. 13a, is now clearly related to axis 2, with type D7 as the most indicative type. Clay is negatively correlated with axis 2, which is related to the difference between types D4 (high clay content) and D7.

Relations between Dry forest communities and their environment. In addition to the observations reported in the previous sections some statistical tests concerning community-environment relations for the Dry forest communities and correlations among the environmental factors are presented. An analysis of variance (ANOVA) was performed to see if there is any significant variation among the community types of the dry forests with respect to any one environmental factor. This was achieved by the Tukey test (Anon. 1990). The results of this analysis are shown in Table 3. Significant variations between community types were obtained for all variables except slope, exposure and sodium.

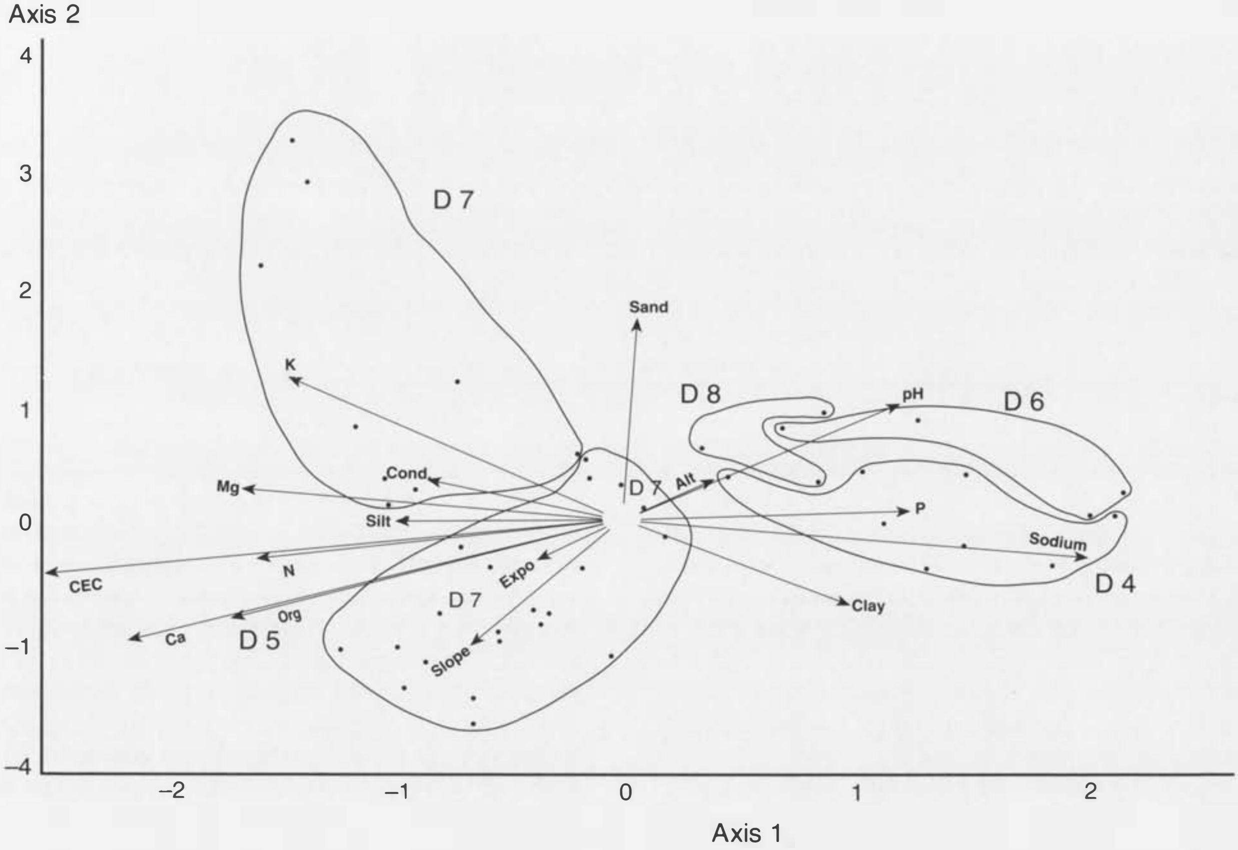

Fig. 13. b. Ordination diagram with axes 1 and 2 of a Canonical Correspondence Analysis, with only the relevés of types D4 - D8 included. Environmental vectors (for abbreviations, see Table 4) enlarged with a factor 3.

Table 3. Tukey's multiple range test between environmental variables and the Dry forest community types D1 - D10. Different letter notations within each row indicate significant differences at $p < 0.05$.

Community type	1	2	3	4	5	6	7	8	9	10
Altitude	2833	2900	2867	2575	2588	2647	2581	2643	2540	2583
	a	a	a	b	b	b	b	b	b	b
Slope	20	21	14	21	28	23	23	28	25	28
	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Exposure	1.3	1.5	1.9	2.3	2.7	2.2	3.0	3.3	1.0	2.3
	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Sand	11.5	14.7	6.0	6.9	5.0	7.7	8.9	6.4	12.7	10.3
	abc	a	bc	bc	c	abc	abc	bc	ab	abc
Silt	72.6	69.7	57.1	65.0	71.0	80.6	76.8	69.3	73.5	82.3
	ab	ab	b	ab	ab	a	ab	ab	ab	a
Clay	15.9	15.7	36.9	28.2	23.9	11.7	13.4	24.4	12.8	7.3
	bc	bc	a	ab	abc	bc	bc	abc	bc	c
pH	6.23	6.08	5.57	6.46	6.07	6.8	6.4	6.8	6.7	6.6
	ab	ab	b	a	ab	a	ab	a	a	a
Electrical conductivity	0.27	0.36	0.15	0.3	0.35	0.41	0.42	0.30	0.40	0.28
	ab	a	b	ab	a	a	a	ab	a	ab
K	0.97	1.09	0.51	0.38	1.11	0.89	1.92	1.55	0.70	0.80
	ab	ab	b	b	ab	ab	a	ab	b	ab
Na	0.64	0.14	0.40	1.32	0.42	1.21	0.30	0.80	0.15	0.27
	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Ca	34.3	22.3	9.67	12.1	37.9	20.6	33.5	23.2	5.50	50.5
	ab	ab	b	b	ab	ab	ab	ab	b	a
Mg	6.16	6.58	2.97	4.20	7.51	6.63	9.34	5.53	5.68	6.80
	ab	ab	b	ab	ab	ab	a	ab	ab	ab
Cation exchange capacity	65.2	58.8	41.7	41.0	63.0	44.9	64.8	49.1	60.6	64.1
	a	abc	c	c	ab	bc	ab	abc	abc	ab
Organic matter	14.1	12.0	7.60	4.94	8.91	5.87	8.81	6.50	16.1	15.1
	ab	abc	bc	c	abc	c	abc	c	a	a
N	0.67	0.52	0.50	0.29	0.43	0.34	0.50	0.30	0.61	0.47
	a	ab	ab	b	ab	ab	ab	ab	ab	ab
P	16.4	43.4	2.10	6.54	5.24	13.2	2.23	13.7	56.7	57.3
	b	a	b	b	b	b	b	b	a	a

The community types can be generally grouped into two main groups, which are differentiated regarding altitudinal variation: types D1 - D3, which are found above ca. 2800 m, and types D4 - D10 found below ca. 2800 m a.s.l. Soil pH shows a more or less inverse trend to that of altitude; it is high at low altitudes and low at high altitudes. Organic matter and phosphorus show similar changes; their quantities are high at low altitudes and decrease towards high altitudes.

The changes among other environmental variables do not follow a general pattern, but rather differ from one type to another. The relationship between the variables was assessed by computing Pearson's product-moment correlation coefficient. The results are presented in Table 4.

Altitude is positively correlated with organic matter, nitrogen and sand, but it is negatively correlated with exposure and pH. Slope shows a strong correlation with calcium and cation exchange capacity. Among the soil inorganic particles, clay is negatively correlated with sand and silt. The factors calcium, magnesium, nitrogen, organic matter, and cation exchange capacity show a strong correlation in most cases; calcium is highly correlated with magnesium, cation exchange, and nitrogen. Cation exchange is strongly correlated with organic matter and nitrogen, while nitrogen and phosphorus are highly correlated with organic matter. Sodium and clay, on the other hand, are negatively correlated with most soil nutrients but slightly positively correlated with each other.

Table 4. Pearson's product-moment correlation coefficient for correlations between environmental variables. *** = $p < 0.001$; ** $p < 0.01$; * = $p < 0.05$; ns = not significant.

	Alt	Slope	Expo	Sand	Silt	Clay	pH	Cond	Na	K	Ca	Mg	CEC	Org	N	P
Altitude	-															
Slope	−0.09 ns	-														
Exposure	−0.30 *	0.14 ns	-													
Sand	0.33 **	−0.04 ns	−0.20 ns	-												
Silt	−0.05 ns	0.30 *	−0.05 ns	−0.02 ns	-											
Clay	−0.07 ns	−0.25 *	0.13 ns	−0.41 ***	−0.91 ***	-										
pH	−0.25 *	0.28 *	0.05 ns	0.21 ns	0.33 **	−0.39 ***	-									
Electrical conductivity	−0.28 *	0.16 ns	0.15 ns	0.09 ns	0.32 **	−0.34 **	0.34 **	-								
Na	−0.05 ns	−0.15 ns	0.07 ns	−0.38 **	−0.11 ns	0.26 *	0.17 ns	0.01 ns	-							
K	0.00 ns	0.20 ns	0.08 ns	0.21 ns	0.26 *	−0.34 **	0.17 ns	0.29 *	−0.48 ***	-						
Ca	0.09 ns	0.44 ***	0.14 ns	−0.03 ns	0.43 ***	−0.38 **	0.21 ns	0.24 *	−0.23 ns	0.33 **	-					
Mg	−0.01 ns	0.29 *	0.06 ns	0.09 ns	0.35 **	−0.36 **	−0.01 ns	0.28 *	−0.37 **	0.42 ***	0.49 ***	-				
Cation exchange capacity	0.13 ns	0.32 **	−0.02 ns	0.15 ns	0.52 ***	−0.54 ***	0.16 ns	0.34 **	−0.39 ***	0.48 ***	0.75 ***	0.58 ***	-			
Organic matter	0.35 **	0.12 ns	−0.18 ns	0.41 ***	0.45 ***	−0.58 ***	0.21 ns	0.09 ns	−0.38 **	0.17 ns	0.47 ***	0.20 ns	0.63 ***	-		
N	0.39 **	0.09 ns	−0.14 ns	0.30 *	0.39 **	−0.48 ***	0.17 ns	0.08 ns	−0.35 **	0.24 ns	0.48 ***	0.19 ns	0.57 ***	0.85 ***	-	
P	0.15 ns	−0.10 ns	−0.22 ns	0.53 ns	0.15 ns	−0.36 ns	0.20 ns	0.04 ns	−0.31 *	−0.12 ns	−0.13 ns	−0.01 ns	0.12 ns	0.48 ***	0.22 ns	-

Ordination of the moist and dry forest relevés together. In order to detect the overall environmental variation underlying the floristic variation in the four Afromontane forests, as well as the floristic relations between the humid and dry forest types, a CCA ordination was performed on all relevés together (with the exception of one Jibat and one Chilimo relevé, as mentioned above). The eigenvalues for axis 1 and axis 2 are 0.53 and 0.32 respectively. These values are considerably higher than in both the Dry forest ordination (see above) and the Humid forest ordination (Tamrat 1994), indicating a good recovery of the now much bigger environmental variation included. Fig. 14a presents the results. Since it is impossible to reproduce the position of the individual relevés with their number, this figure only presents the coherence of positions within vegetation types. Table 5 shows the allocation of the individual 144 relevés to the 18 vegetation types.

The main division is again according to altitude, with types H2-H7, D1-D10 and H1 separated. Also, pH and phosphorus are important along axis 1. Table 6 gives the canonical coefficients and *t*-values of the regression coefficients for the environmental variables on the axes 1 and 2.

Table 5. Allocation of 144 relevés to the 18 vegetation types. H = humid forest types; D = dry forest types. J = Jibat forest; Ch = Chilimo forest; M = Menagesha forest; W = Wof-Washa forest.

H1	J 44-50
H2	J 1, 2, 8, 9, 11, 15, 18-21, 35, 51-58, 60, 61, 75
H3	J 13, 14, 16, 17, 22-25, 40-43, 59, 63-69, 73, 74
H4	J 3-7, 10, 12, 28, 32-34, 36-38, 62, 72
H5	J 29-31, 39
H6	J 26, 27
H7	J 70, 71
H8	J 76
D1	M 117, 121, 122; W 126-128, 130, 131, 135
D2	W 129, 134, 137-139
D3	Ch 83; M 110, 111
D4	M 113-116, 120, 123-125
D5	Ch 77-80, 82, 84, 86-89, 95-100, 102-105
D6	M 108, 109, 118
D7	C 81, 85, 90-94, 101; W 133
D8	M 106, 107, 112, 119
D9	W 132, 141-144
D10	W 136, 140

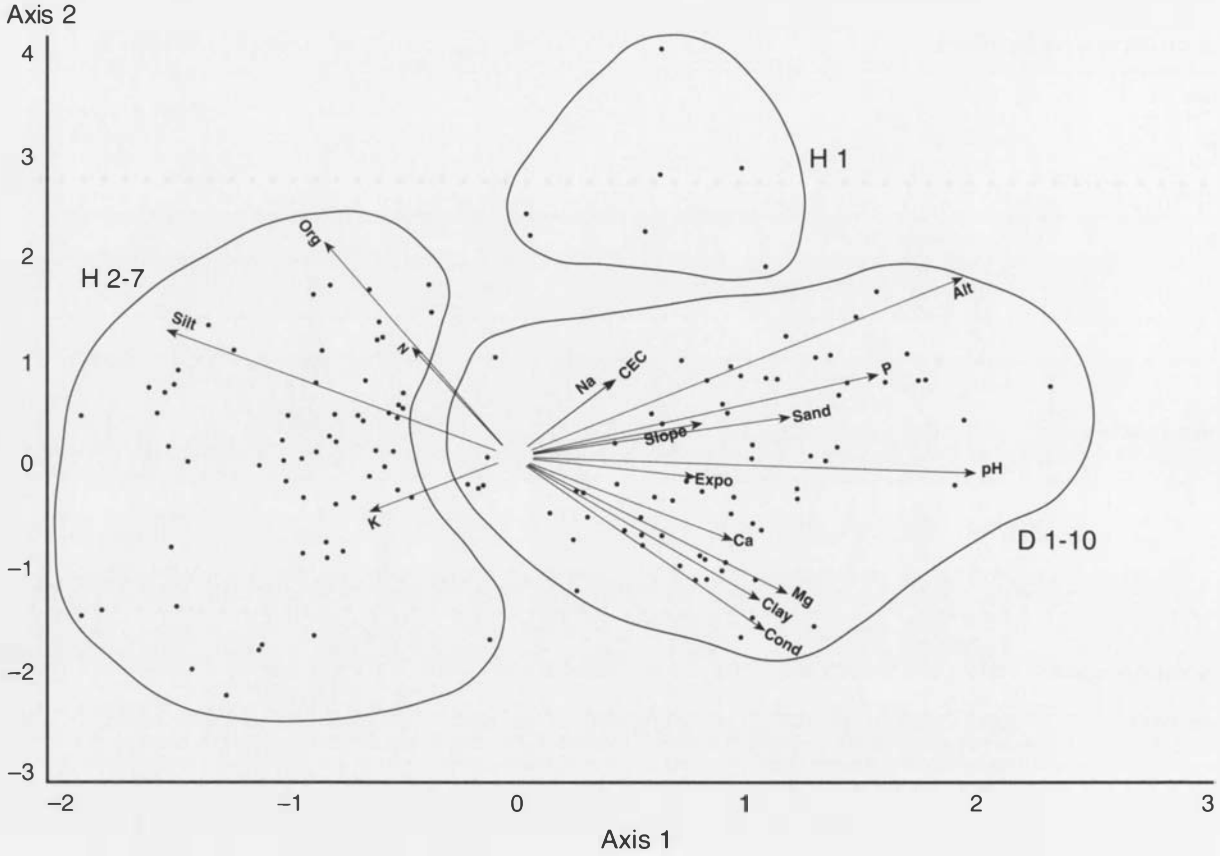

Fig. 14. a. Ordination diagram with axes 1 and 2 of a Canonical Correspondence Analysis of all relevés and environmental data of the humid forest of Jibat and the dry forests of Chilimo, Menagesha and Wof-Washa. Environmental vectors (for abbreviations, see Table 4) enlarged with a factor 3.

Table 6. Canonical coefficients (cc) of environmental variables on axes 1 and 2 of the Canonica Correspondence Analysis of (a) all Humid and Dry forest relevés except that of type H8; (b) all Humid and Dry forest relevés, except those of types H8 and H7. *t*-values of the regression coefficients (ter Braak 1988) are added; critical value (df ≥ 18, $\alpha = 0.05$) = 2.1.

	a				b			
Axis	1		2		1		2	
Eigenvalue	0.36		0.29		0.26		0.18	
	cc	t	cc	t	cc	t	cc	t
Altitude	0.5	9.9	0.4	6.1	0.5	10.2	0.1	2.0
Slope	0.0	0.7	0.1	1.7	0.0	0.5	0.1	2.1
Exposure	0.1	1.0	0.1	1.1	0.1	1.2	0.0	– 1.0
Sand	–0.3	–0.9	–0.9	–2.4	–0.7	–1.7	–0.4	–0.9
Silt	–0.8	–0.9	–2.6	–2.6	–1.9	–1.7	–1.9	–1.5
Clay	–0.5	–0.6	–2.9	–2.8	–1.6	–1.5	–2.2	–1.7
pH	0.3	5.2	0.1	0.8	0.4	5.8	–0.2	–2.7
K	–0.2	–2.7	–0.1	–1.4	–0.2	–3.4	0.0	0.0
Na	–0.1	–0.9	0.0	–0.3	–0.1	–1.7	0.1	1.0
Ca	0.0	–0.4	–0.2	–2.2	–0.1	– 0.1	–0.1	–0.6
Electrical conductivity	0.1	0.8	–0.3	–4.5	0.0	0.1	–0.2	–2.1
Mg	0.1	2.3	–0.3	–4.7	0.1	1.8	–0.3	–4.3
Cation exchange capacity	0.2	2.3	0.1	0.8	0.2	2.7	–0.1	– 1.2
Organic matter	–0.4	–4.5	0.4	3.8	–0.3	–3.9	0.4	3.9
N	0.1	1.9	–0.2	–2.2	0.1	1.5	–0.2	–2.2
P	0.2	3.8	0.1	1.6	0.2	2.9	0.6	7.5

The variation according to altitude runs slightly diagonally from the lower left to the higher right part of the diagram. Perpendicular to this variation there is variation according to the amount of organic matter. The relevés of the Jibat type H1, *Arundinaria alpina*, are characteristic of a combination of high altitudes and high amounts of organic matter.

In order to obtain a clearer structure in the remaining H-types and the D-types, the CCA was repeated after removal of the seven H1 relevés (Fig. 14b). The eigenvalues for axis 1 and axis 2 are 0.54 and 0.29, i.e. roughly the same as in the previous ordination. The individual position of the relevés is indicated again without numbers, but now the types the relevés belong to, are indicated with separate numbers. The main structure in the diagram suggests the separate position of H-types within the Jibat forest, D-types within the Wof-Washa forest and D-types within a complex of the Chilimo and Menagesha forests. Within these main groups the community types are not very well separated. This illustrates the difference between the two procedures TABORD and CCA: in TABORD the overall floristic similarity of relevés is

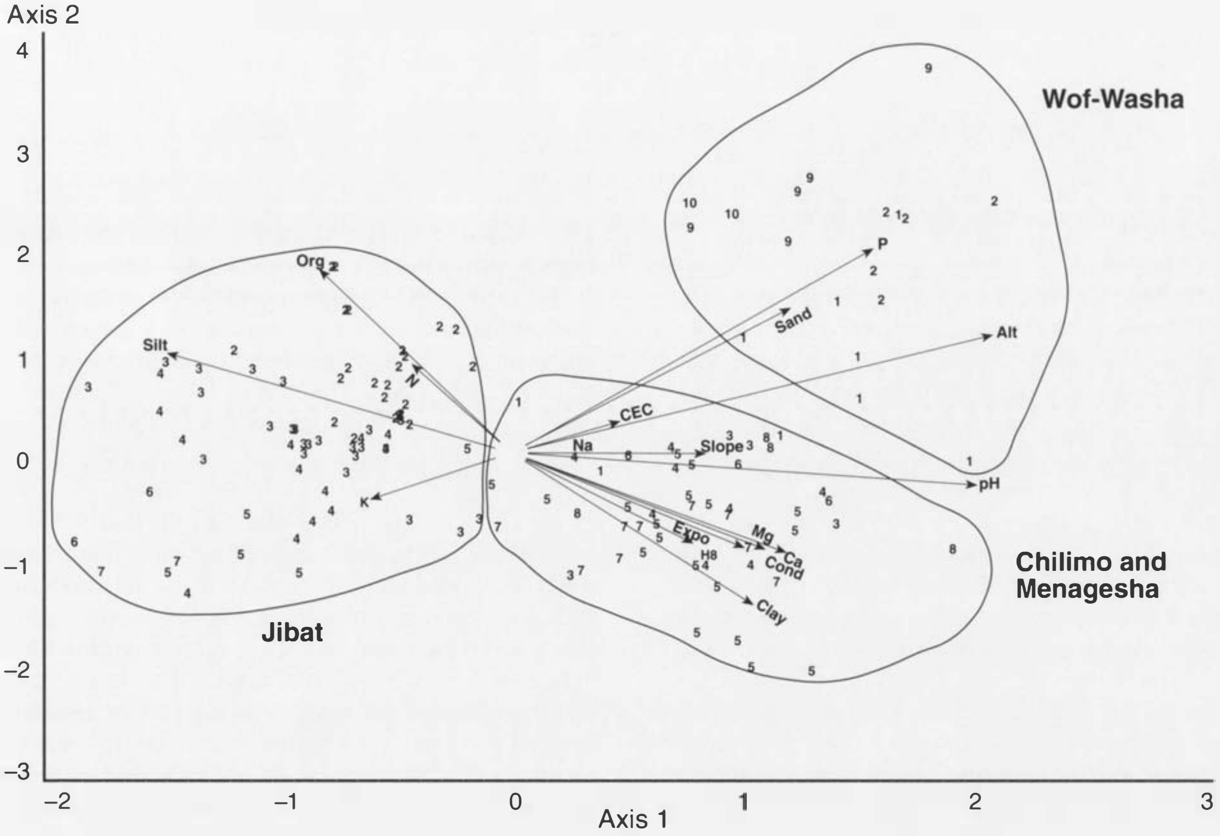

Fig. 14. b. Ordination diagram with axes 1 and 2 of a Canonical Correspondence Analysis, relevés of high-altitude Jibat types H1, *Arundinaria alpina,* and H8, *Erica arborea,* omitted. Position of the types H2 - H7 and D1 - D10 is indicated. Environmental vectors (for abbreviations, see Table 4) enlarged with a factor 3.

decisive, while in CCA the differences between the relevés regarding the ecologically differentiating species are more important. Still, some general conclusions are possible. First, the main differentiation is between the moist forest types and the dry forest types, which are clearly separated along axis 1. As in the ordinations of the separate forest types, altitude is a main differentiating factor, which seems somewhat surprising, because the altitudinal spectrum of H-types is relatively broad. However, the high-altitude H-types were removed from the analysis! A further differentiating contrast is between the soils of Jibat, with a high silt content, on the one hand, and either a higher clay or a higher sand content predominating in the dry forests (Table 6). In spite of the variation in these textural components, the soil class for most types is silty loam.

Along axis 2, most of the Wof-Washa dry types are separated from the types of Chilimo and Menagesha, which themselves are not separated. Type D1, *Juniperus procera-Myrsine africana*, is represented in both Wof-Washa and Menagesha. Environmentally, the differentiation is determined mainly by pH, phosphorus and soil texture.

Based on the similarity between types and while also taking the position of the relevés in Fig. 14b into account, an arrangement of types is possible in the following way: H7 → H6 → H5 → H4 → H3 → H2 → D5 → D7 → D3 → D8 → D6 → D4 → D1 → D2 → D10 → D9. This sequence is adopted in Table 1. Type H8, *Erica arborea* - represented by only one relevé - is found in the middle of types mainly found in the Menagesha forest, which share *Erica arborea* and *Myrsine africana* with it.

Although the dry and humid forest types are generally clearly separated, there are some links between the two groups. One link is between type H2 and nearby relevés of the Chilimo types D5 and D7, with *Maytenus addat* and *Olinia aequipetala* as linking species, the other link connects types H2 and H3 with the Wof-Washa type D10, with *Galiniera coffeoides* and *Ilex mitis* as connecting species.

5 Analysis of the vegetation structure

5.1 Introduction

The importance of the inclusion of structural characteristics in vegetation description has been stressed repeatedly by, among others, Richards et al. (1940), Richards (1952, 1973, 1983), Cain & Castro (1959), Shimwell (1972), Webb et al. (1976), Werger & van der Maarel (1978), Barkman (1979), Werger & Sprangers (1982), and Stoutjesdijk & Barkman (1992). However, there is no unanimity as to how to define and analyse structure. Barkman (1979) defined structure as all the morphological characters of the vegetation, except the qualitative and quantitative properties of the plant taxa included in the vegetation. He includes the following components in an analysis of structure: life form, growth form, height class distribution, leaf type and leaf size class distribution. He emphasized the distinction between horizontal structure (pattern) and vertical structure (stratification). Popma et al. (1988) emphasized the vertical distribution of density, basal area, cover and leaf type in the description of tropical rain forest. Leemans (1989) analyzed density, basal area, maximum tree height, and minimum and maximum bole height in his study of stand structure in Swedish boreal forests.

In this study, the emphasis will be on the vertical distribution of structural properties, particularly stratification. The existence of stratification in tropical forests has been much discussed (e.g. Richards 1952, 1983, Grubb et al. 1963, Hallé et al. 1978); generalizations are difficult because concepts and criteria differ widely among the various studies (Popma et al. 1988). Richards (1952) stated that there is always some stratification in tropical forests. He defined a stratum (or storey) as a layer of trees whose crowns vary in height around a mean. Each of the layers defined in this way should have a floristic composition of its own, but often the trees characterizing the upper story are also represented in lower strata – with lower or younger trees. Hallé et al. (1978) expressed the opposite view; there are "no strata in the forest as subdivisions of the total population", but only horizontal 'sets' of 'trees of the present'. They classified trees into three different groups, based on their sylvigenetic roles. 1. 'Trees of the present' lack any potential for further expansion and persist at a stationary height, without adding to their vertical or horizontal dimension. 2. 'Trees of the future' are found in the lower parts of the forest, being either in a phase of rigorous expansion, or suppressed and awaiting conditions of rapid growth. 3. 'Trees of the past' are damaged beyond repair and have not have any chance to grow, not even to survive in a stationary state.

Richards (1952) approached forest stratification through the construction of frequency distribution histograms for classes of values for important characteristics, notably height classes. Grubb et al. (1963), also working with frequency distributions, distinguished between stratification of individuals and stratification on the species level. Bourgeron (1983) added a third aspect, the stratification of leaf mass. Generally, both the occurrence of peaks and of empty classes in the height distribution may imply stratification. As Grubb et al. (1963) and later Richards (1983) pointed out, the study of species stratification is very complicated. It is especially difficult to indicate the average height of mature trees of a species, because genetic and environmental factors interfere. Another point made by Grubb et al. (1963) is that the detection of strata depends on the selection of height classes; when based on narrow height classes, strata will be easily recognized, but the use of wide height classes may obscure stratification.

Thus, the differences of opinion regarding the existence of strata originate, at least in part, from apparent differences in the concept of stratum and in the methods to detect them, and also from the lack of a clear view of the forest in profile. The latter problem can be overcome through the construction of profile diagrams, drawings of both the vertical and horizontal extension of trees in a transect across the forest, albeit that such profiles have their shortcomings. Paijmans (1970) pointed out that the selection of the transects to be analyzed is subjective and that only two dimensions can be involved. Richards (1983) considered profile diagrams illustrative, but only quantitative, i.e. difficult to use for quantifications of the forest structure. Grubb et al. (1963) considered profile diagrams of limited use because they mainly show the distribution of tree crowns, whereas height-class distributions give information on the entire height profile of the forest. Furthermore, the vertical structure encountered in a transect, which is always very narrow and usually not very long, will vary from one site to another as a result of the occurrence of regeneration patterns (Uhl & Murphy 1981) and of gaps (Whitmore 1984). Finally, profile diagrams depict the forest architecture at one moment in time and have therefore only a static value (Oldeman 1983).

Despite the shortcomings of profile diagrams, they will be used in this study, particularly in order to characterize the stratification of the different forests.

5.2 Methods

All tree and shrub species taller than 2m and more than 2 cm in diameter were measured for height and diameter at breast height (DBH), i.e. 1.3 m above ground level. The heights were measured with a Suunto clinometer, the diameters with a DBH measuring tape. Where slope, topography and/or crown structure made it difficult to use the height meter, heights were estimated visually. In cases where tree boles were buttressed, measurements were related to the point just above the buttresses. If the tree branched at about breast height, the diameter was measured separately for the branches.

Basal area, measured as the cross-section area of a tree at breast height, was used as a relative importance measure (Cain & Castro 1959). Ground-level measurement of the basal area was avoided because some individual trees showed a convoluted outline due to buttresses.

Density figures for the different forests and forest types were calculated on the basis of the countings of the woody individuals. Height, DBH and basal area measurements were used to construct frequency distributions for the various categories the measurements can be allocated to.

The most commonly recommended way of constructing profile diagrams is to fell trees along a specified strip and perform the actual measurements on the pieces (Richards 1952; Cain & Castro 1959). Paijmans (1970) noted that measurements on felled trees give better estimates than measurements of intact trees. In the present study this destructive sampling was impossible; hence measurements were made without the felling of trees.

A transect of 61 m × 7.6 m (200 ft × 25 ft), following Richards (1952), was selected in the forest and a drawing of trees and shrubs inside the plot was made. All trees and shrubs > 2 m in height and > 2 cm in diameter were included in the drawing. The relative distribution of individuals on the ground was mapped and incorporated in the profile diagram. The relative position of the trees within the strip, their diameters, crown mass and crown shape were all drawn to a visually determined scale. Profile diagrams were made at the following six sites:

- a very old *Juniperus procera* stand (community type D1, *Juniperus procera-Myrsine africana-Ehrharta erecta)* in the Menagesha forest at 2650 m a.s.l.;
- a *Juniperus procera* stand (community type D2, *Juniperus procera-Maytenus arbutifolia-Peucedanum winkleri*) in the Wof-Washa forest at 2720 m a.s.l.;
- a *Juniperus procera* stand (community type D1, *Juniperus procera-Myrsine africana-Ehrharta erecta*) in the Wof-Washa forest at 2820 m a.s.l.;
- an open *Podocarpus gracilior* stand in the Wof-Washa forest (community type D7, *Podocarpus gracilior-Allophylus abyssinicus*) at 2710 m a.s.l.;
- a *Podocarpus-Juniperus* stand (community type D9, *Podocarpus gracilior-Maytenus arbutifolia*) in the Wof-Washa forest at 2910 m a.s.l.;
- an *Euphorbia obovalifolia* stand (community type D10, *Euphorbia obovalifolia-Podocarpus gracilior*) in the Wof-Washa forest at 2540 m a.s.l.

Two profiles were taken from a *Juniperus procera* stand to compare the forest structure at two different altitudes.

5.3 Results

5.3.1 Tree density

Table 7 presents data on the density of forest trees, expressed as numbers per hectare of individuals of more than 10 cm and more than 20 cm DBH respectively, as well as their ratio. The forest at Chilimo has the highest density of trees >10 cm DBH, followed by the Jibat, Menagesha and Wof-Washa forests. The ratio of ‘density > 10 cm’ to ‘density > 20 cm’ is taken as a measure of the distribution of the size classes (Grubb et al. 1963). Among the dry Afromontane forests, tree density at Chilimo is much higher than at Menagesha and Wof-Washa in both diameter classes. The moist Afromontane (Jibat) forest is next to Chilimo in DBH class > 10 cm, but much denser than all the dry forests in DBH class > 20 cm.

The very high *a*/*b* ratio in the Chilimo forest indicates the predominance of small-sized individuals; this is a result of to the excessive cutting, which took place here a long time ago. In the Wof-Washa forest, on the other hand, the proportions of small-sized and large-sized individuals do not differ much, which indicated that this forest has developed under natural conditions and without major disturbances.

5.3.2 Tree height and diameter

The distribution of trees in different height classes is shown in Table 8. A considerable proportion (i.e. > 70%) of the individuals in the Chilimo and Menagesha forests belongs to the lowest height classes (i.e. 6 - 9 m and 9 -12 m). In the Jibat forest 49.5%, and in Wof-Washa 44.6% of

Table 7. Tree density (number of trees/ha) in the four forests; *a* = for trees > 10cm DBH; *b* = for trees > 20 cm DBH; *a*/b = ratio between *a* and *b*.

	a	*b*	*a*/*b*
Jibat	565	287	2.0
Chilimo	638	250	2.6
Menagesha	484	208	2.3
Wof-Washa	329	215	1.5

Table 8. Height-class (m) distribution of trees in the four forests; figures are % values within each of the forests.

Height class	Jibat	Chilimo	Menagesha	Wof-Washa
6 - 9	25.5	42.1	38.5	23.3
9 - 12	24.0	30.8	32.0	21.3
12 - 15	15.2	15.3	10.8	13.7
15 - 18	14.0	7.5	11.0	13.1
18 - 21	7.2	3.4	2.2	6.1
21 - 24	3.7	< 1	2.2	1.6
24 - 27	3.5	-	1.0	8.0
27 - 30	2.5	-	< 1	8.0
> 30	4.3	-	2.0	4.8

the individuals are found in the lowest height classes. Only few individuals (< 1%) attain heights of more than 21 m in the Chilimo forest. For Menagesha this figure is < 6.0 %, but in Jibat and Wof-Washa the figures are 14.0 % and 21.6% respectively. In the Menagesha forest, individuals reaching heights of 30 m are not uncommon; these are old and big individuals which survived in this natural forest stand. The Jibat and Wof-Washa forests on the other hand, are well-represented by individuals distributed in all height classes, including the > 30 m class.

DBH measurements reveal a trend similar to that of the height distribution (Table 9). Most trees have a diameter < 20 cm. Most of the individuals in the Chilimo and Menagesha forests, i.e. 61% and 57% respectively, were in the DBH class < 20 cm. In the Chilimo forest there are hardly any individuals with a DBH > 80 cm, while in the Menagesha forest 3.6% of the trees have DBH values of > 80 cm. A very small proportion of the stems in the Jibat forest (i.e. < 1%) attains diameters of > 140 cm, but 88.4% belong to the DBH class 10 - 50 cm. The largest trees are found in the Wof-Washa forest where individuals may reach a DBH of up to 200 cm. About 64.4% of the individuals are in the 10 - 50 cm classes, while about 3.6% belong to the >140 cm class; one individual with a diameter of 210 cm was encountered.

The variation in height and DBH distribution can be attributed in part to the history of the forests. The forests of Chilimo and Menagesha have been heavily exploited through selective cutting, particularly the Chilimo forest. At present these forests are in different stages of secondary development. The Wof-Washa forest on the other hand, has never been under such intense disturbance except very locally. The large number of very big trees and the relatively small proportion of small-sized individuals in this forest indicates that the Wof-Washa forest is in advanced stage of development. Although some commercial exploitation has occurred in the Jibat forest, there are still parts left which remained largely undamaged. The presence of some large trees and the prevalence of small to medium-sized individuals in this forest may indicate that the forest is in a late stage of secondary development.

Table 9. DBH-class (cm) distribution of trees in the four forests; figures are % values within each forest.

DBH-class	Jibat	Chilimo	Menagesha	Wof-Washa
10 - 20	48.9	60.8	56.9	32.6
20 - 50	39.5	36.5	32.8	31.7
50 - 80	9.8	2.6	6.5	14.6
80 - 110	1.4	-	2.5	11.7
110 - 140	< 1	-	1.1	5.9
> 140	< 1	-	-	3.6

5.3.3 Basal area

A comparison of the basal areas and densities of the forests is presented in Table 10. The Wof-Washa forest has the highest basal area for trees > 10 cm in DBH, followed by the Jibat, Menagesha and Chilimo forests. The total basal area for the Wof-Washa forest is 101.8 m^2/ha, while it is 49.8 m^2/ha, 36.1 m^2/ha, and 30.1 m^2/ha for the forests of Jibat, Menagesha and Chilimo respectively.

Fig. 15a-d presents block diagrams of the numbers of trees in 30-cm DBH classes (above the horizontal line) and basal area in m^2 (below the line). There is a considerable decrease in number of individuals with increasing DBH. This decrease is very drastic in the forests of Chilimo and Menagesha, but less so in Jibat and Wof-Washa. Most of the trees in the Chilimo forest are small-sized, as shown by the peak in basal area in the lowest DBH classes (i.e. up to 50 cm). Some trees in the Menagesha forest are of medium size. The trees belonging to higher DBH classes are fewer but they contribute nevertheless considerably to the total basal area. In Wof-Washa, the DBH classes > 50 cm are better represented

Table 10. Structural characteristics in the four forests, differentiated for woody individuals in different DBH-classes.

Characteristic	Jibat	Chilimo	Menagesha	Wof-Washa
Basal area (m^2/ha), DBH > 10 cm	47.5	27.3	32.4	100.3
Density (ind./ha), DBH < 10 cm	1254	1606	2010	696
Density (ind./ha), 10 cm < DBH < 20 cm	275	388	276	107
Density (ind./ha), DBH > 20 cm	287	250	208	215

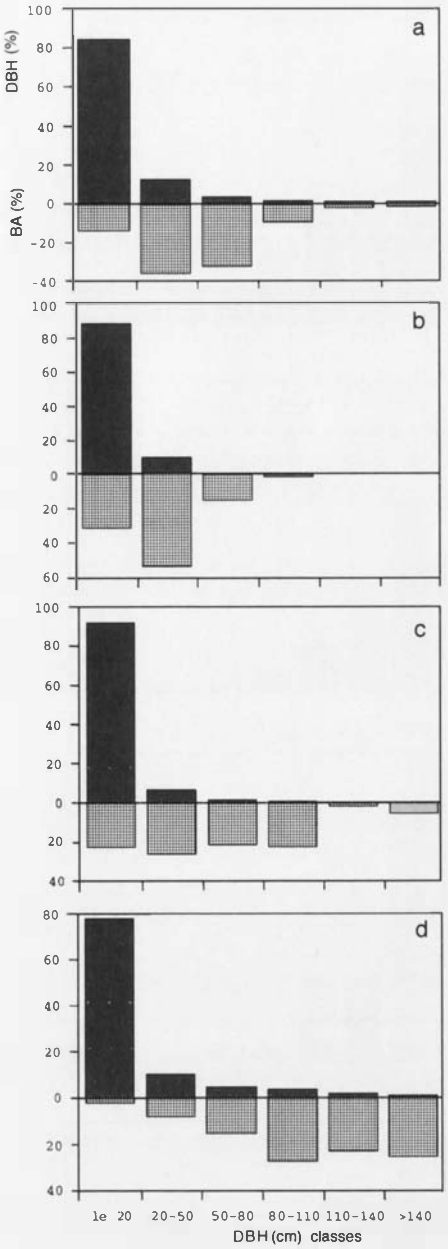

Fig. 15. Frequency distribution of trees in DBH classes (all trees included) in the forests of a. Jibat; b. Chilimo; c. Menagesha; d. Wof-Washa. Blocks above the 0-line: figures based on relative DBH (%); blocks below the 0-line: figures based on relative basal area (%).

and hence they contribute much to the total basal area. All the forests have more than half their total number of individuals in the smallest DBH class (i.e. < 20 cm). The contribution of these individuals to the basal area is only pronounced in the forests of Chilimo and Menagesha. Many individuals in the lowest DBH classes are of a small stature; hence the basal area contributed by these classes is small. The basal area contribution by the lowest and the highest DBH classes in any one forest is very low as compared to the contribution of the intermediate classes, irrespective of the state of successional stage of the forest.

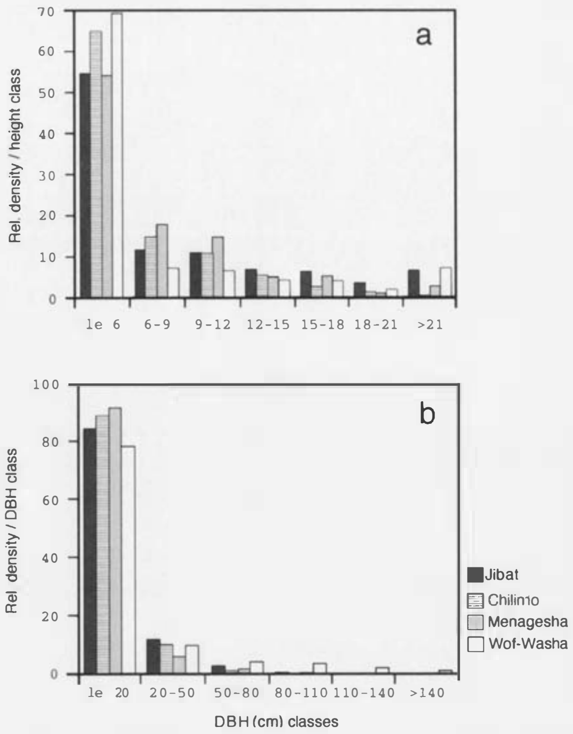

Fig. 16. Frequency distribution of a. density contributions by height class for the four forests, and b. density contributions by DBH class.

The density distribution in different height- and DBH classes shows a similar pattern (Fig. 16a,b). Most of the individuals in all forests are found in the lowest DBH class, which is also reflected by the high aggregation of individuals in the lowest height class. Such a relationship is evident, as very few individuals attain a large diameter when they are short.

The basal area and density distributions of five species in each of the forests is shown in Table 11. These species rank highest as to their contribution to the total basal area in the respective forests. The basal area contribution of these species in the Jibat and Chilimo forests is similar, 65.6% and 73.8% respectively. However, the absolute basal area value for Jibat is much higher than in Chilimo (33 against 22 m^2/ha). The Chilimo forest is successionally younger and consists of smaller individuals. None of the five major species in the Jibat and Chilimo forests shows an overriding dominance over the others in terms of basal area. On the other hand, in the Menagesha and Wof-Washa forests, one of the important species, *Juniperus procera*, dominates completely, contributing no less than 60.4% and 61.8% of the total basal area respectively. Note, that the fifth species in Wof-Washa, *Hagenia abyssinica*, is represented with a low

Table 11. Basal area and density of the five most important species in each of the four forests.

	Basal area		Density	
	m²/ha	%	stems/ha	%
Jibat				
Ilex mitis	9.4	18.9	179	9.9
Syzygium guineense	7.9	15.9	137	7.5
Prunus africana	5.6	11.2	36	2.0
Apodytes dimidiata	5.0	10.0	129	7.1
Olinia aequipetala	4.8	9.6	79	4.3
Total	32.7	65.6	560	30.8
Chilimo				
Olea europaea	5.5	18.3	139	6.2
Podocarpus gracilior	5.3	17.6	308	13.7
Juniperus procera	4.5	15.0	150	6.7
Olinia aequipetala	4.4	14.6	195	8.7
Scolopia theifolia	2.5	8.3	493	22.0
Total	22.2	73.8	1285	56.6
Menagesha				
Juniperus procera	21.8	60.0	164	6.6
Olea europaea	4.5	12.5	133	5.3
Olinia aequipetala	2.8	7.8	163	6.5
Spiniluma oxyacantha	1.9	5.3	378	15.2
Scolopia theifolia	1.0	2.8	430	17.3
Total	32.0	88.8	1268	50.9
Wof-Washa				
Juniperus procera	62.9	61.8	78	7.7
Podocarpus gracilior	16.3	16.0	144	14.0
Ilex mitis	8.4	8.3	83	8.1
Euphorbia obovalifolia	5.2	5.1	50	4.9
Hagenia abyssinica	2.3	2.3	3	0.3
Total	95.1	93.5	358	35.0

value in Table 1 (Type D3). The relatively high basal area of this species is based on the occurrence of only few, but very large trees, which did not reach a high cover-abundance value in the relevés of this type.

The density distribution of the five most important species does not follow the same trend as that of the basal area. Species with the highest basal area/ha do not always have the highest density, indicating size differences between the species (e.g. *Prunus africana* and *Apodytes dimidiata* in the Jibat forest). In other cases, differences in growth forms could be important; the shrubby tree *Scolopia theifolia* is the densest of the five species in the Chilimo forest, but its contribution to the basal area is the least. In the forests of Menagesha and Wof-Washa, one single species, *Juniperus procera*, attains the highest sizes and is by far the most dominant, contributing more than 60% of the total basal area. *J. procera* is also the densest species in the Menagesha forest, while *Podocarpus gracilior* is denser than *J. procera* in the Wof-Washa forest. The low

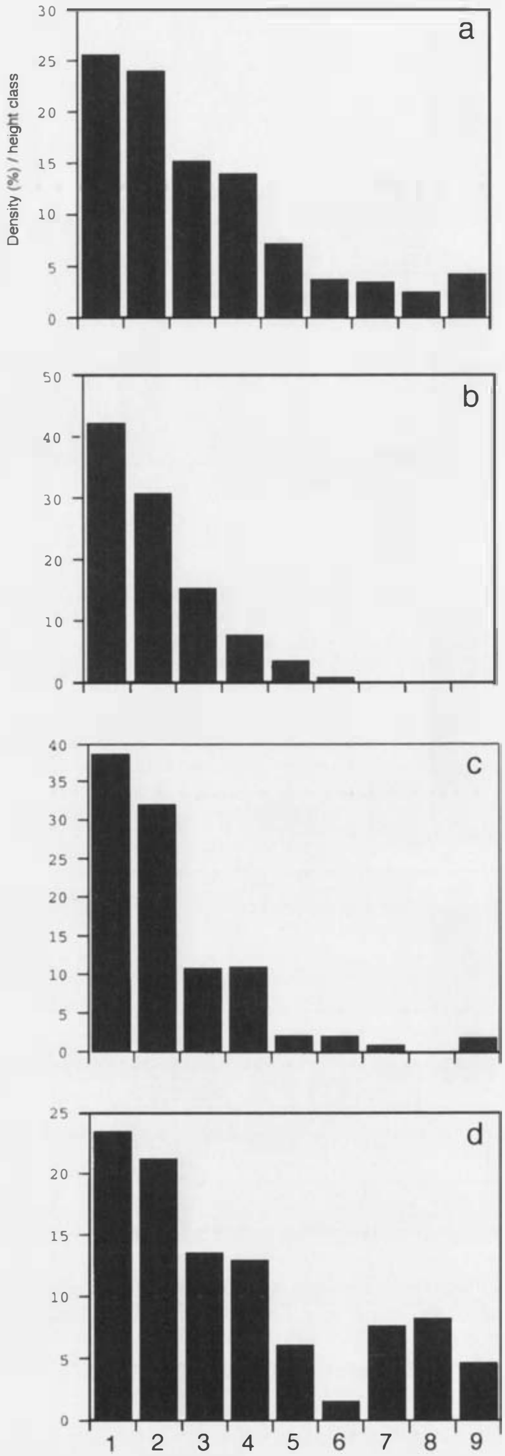

Fig. 17. Frequency distribution of tree numbers in height classes for a. Jibat; b. Chilimo; c. Menagesha; d. Wof-Washa. Class 1 = 6 - 9 m; 2 = 9 - 12 m; 3 = 12 - 15 m; 4 = 15 - 18 m; 5 = 18 - 21 m; 6 = 21 - 24 m; 7 = 24 - 27 m; 8 = 27 - 30 m; 9 = >30 m.

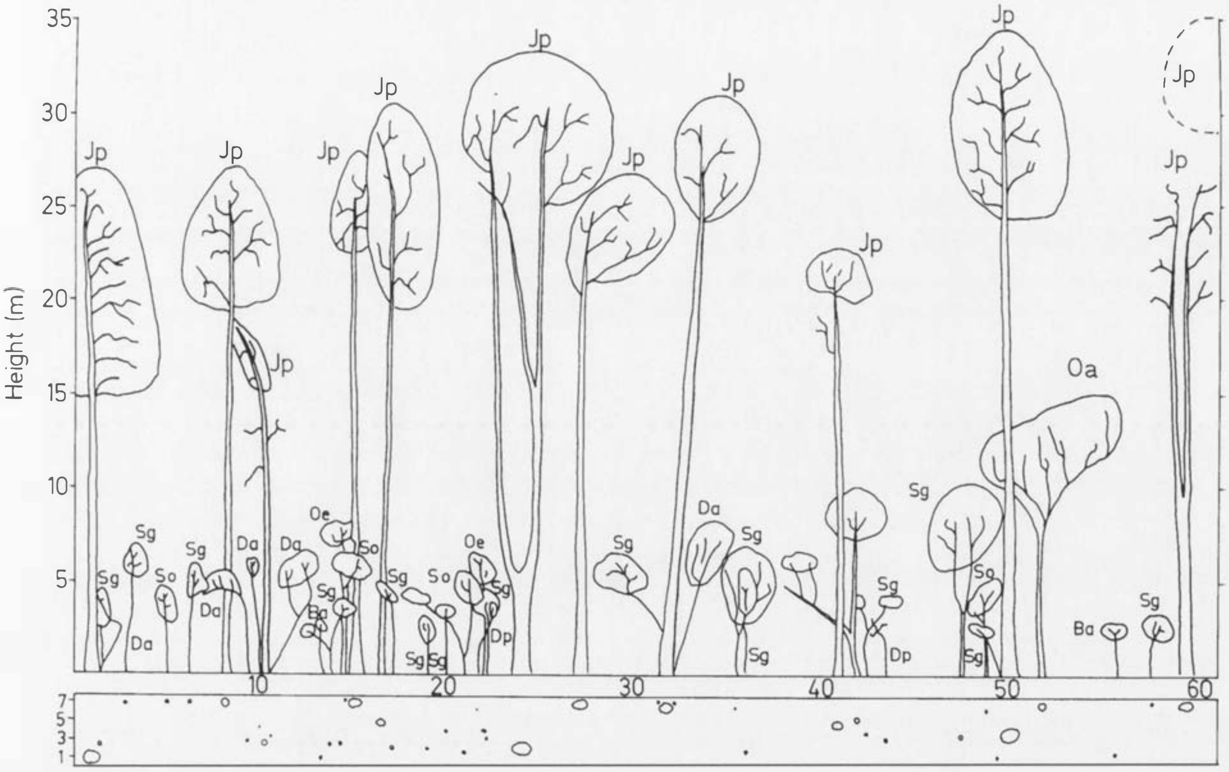

Fig. 18. Profile diagram of a *Juniperus* stand (61 m × 7.6 m) in the Menagesha forest at 2650 m a.s.l. Ba = *Bersama abyssinica*; Da = *Dovialis abyssinica*; Dp = *Discopodium penninervium*; Jp = *Juniperus procera*; Oa = *Olinia aequipetala*; Oe = *Olea europaea*; Sg = *Syzygium guineense*; So = *Spiniluma oxyacantha.* Interrupted line around Jp to the right = canopy extension from outside the strip.

density in the latter forest might be due to its very old age; indeed, trees are showing signs of old age and while *J. procera* has a poor regenerating capacity under its own canopy, *P. gracilior* is successfully regenerating in this stand; hence the density dominance of the latter species.

As basal area provides a better measure of the relative importance of tree species than simple stem counts (Cain & Castro 1959); species with the largest contribution in basal area can be considered as the most important in these forests.

The structural comparisons presented above, indicate a variability in the successional stage of the forests. Wof-Washa is a forest that has reached maturity. The other two dry forests (i.e. Chilimo and Menagesha), and the humid forest of Jibat are in different stages of secondary development, Jibat probably in a late-successional stage.

5.3.4 Stratification

In terms of tree height, the forests of Jibat, Chilimo and Menagesha do not show a stratification (Fig. 17a-c). In the Wof-Washa forest, however, the height distribution suggests the presence of at least two strata, one from 6 - 18 m and one above 24 m (Fig. 17d).

The profile diagram from the Menagesha forest refers to a very old *Juniperus* stand at 2650 m a.s.l. (Fig. 18). The canopy layer is entirely composed of old *Juniperus* trees. Most of these trees have started dying-back from the tips, as observed from the stag-heads. The crowns are degenerating and on some trees they are completely absent (see tree at the extreme right-hand side of the figure). The characteristic feature of this profile is the well-defined canopy at 20 - 35 m. The understorey consists of shrubs and small trees with dense crowns between 4 and 7 m, with mainly *Syzygium guineense* and *Spiniluma oxyacantha.*

Figs. 19 and 20 show the profile diagrams from the *Juniperus* stands in the Wof-Washa forest at 2720 and 2820 m a.s.l. respectively. Both profiles depict a *Juniperus* stand with a mixed understorey. In the former, there is a canopy stratification, but only at the right-hand side of the strip. In the *Juniperus* stand depicted in Fig. 20, the understorey trees and shrubs are better developed than in the stand depicted in Fig. 19. Their canopies merge with that of the bigger trees. The apparent gap at the right-hand side of the diagram, which is being filled up with understorey species, is actually covered by a taller canopy of *Juniperus*, extending from just outside the strip. Overall, there is no distinct layering in this plot.

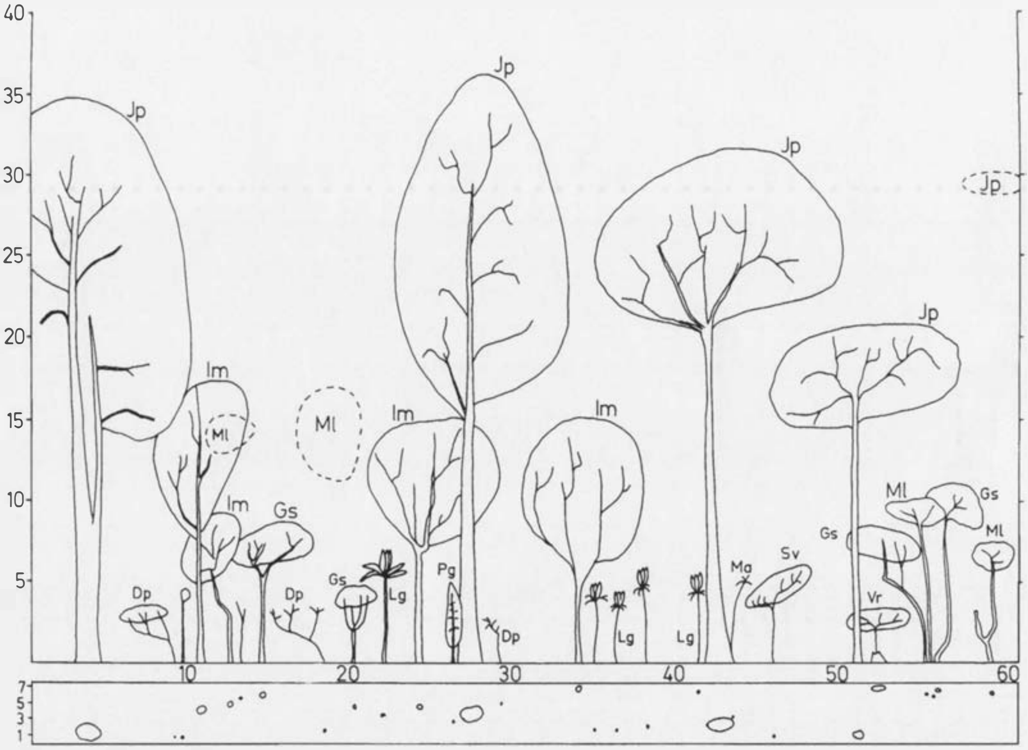

Fig. 19. Profile diagram of a *Juniperus* stand (61 m×7.6 m) in the Wof-Washa forest at 2720 m a.s.l. Dp = *Discopodium penninervium*; Gs = *Galiniera coffeoides*; Im = *Ilex mitis*; Jp = *Juniperus procera*; Lb = *Lobelia gibberoa*; Ml = *Maesa lanceolata*; Sv = *Schefflera volkensii*. Interrupted lines = canopy extensions from outside the strip.

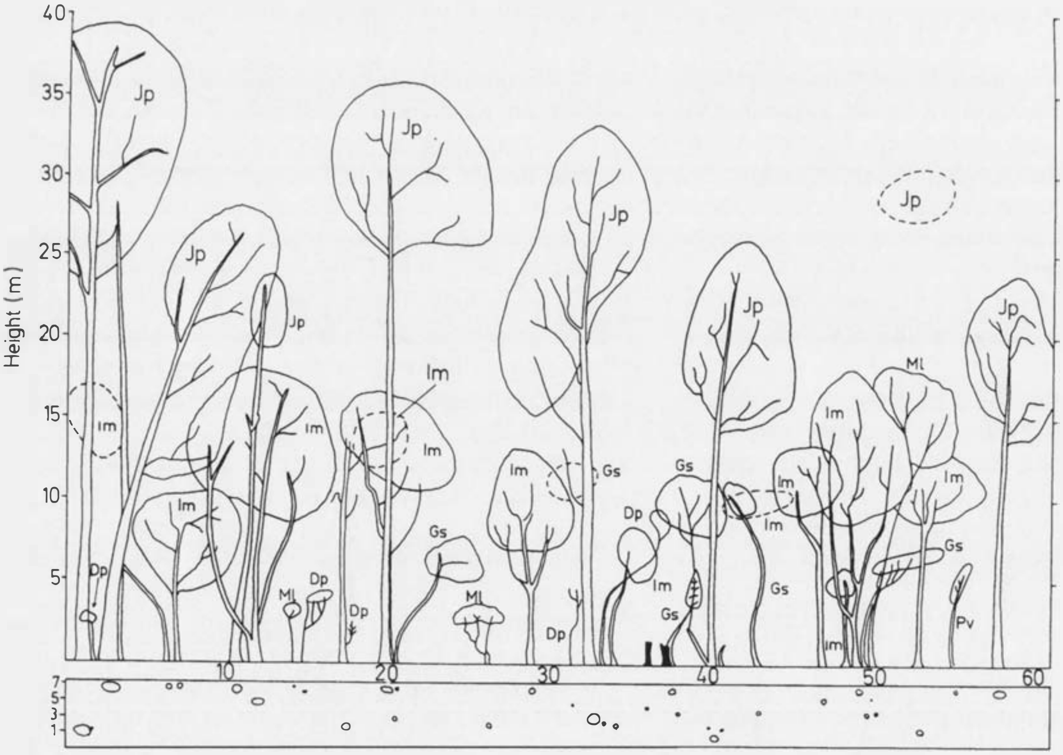

Fig. 20. Profile diagram of a *Juniperus* stand (61 m×7.6 m) in the Wof-Washa forest at 2820 m a.s.l. Dp = *Discopodium penninervium*; Gs = *Galliniera coffeoides;* Im = *Ilex mitis*; Jp = *Juniperus procera*; Ml = *Maesa lanceolata*; Pv = *Pittosporum viridiflorum*.Interrupted lines = canopy extensions from outside the strip.

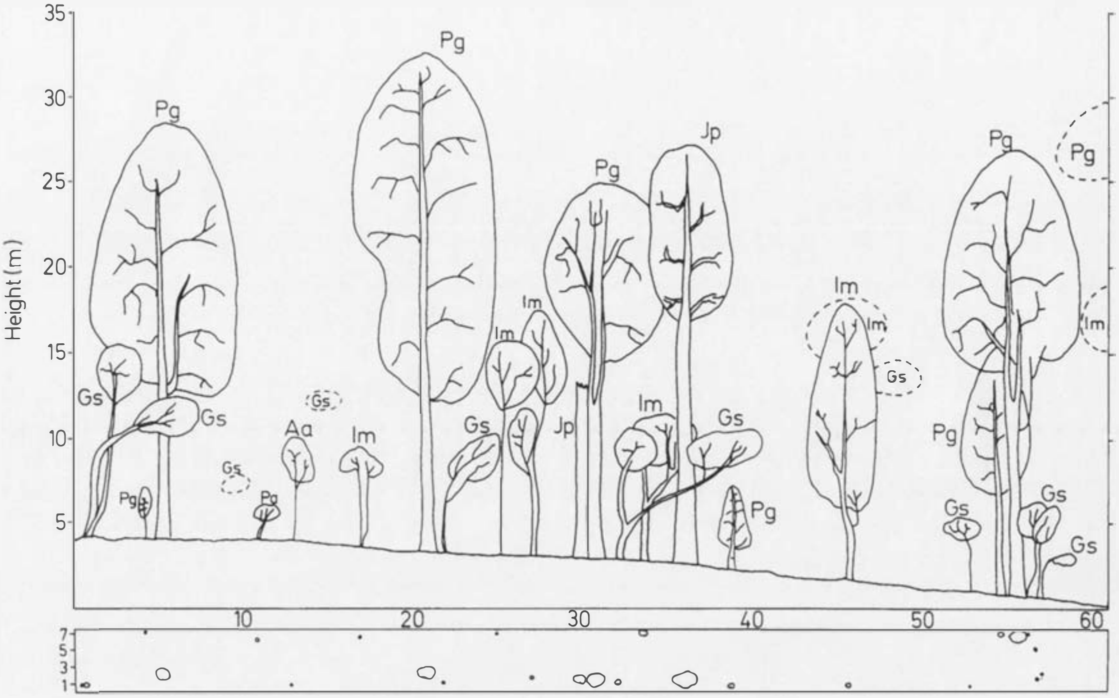

Fig. 21. Profile diagram of a *Podocarpus* stand (61 m × 7.6 m) in the Wof-Washa forest at 2710 m a.s.l. Aa = *Allophyllus abyssinicus*; Gs = *Galiniera coffeoides*; Im = *Ilex mitis*; Jp = *Juniperus procera*; Pa = *Pavetta abyssinica*; Pg = *Podocarpus gracilior*. Interrupted lines = canopy extensions from outside the strip.

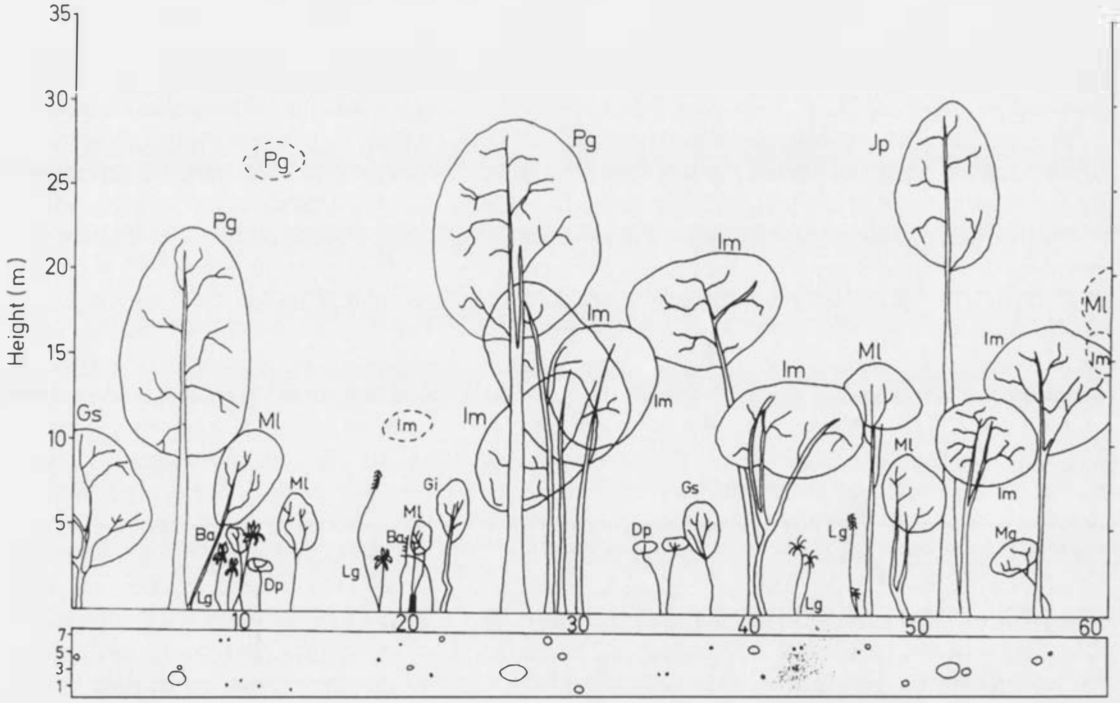

Fig. 22. Profile diagram of a *Podocarpus-Juniperus* stand (61 m × 7.6 m) in the Wof-Washa forest at 2590 m a.s.l. Ba = *Bersama abyssinica*; Dp = *Discopodium penninervium*; Gs = *Galiniera coffeoides*; Im = *Ilex mitis*; Jp = *Juniperus procera*; Lb = *Lobelia gibberoa*; Ma = *Maytenus arbutifolia*; Ml = *Maesa lanceolata*; Pg = *Podocarpus gracilior*. Interrupted lines = canopy extensions from outside the strip.

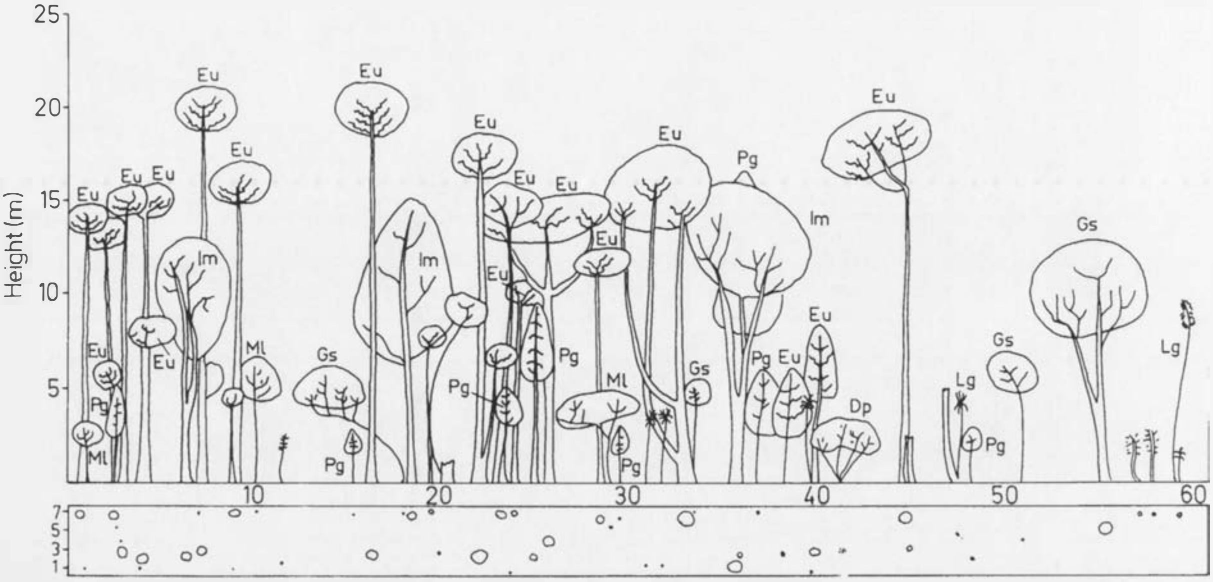

Fig. 23. Profile diagram of an *Euphorbia obovalifolia* stand (61 m × 7.6 m) in the Wof-Washa forest at 2540 m a.s.l. Dp = *Discopodium penninervium*; Eu = *Euphorbia obovalifolia*; Gs = *Galiniera coffeoides*; Im = *Ilex mitis*; Lb = *Lobelia gibberoa*; Ml = *Maesa lanceolata*; Pg = *Podocarpus gracilior*. Interrupted lines = canopy extensions from outside the strip.

Fig. 21 shows the profile diagram of the *Podocarpus* forest. The dominant tree is *Podocarpus gracilior*. There are large openings between the canopy trees. Apart from the young trees, the shrub layer is missing here, which is probably due to the effect of grazing animals and human activity. The canopies of the young trees smoothly merge with those of the upper trees without any signs of a distinct stratification.

The profile diagram from the mixed *Podocarpus-Juniperus* stand in the Wof-Washa forest is shown in Fig. 22. The stand is situated towards the lower periphery of the forest where it is drier. Except for the one emergent *Juniperus procera* tree at the left-hand side of the diagram, there is a continuous canopy cover between 5 - 15 m, with *Ilex mitis* and *Maesa lanceolata*. However, no distinct canopy stratification is displayed by the individual species involved.

The profile diagram from the *Euphorbia* stand in the Wof-Washa forest is shown in Fig. 23. The stand is situated on the banks of a river along the boundary between the montane forest and the dry lowland vegetation. The *Euphorbia* trees are of varying height, and except for openings in the canopy where the larger individuals have been cut (see right-hand edge of the diagram), the crowns form a more or less continuous layer at about 12 - 13 m. The understorey is mainly composed of regenerating *Podocarpus gracilior* and *Galiniera coffeoides*. No layering is evident here.

5.3.5 Species population structure

As an addition to, and differentiation of, the general picture presented by the profile diagrams and especially the general frequency distribution of trees in DBH classes (Fig. 15a-d), some frequency distributions of representative trees in the different forests are presented. The population structure of 14 species from the humid forest and 21 species from the dry forest communities were analyzed. The patterns of species population structure that emerge can be interpreted as an indication of variation in population dynamics in the forest (Popma et al. 1988).

Five general patterns of population structure were recognized in the six community types from the Jibat forest, i.e. types H2-H7 [species from the *Arundinaria* (type H1) and *Erica* (type H8) types were not analyzed)]. The first pattern (Fig. 24a) is formed by the species with a more or less even frequency distribution in all DBH classes. This pattern suggests a good reproduction and recruitment. Only one species, *Rapanea simensis* (type H2), belongs to this group.

The second type (Fig. 24b) shows a Gauss-type distribution pattern, with the first and second DBH classes having a low frequency, a gradual increase in the number of individuals towards the medium classes, and then a subsequent decrease in frequency towards the higher DBH classes. Three species show this pattern: *Galiniera coffeoides* (types H2, H3, H4 and H6), *Dracaena afromontana* (types H3 and H7), and *Nuxia congesta* (type H4). This pattern indicates a poor reproduction, but we can only speculate about the reason for the decline in

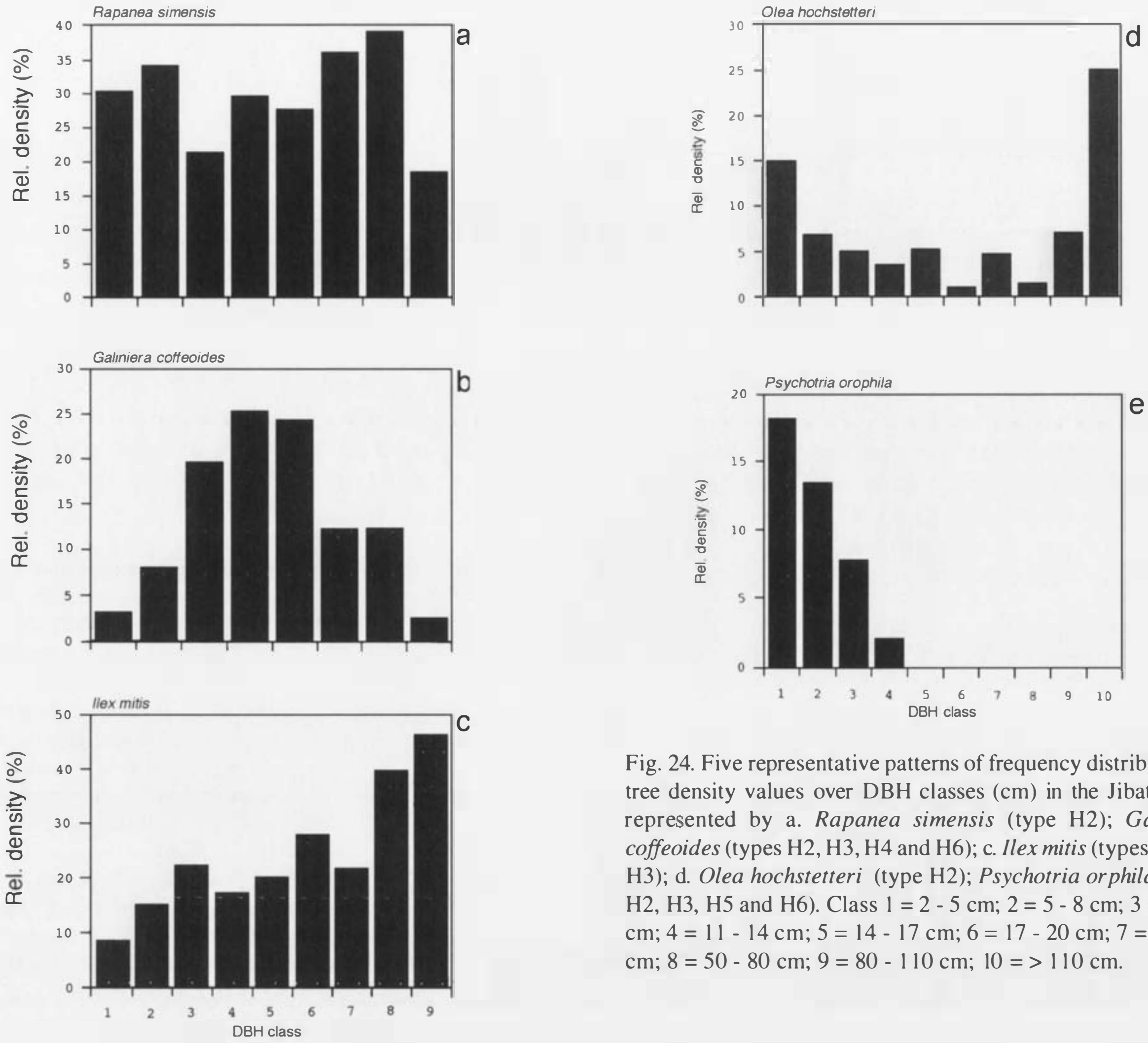

Fig. 24. Five representative patterns of frequency distribution of tree density values over DBH classes (cm) in the Jibat forest, represented by a. *Rapanea simensis* (type H2); *Galiniera coffeoides* (types H2, H3, H4 and H6); c. *Ilex mitis* (types H2 and H3); d. *Olea hochstetteri* (type H2); *Psychotria orphila* (types H2, H3, H5 and H6). Class 1 = 2 - 5 cm; 2 = 5 - 8 cm; 3 = 8 - 11 cm; 4 = 11 - 14 cm; 5 = 14 - 17 cm; 6 = 17 - 20 cm; 7 = 20 - 50 cm; 8 = 50 - 80 cm; 9 = 80 - 110 cm; 10 = > 110 cm.

the number of big-sized trees.

The third type (Fig. 24c) shows a pattern where the frequency is very low in the first and second DBH classes, but increases towards the higher classes. This pattern indicates poor reproduction. This group includes: *Olinia aequipetala* (type H2), *Ilex mitis* (types H2 and H3), *Apodytes dimidiata* (types H3, H4 and H5), *Rapanea simensis* (type H3), *Syzygium guineense* (types H3 and H4), *Olea hochstetteri* (types H4 and H5), and *Galiniera coffeoides* (type H5).

The fourth type (Fig. 24d) shows a U-shaped pattern; the frequency is high in the lowest and highest DBH classes but very low in the intermediate classes. Only one species, *Olea hochstetteri* (type H2), belongs to this group. This pattern probably indicates selective cutting and removal of medium-sized individuals of this species.

The fifth type (Fig. 24e) shows a pattern that is formed by species with the highest frequency in the first or second DBH classes and a gradual decrease towards the bigger classes. Species in this group include *Psychotria orphila* (types H2, H3, H5 and H6), *Rytyginia neglecta* (type H4) and *Lepidotrichilia volkensii* (type H4).

Six general patterns of population structure were recognized in the ten community types from the dry montane forests of Chilimo, Menagesha and Wof-Washa, i.e. types D1-D10. The first type (Fig. 25a) shows a somewhat J-shaped pattern where frequency is very low in the lowest DBH classes and gradually increases towards the higher classes (as type 3 in Jibat). Species in this group include *Juniperus procera* (types D1, D2 and D5), *Olea europaea* (types D1, D5 and D7), *Pittosporum abyssinicum* (type D1), *Pittosporum viridiflorum* (type D3), *Maytenus addat* (type D4), *Rhus glutinossa* (type D5), *Olinia aequipetala* (type D5 and D7), *Maesa lanceolata* (type D9), and *Euphorbia obovalifolia* (type D10). This pattern indicates poor reproduction.

The second type (Fig. 25b) shows a pattern where individuals are frequent only in the highest DBH classes. This indicates very big and old individuals which are no longer reproducing or regenerating. This pattern is shown

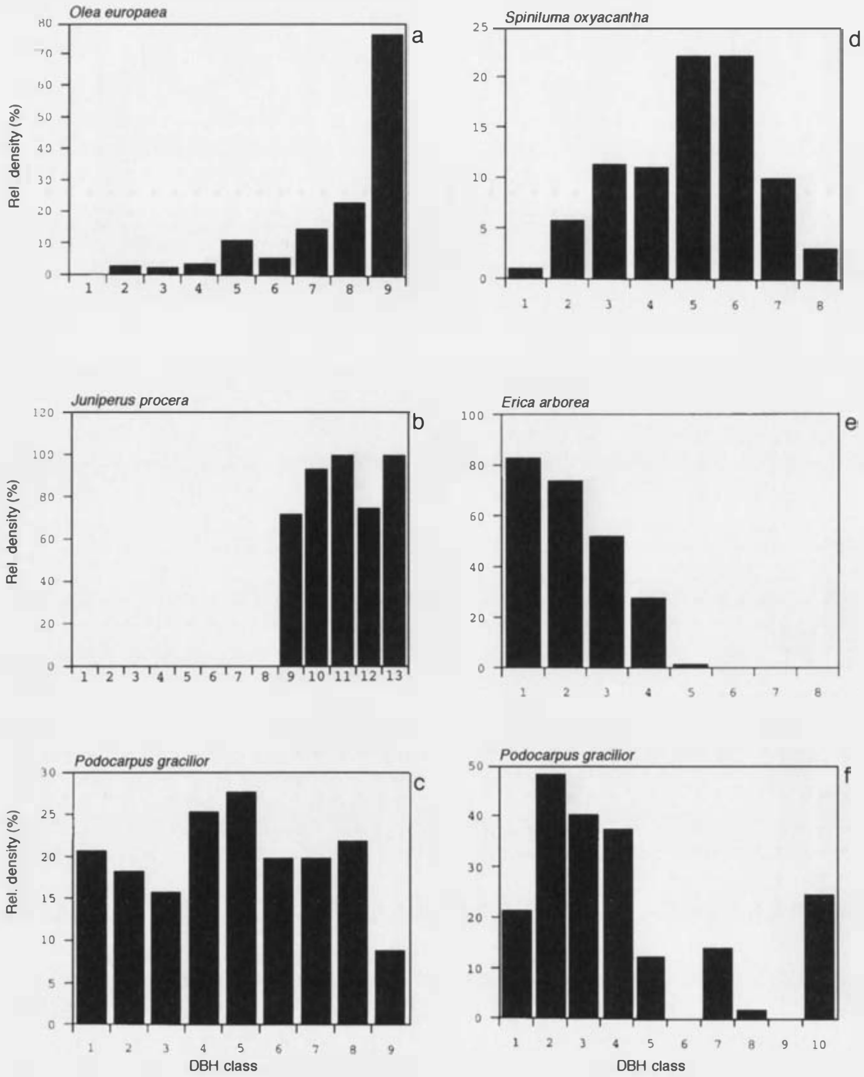

Fig. 25. Six representative patterns of frequency distribution of tree density values over DBH classes in the Chilimo forest, represented by a. *Olea europaea* (types D1, D5 and D7); b. *Juniperus procera* (types D1, D8 and D9); c. *Podocarpus gracilior* (D5 and D7); d. *Spiniluma oxyacantha* (type D1, D4 and D7); e. *Erica arborea* (type D3); f. *Podocarpus gracilior* (type D10). Class 1 = 2 - 5 cm; 2 = 5 - 8 cm; 3 = 8 - 11 cm; 4 = 11 - 14 cm; 5 = 14 - 17 cm; 6 = 17 - 20 cm; 7 = 20 - 50 cm; 8 = 50 - 80 cm; 9 = 80 - 110 cm; 10 = 110 - 140 cm; 11 = 140 - 170 cm; 12 = 170 - 200 cm; 13 = > 200 cm.

only by *Juniperus procera* (types D1, D8 and D9).

The third type (Fig. 25c), which is identical to Jibat type 1, shows a pattern where there is an even frequency distribution in all classes. Species in this group include *Podocarpus gracilior* (D5 and D7), and *Scolopia theifolia* (types D5 and D7). This pattern indicates a good reproduction and a good recruitment.

The fourth type (Fig. 25d) (Jibat type 2) shows a Gauss distribution. Species in this group include: *Erica arborea* (type D1), *Olinia aequipetala* (type D1 and D8), *Spiniluma oxyacantha* (type D1, D4 and D7), *Podocarpus gracilior* (type D1 and D4), *Maytenus arbutifolia* (type D2), *Allophylus abyssinicus* (type D8), *Sideroxylon gilletti* (type D8), *Galiniera coffeoides* (type D9), and *Maesa lanceolata* (type D10). These species have a poor eproduction.

The fifth type (Fig. 25e) (Jibat type 5) shows a pattern where the frequencies are highest in the lowest DBH classes, and then decrease towards the higher classes. Species in this group include *Erica arborea* (type D3), *Maytenus addat* (type D5 and D7), *Myrsine africana* (type D5), *Ilex mitis* (type D6), and *Maytenus arbutifolia* (type D6). This pattern indicates a good reproduction but a bad recruitment.

The sixth type (Fig. 25f) shows a pattern where frequency is high at lower DBH classes but becomes irregular towards higher classes. This pattern indicates a good reproduction but discontinuous recruitment. Two species that show such a pattern are *Ilex mitis* (type D6) and *Podocarpus gracilior* (type D10).

Few species do not strictly conform to any one of the described patterns above, but rather show intermediate trends in-between. These species include *Apodytes dimidiata* (type H2), *Croton machrostachyus* and *Ilex mitis* (type H3), *Rapanea simensis* (type H4), *Olea hochstetteri, Rytyginia neglecta & Syzygium guineense* (type H5), *Ilex mitis* (type H6), *Erica arborea* (type D1), *Olinia aequipetala* (Type D4), and *Rapanea simensis* (Type D7).

5.4 Discussion

The profile diagrams illustrating the forests provide a general impression of the structure of the forests under study. The profile from the old *Juniperus* stand from the forest of Menagesha shows two distinct strata of canopy layers. This observation is in line with that of Grubb et al. (1963), who noted that a stratification into two tree layers is common in species-poor forests in Ecuador where only one or two species are represented with large trees. No such stratification could be detected in the other forests. Generally, there is considerable variation in the height structure within a forest, or even within one stand. Maybe, the search for distinct layers is not meaningful (cf. Grubb et al. 1963; Paijmans 1970; Uhl & Murphy 1981). Still, variation in tree height is an important ecological phenomenon which effects the microclimate (e.g. Grubb et al. 1963, Stoutjesdijk & Barkman 1992) and the distribution of epiphytes and climbers.

Gaps in the canopy are evident in the profile diagrams (Figs. 18-23). Since the individuals included in the diagrams were obviously intact, the gaps cannot be attributed to any recent tree fall or a snapped-off large branch, or the death of a tree from old age. In fact, these gaps are filled by the canopy of trees from outside the sample plot (see stippled outlines in Figs. 18-23).

The patterns of species population structure suggest at least two major types of trees: (1) species able to regenerate in the forest understory and (2) large and probably old trees with difficulties to reproduce in the understory environment. A third type, including species with both a good reproduction and a good recruitment in the dry and humid forests are rare. *Rapanea simensis* (humid forest) and *Podocarpus gracilior* (dry forests) have such viable populations. Both species have a good regeneration under the canopy of mature trees. Several species have a good regeneration but most of the seedling individuals do not thrive long enough to grow into adults.

The patterns in the population structure of some species are suggestive of the past occurrence of disturbance. In cases of trees with a U-shaped population structure (e.g. Fig. 24d), medium-sized individuals from the population have probably been selectively cut. *Olea hochstetteri* is one such species in the Jibat forest that was exploited in this way. In some populations, only the older and bigger individuals are considered for cutting, and such species may display the kind of population pattern as depicted in Fig. 24b and 25d. This pattern could also mean that older individuals are eliminated by other, more succesful competative species. Thus, such a pattern can not be definitively explained on the basis of the present observations alone.

Juniperus procera does not show a good regeneration capacity; the individuals whose population pattern is shown in Fig. 25b are very old trees that have started to die back. This particular pattern is from a very old stand (ca. 400 yr) that is now under protection, and it reveals the incapability of the species to regenerate under its own canopy. However, where there has been a complete clearing of the original forest as in Chilimo, a second generation of *Juniperus* trees has grown up and is thriving. The quantity and spectral distribution of light reaching the ground is critical for the regeneration of *Juniperus procera*, and as a result regeneration in most of the forests where the species occurs is always more abundant at the margins of stands (Kerfoot 1963). White (1983a) also mentioned that Juniperus procera is strongly light-demanding and cannot regenerate in its own shade.

The structural comparisons discussed above indicate variability in successional stages attained by the forests. Wof-Washa is a forest that has reached maturity. The other two dry Afromontane forests (i.e. Chilimo and Menagesha), and the humid Afromontane forest of Jibat are in different secondary developmental stages with the latter probably in a late secondary stage of development.

6. Phytogeographical description

6.1 Survey of tree and shrub species

A total of 201 species were recorded from the four Afromontane forests of the Central Plateau (Appendix 1). This list, however, is not assumed to be complete; more species will probably be added as the taxonomic work on the flora proceeds. This is particularly relevant to herbaceous and graminoid species which need repeated collections to produce a more exhaustive list. The tree and shrub species, on the other hand, are easier to identify even when flowers or fruits are missing, and it is not expected that many additional species will be found. The following description is, therefore, based on the tree and shrub species. The distribution of 70 tree and shrub species is shown in Table 12. The assignment of species to floral elements follows the description of Chapman & White (1970), and White (1979).

Most of the tree and shrub species are characteristic Afromontane species. Only three (i.e. 4%) of the species (*Ehretia cymosa*, *Ficus sur*, and *Oxyanthus speciosus*) are Guineo-Congolian floral elements, and these were all recorded from the humid Jibat forest. The Guineo-Congolian elements are not widely distributed on the Central Plateau of Shewa and are mostly found in specialized habitats such as along river courses (e.g. *Ficus sur*). The presence of these species in the Jibat forest has to do with the close proximity of the forest to the lowland floral region, and the presence of suitable habitats at lower altitudes in the forest. Chapman & White (1970) described such species from Malawi and noted that they could extend upwards into the submontane forests of the Afromontane Region.

The Afromontane 'nephews' (*sensu* Chapman & White 1970), those species with relatives in the lowland phytochoria, have only been recorded from the moist montane forest of Jibat. These species include *Aningeria adolfi-friederici*, *Prunus africana* and *Olea welwitschii*. Lind & Morrison (1974) considered these species as typical of moist montane forests in East Africa.

Apodytes dimidiata and *Rapanea simensis* have not been recorded from the Wof-Washa forest, while on the other hand, *Halleria lucida* was only recorded from here. All three species belong to the Afromontane 'orphans', species with no relatives in the humid tropics at present, although they may have relatives elsewhere in the tropics.

The dry montane forests mostly contain those Afromontane endemics that belong to the category Afromontane flora *sensu stricto*. These species include *Juniperus procera*, *Olea europaea*, *Hagenia abyssinica*, *Halleria lucida*, *Podocarpus gracilior*, *Apodytes dimidiata*, *Ilex mitis* and *Rapanea simensis*. Some of these species have also a wider distribution and can be found in the moist lowland forests as well. A few characteristic Afromontane endemic species (e.g. *Juniperus procera*, *Olea europaea* and *Olinia aequipetala*), however, were only recorded from the dry montane forests. *Juniperus procera* and *Olea europaea* are characteristic species of dry Afromontane forests. *Olea europaea*, and *Maytenus undata* are known to possess strong xeromorphic features which enables them to survive during severe dry conditions (Coetzee 1978); the latter species has only been recorded from the Wof-Washa forest.

In addition to the Afromontane endemics, other species belonging to connecting elements have also been identified from the plateau forests in Central Ethiopia. These include the 'ecological transgressors', e.g. *Cassipourea malosana* and *Ekebergia capensis*, and forest pioneer connecting species, e.g. *Trema orientalis, Maesa lanceolata*, *Clausena anisata* and *Bersama abyssinica.* The former can be found dispersed over a wider geographical area, while the latter are found in disturbed habitats along forest edges.

Bronner (1990) mentioned that the tree species *Olea hochstetteri* and *Nuxia congesta*, and the grasses *Oplismenus compositus* and also *Ehrharta erecta* are wide-ranging species in the Mathews Range in Kenya. According to the present study, *Oplismenus* is dominant in Humid forest types, while *Ehrharta* is dominant in the Dry forest types.

The *Euphorbia* community type from Wof-Washa forest constitutes a distinct vegetation type along the fringes of the forest. Iversen (1991) stated that *Euphorbia* thickets invading degraded slopes of the mountains can be secondary, while von Breitenbach (1963) correlated their presence with drier conditions at higher altitudes. The plausible explanation of their presence here is the latter, a dry environment, as there is no clear evidence of past disturbance at this site.

In Cameroon's mountains, *Hypericum revolutum*, *Agauria salicifolia* and *Ilex mitis* are mentioned as forest fringe and forest outlier species (Richards 1963); here fires are frequent and light conditions more favourable.

Some of the montane forest species in the present study have also been recorded from shrubland vegetation on the Central Plateau of Ethiopia (Zerihun & Backéus 1991). These species include *Erica arborea*, *Juniperus*

Table 12. Distribution of trees and shrubs in the plateau forests of Shewa. J = Jibat; C = Chilimo; M = Menagesha; W = Wof-Washa; G-C = Guineo-Congolian flora element; L = Linking species; Tr = Ecological transgressor. All other species are considered Afromontane species.

Species		J	C	M	W
Trees >10 m					
Albizia sp.		x			
Aningeria adolfi-friederici		x			
Allophylus abyssinicus		x	x	x	x
Apodytes dimidiata		x	x	x	
Cassipourea malosana	(Tr)	x			x
Cordia abyssinica	(L)	x			
Croton macrostachyus		x			
Ekebergia capensis		x	x	x	x
Ficus sur	(G-C)	x			
Galiniera coffeoides		x			x
G. saxifraga					x
Hagenia abyssinica		x	x	x	x
Ilex mitis		x	x	x	x
Juniperus procera			x	x	x
Lepidotrichilia volkensii		x			
Millettia ferruginea		x			
Myrica salicifolia		x	x	x	
Nuxia congesta		x	x	x	x
Olea europaea			x	x	x
O. hochstetteri		x			
O. welwitschii		x			
Olinia aequipetala			x	x	x
Pittosporum mannii		x			
P. viridiflorum		x	x	x	x
Podocarpus gracilior		x	x	x	x
Polyscias fulva		x			x
Prunus africana		x	x	x	
Rapanea simensis		x	x	x	
Schefflera volkensii		x	x	x	x
Syzygium guineense		x			
Small trees and shrubs < 10 m					
Agauria salicifolia				x	
Bersama abyssinica		x	x	x	x
Brucea antidysenterica		x			
Buddleja polystachya		x			
Calpurnea aurea		x	x		
Canthium oligocarpum		x			
Carissa edulis			x	x	
Clausena anisata		x	x		
Discopodium penninervium				x	x
Dovyalis abyssinica		x	x	x	x
Dracaena afromontana		x			
Ehretia cymosa	(G-C)	x			
Embelia schimperi		x			
Erica arborea		x	x	x	x
Erythrococca trichogyne		x			
Euphorbia obovalifolia					x
Euclea schimperi	(Tr)	x			
Flacourtia sp.	(L)	x			
Halleria lucida				x	x
Hypericum revolutum		x	x	x	x
Jasminum abyssinicum		x			
Lobelia gibberoa				x	x
Maesa lanceolata					x
Maytenus addat		x	x	x	
M. arbutifolia		x	x	x	x
M. undata					x
Myrsine africana		x	x	x	x
Oxyanthus speciosus	(G-C)	x			
Pavetta abyssinica			x		x
Psychotria orophila		x			
Rhamnus prinoides		x			
Rhus glutinosa			x	x	
Rosa abyssinica			x		
Rytigynia neglecta		x			
Scolopia theifolia			x	x	
Spiniluma oxyacantha			x	x	
Teclea nobilis		x			
Trema orientalis		x			
Turraea holstii		x			

procera, Olea europaea, Pittosporum viridiflorum, Prunus africana, Maytenus arbutifolia, Myrsine africana, Scolopia theifolia and *Spiniluma oxyacantha*. The species must have a high tolerance of variations in temperatures, humidity and moisture availability to be able to survive in different vegetation types such as forests and shrublands. This shrubland type has been described as a secondary community that has expanded from lower altitudes and drier sites as the forests gradually disappeared (Zerihun & Backéus 1991). The possible occurrence of some dry montane forest species in secondary vegetation was noted earlier by Hamilton (1972).

6.2 Comparison between East-African montane forests

An attempt was made to compare some montane forests in Ethiopia and East Africa on the basis of the similarities in species distribution. A complete list of the species is not available, but the data at hand are considered to enable a regional comparison. A similarity analysis was carried out to evaluate the relationship between the forests based on the presence of tree and shrub species. The similarity index used is Sørensen's Similarity Coefficient $2c/(a+b)$, where c is the number of species shared by the forests

Table 13. Floristic similarity between the four forests described in this study and four comparable other forests: Belette forest (Friis et al. 1982), Mt. Elgon (Hamilton & Perrot 1981), Chilalo forest (Kebrom 1984), Harenna forest (Lisanework 1987). *N* = number of species included in the comparison.

Forest	Altitude (m)	*N*	1	2	3	4	5	6	7	8
Jibat	2200 - 2900	58	-							
Chilimo	2400 - 2800	30	0.31	-						
Menagesha	2400 - 3000	30	0.29	0.45	-					
Wof-Washa	2400 - 3000	27	0.26	0.34	0.39	-				
Belette	ca. 2800	28	0.35	0.17	0.15	0.24	-			
Harenna	ca. 2200 - 3300	48	0.36	0.19	0.19	0.18	0.27	-		
Chilalo	2400 - 3700	22	0.24	0.30	0.31	0.28	0.09	0.13	-	
Mt. Elgon	ca. 2000 - 3450	28	0.26	0.24	0.24	0.29	0.32	0.25	0.12	-

compared, *a* is the number of species in one forest, *b* is the number of species in the other forest. The results of the analysis are presented in Table 13.

The forests of Chilimo and Menagesha show a higher similarity to each other than to any other forest. Considering the geographical proximity of these forests to each other, and the similar human influence they have been exposed to, it is expected that they will not show much variation. The Wof-Washa and Jibat forests are in two different climatic zones, with the forests of Chilimo and Menagesha distributed in the intervening range.

The Chilalo forest, another remnant forest on the SE Plateau and situated very close to a regional town, is believed to be under severe human influence too. The presence of the exotic species, *Eucalyptus globulus*, in this forest indicates a far-reaching human influence in the forest. This forest is more similar to the dry forests of the Central Plateau than to the Harenna forest, which is also situated on the SE Plateau.

There is a very close relationship between the moist montane forests; the Jibat forest is equally related to the forests of Belette and Harenna. These forests are situated in the same ecological zone; they are found on the moister sides of the NW (Jibat & Belette) and SE (Harenna) Ethiopian Plateaux. A very close floristic relationship between these forests was earlier noted by Friis (1992).

The forests of Belette and Harenna are more related to the forest on Mt. Elgon (Uganda) than to the dry montane forests of Ethiopia. These forests are exposed to a similar moister climate, when compared to the dry Afromontane forests in Ethiopia. Gillett (1955) noted the flora of southern Ethiopia to be more similar to the flora of the East African highlands (Kenya and Uganda) than to that of northern Ethiopia.

The forests that show the least similarity are those of Belette and Chilalo. The former forest is situated in the wettest region of the country while Chilalo forest is situated on the leeward side of the SE Plateau.

Within Ethiopia, the forests in the southwest are species-rich and start to decrease to the north. The species richness of the lowland forests of Ethiopia in particular, however, is not comparable to that of the forests of East Africa. The general poverty in woody species in the Ethiopian flora has already been mentioned (e.g. White 1978; Hamilton 1989). Chapman & White (1970) characterize the moist montane forests of Malawi as differing from the dry montane forests in having a much higher proportion of species with relatives in the lowland. A distinct pattern in floristic impoverishment from west to east in the distribution of lowland forest trees in Uganda was also shown by Hamilton (1974).

There is a very long history of human inhabitation in East Africa, with the result that the natural vegetation has largely changed into a mosaic of remnant vegetation, woodlands, and various seral stages in the development of vegetation. Vegetation changes due to human impact as far back as ca. 2000 years ago have been noted to have taken place in Ethiopia (Bonnefille & Hamilton 1986). Only a few pollen studies have been carried out to reconstruct the vegetation history of the plateau so far (Hamilton 1982, Bonnefille & Hamilton 1986, Kedamawit 1986, Bonnefille & Buchet 1987). Still, more palynological work is needed to enable the complete reconstruction of past vegetation types.

7 General Discussion

If we consider all forest community types described for the Central Plateau in general, the main differentiation appears to follow the altitudinal gradient. The altitudinal ranges (m) for the four forests are as follows:

Jibat 2000 — 2950
Wof-Washa 2100 — 3600
Menagesha 2300 — 3000
Chilimo 2400 — 2900

The importance of an altitudinal gradient in the distribution of vegetation on East African mountains has been shown repeatedly (O. Hedberg 1951; Lind & Morrison 1974; Hamilton & Perrot 1981; Hamilton 1982; Dowsett-Lemaire 1988; Tewolde 1989). Three vegetation belts were described as characteristic for East African mountains (O. Hedberg 1951); the Montane forest belt, the Ericaceous belt and the Alpine belt. The Montane forest belt, and the Ericaceous belt to some extent, are represented in the Wof-Washa forest. The Montane forest belt is further subdivided into three zones (O. Hedberg 1951); the Montane rain-forest zone, the Bamboo zone and the *Hagenia-Hypericum* zone. The Montane rain forest and Bamboo zones have been described from the Jibat forest.

The *Arundinaria alpina* type in the humid Jibat forest, and the *Erica arborea* type in the dry Afromontane forests Chilimo, Menagesha and Wof-Washa, prevail at the highest elevations (>2700 m a.s.l.). At Wof-Washa, where the highest elevation is encountered, the *Erica* individuals decrease in size towards the upper limit of their occurrence and merge with the Afroalpine vegetation at about 3000 m a.s.l. There is a distinct *Arundinaria alpina* zone in the Jibat forest. It was noted that the mountain bamboo forms a natural zone in moist montane forests (Trapnell & Langdale-Brown 1962; Lind & Morrison 1974; Hamilton & Perrot 1978).

Erica arborea is favoured by fire, according to personal observations in the Jibat forest. Under natural conditions it forms a distinct community towards the upper edges of the forest, as found in Menagesha (above ca. 2800 m a.s.l.) and Wof-Washa forests (above ca. 3000 m a.s.l.).

The *Hagenia-Hypericum* zone *sensu stricto* is not distinct although the species assemblage is represented in the dry forests, except in the Chilimo forest. White (1978) mentioned that the Montane forests and Ericaceous belts can be differentiated on the highest mountains, where (as elsewhere) the two floras intermingle. Above ca. 3300 m a.s.l., species of the Alpine belt (e.g. *Lobelia giberroa*) start to appear on the upper ranges of the Wof-Washa forest. However, since the vegetation above the upper ranges of the montane forest has not been floristically analysed, it is difficult to say whether a well-defined Alpine zone really exists here.

The mountain bamboo (*Arundinaria alpina)* has only been described for the Jibat forest. However, a very small population of this species was found about 25-30 km from the Wof-Washa forest, situated in a valley surrounded by a completely degraded slope, and devoid of any natural vegetation. Local people state that this patch was larger in the past. Mountain bamboo is known as a component of humid montane forests (Lind & Morrison 1974), although its occurrence on African mountains depends on incompletely understood edaphic, biotic and climatic factors (Richards 1963).

The *Aningeria adolfi-friederici* forest type is distributed widely in wet montane forests of East Africa at altitudes of ca. 1500 - 2400 m (Lind & Morrison 1974). This community type has only been described from the Jibat forest and was absent from the dry Afromontane forests of the Plateau. However, due to its good wood quality this tree has been under high exploitation pressure and at present it is only sparsely distributed in the Jibat forest.

The species composition of the community types of the humid Afromontane Jibat forest is quite different from that of the dry Afromontane Chilimo, Menagesha and Wof-Washa forests. The contrast is evident both in the tree and field layer. The humid Afromontane forests are mixed types, with several deciduous species present as dominants. The local distribution of many species appears to be related to variation in altitude and other environmental, particularly soil fertility factors, and distinct community types can be distinguished.

The dry Afromontane forests differ from the humid ones by being evergreen and mainly dominated by two conifers: *Juniperus procera* and *Podocarpus gracilior.* Although the humid and dry Afromontane forests have certain species in common, the overriding conclusion is that the two types are floristically quite distinct. Species only occurring in the Jibat forest include: *Albizia* sp., *Aningeria adolfi-friederici, Arundinaria alpina, Millettia ferruginea* and *Olea hochstetteri.* Species that have only been encountered in the dry Afromontane forests include *Euphorbia obovalifolia, Haleria lucida, Maytenus arbutifolia, M. undata, Olea europaea, Oxyanthus speciosus,* *Podocarpus gracilior, Scolopia theifolia, Sideroxylon gillettii, Spiniluma oxyacantha,* and *Turraea holstii.*

The presence of an altitudinal zonation in forest vegetation in East Africa has been claimed by O. Hedberg (1951, 1955, 1978), and Moreau (1966), and more recently by Friis & Lawesson (1993), while Hamilton (1975) proposed the opposite view, especially regarding the forests in Uganda. The presence of altitudinal zonation, typical of the East African mountains (O. Hedberg 1951), is described from the Semien Mountains in the northern highlands of Ethiopia by Verfaillie (1978). There are two main reasons why it is not possible to make conclusive deductions regarding the mountains and escarpments of the Central Plateau of Ethiopia studied in the present work. Firstly, the extent of disturbance in most of the forests has been noted to be very large, thus obscuring the original state of the natural vegetation. Secondly, the altitudinal range in the mountains and escarpments may not be high enough to enable such a comparison to be made.

No attempt has been made in the present study to collect the epiphtyic plants in the sample plots. However, a visual estimate of their abundance has been recorded in the field. The general pattern in the distribution of the epiphytes can be summarized as follows. Epiphytic plants, predominantly mosses and lichens, are more prevalent in the forest of Jibat than in the other three forests. The tree lichen *Usnea* sp., on the other hand, is predominant in the forests of Wof-Washa, Menagesha and Chilimo, especially on the tree species *Juniperus procera.* This difference can probably be explained by the higher precipitation and humidity in the humid Jibat forest. Estimations of epiphytes can be used as a diagnostic characteristic in order to detect old secondary and climax forest communities (see Budowski 1970): epiphytes are common on trunks and branches of trees of old secondary communities, but few species are represented, while in climax communities the specimens are few but many species are present. Since the observations in this study have not been quantified, it is not possible to derive at such a conclusion.

The number of logs, tree stumps and dead but standing trees in each sample plot were counted as possible indicators of disturbance and senescence. The following is a summary of the recordings - figures are numbers of individuals/ha -

Forest	Logs	Stumps	Standing dead
Jibat	64	10	123
Chilimo	102	160	13
Menagesha	18	50	5
Wof-Washa	109	47	5

The smaller number of stumps in Jibat suggests a less intense selective cutting in this forest. However, it has to be noted that, in this forest, sites under human interference have been avoided during sampling and the effects of exploitation can not be seen from the distribution of the stumps alone. It has earlier been noted that there is some selective cutting going on in the Jibat forest (see Fig. 6). The very large number of standing dead trees indicate that this forest is still in a developmental stage. The very high number of stumps in the Chilimo forest indicates the extent of exploitation in the forest. The forests of Menagesha and Wof-Washa are similar, except for the very low number of logs in the former. Most of the stumps in the forest are very large, and the forest could probably have attained a structure similar to that of the Wof-Washa forest at present if it had been left untouched.

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Appendix 1. Species recorded from the remnant forests of the Central Plateau of Shewa, Ethiopia. b = bamboo; cl = climber; f = fern; g = graminoid; h = herb; s = shrub; sp = pioneer shrub; t = tree; tp = pioneer tree.

Acanthaceae	
Acanthus sp.	s
Hypoestes triflora	h
H. forskali	h
Isoglossa punctata	h
I. somalensis	h
Justicia flava	h
J. schimperiana	h
Mimulopsis solmsii	h
Adianthaceae	
Cheilanthes afromontana	f
Agavaceae	
Dracaena afromontana	s
Amaranthaceae	
Achyranthes aspera	h
Celosia argentea	h
Anacardiaceae	
Rhus glutinosa	s
Apiaceae	
Agrocharis incognita	h
A. melanantha	h
Centella asiatica	h
Peucedanum winkleri	h
Sanicula elata	h
Apocynaceae	
Carissa edulis	s
Aquifoliaceae	
Ilex mitis	t
Araliaceae	
Polyscias fulva	t
Schefflera volkensii	t
Asclepiadaceae	
Leptadenia sp.	cl
Periploca linearifolia	cl
Aspidiaceae	
Dryopteris inaequalis	f
Aspleniaceae	
Asplenium abyssinicum	f
A. aethiopicum	f
A. bugoiense	f
A. erectum	f
A. monanthes	f
A. theciferum	f
Asteraceae	
Athrixia rosmarinifolia	h
Bidens pilosa	h
Carduus leptacanthus	h
Cirsium deuderii	h
Conyza hypoleuca	s
Crassocephalum sp.	h
Crepis sp.	h
Echinops sp.	s
Asteraceae *(cont.)*	
Gerbera piloselloides	h
Guizotia scabra	h
Haplocarpha sp.	h
Inula confertiflora	h
Inula sp.	h
Laggera sp.	h
Microglossa pyrifolia	h
Mikaniopsis clematoides	cl
Prenanthes subpaltata	h
Senecio sp.	s
Tolpis virgata	h
Vernonia amygdalina	s
V. rueppellii	s
Balsaminaceae	
Impatiens aethiopica	h
I. hochstetteri	h
Boraginaceae	
Cordia africana	t
Cynoglossum amplifolium	h
Ehretia cymosa	s
Heliotropium sp.	h
Caryophyllaceae	
Cerastium afromontanum	h
C. octandrum	h
Stellaria media	h
S. senii	h
Celastraceae	
Hippocratea sp.	cl
Maytenus addat	s
M. arbutifolia	s
M. undata	s
Commelinaceae	
Commelina latifolia	h
Convolvulaceae	
Convolvulus sp.	h
Crassulaceae	
Crassula alsinoides	h
Kalanchoe petitiana	h
Kalanchoe sp.	h
Cupressaceae	
Juniperus procera	t
Cyperaceae	
Carex chlorosacus	g
C. spicato-paniculata	g
Carex sp.	g
Cyperus fischerianus	g
Cyperus sp.	g
Kyllinga apendiculata	g
Dennstaedtiaceae	
Blotiella glabra	f
Pteridium aquilinum	f
Ebenaceae	
Euclea schimperi	t
Ericaceae	
Agauria salicifolia	s
Erica arborea	t
Euphorbiaceae	
Clutia abyssinica	s
Croton macrostachyus	t
Erythrococca trichogyne	s
Euphorbia obovalifolia	t
Fabaceae	
Albizia sp.	t
Calpurnea aurea	s
Crotalaria incana	h
C. rosenii	h
Crotalaria sp.	s
Desmodium sp.	h
Indigofera sp.	h
Millettia ferruginea	t
Parochetus communis	h
Trifolium sp.	h
Vigna sp.	h
Flacourtaceae	
Dovyalis abyssinica	s
Flacourtia indica	s
Flacourtia sp.	s
Scolopia theifolia	t
Geraniaceae	
Geranium aculeolatum	h
G. arabicum	h
Hypericaceae	
Hypericum lanceolatum	s
H. revolutum	s
Icacinaceae	
Apodytes dimidiata	t
Lamiaceae	
Ajuga remota	h
Ocimum sp.	h
Plectranthus assurgens	s
Salvia merjamie	h
S. nilotica	h
Satureia abyssinica	h
Stachys aculeolata	h
Thymus sp.	h
Liliaceae	
Gloriosa simplex	cl
Loganiaceae	
Buddleja polystachya	s
Nuxia congesta	t
Meliaceae	
Ekebergia capensis	t
Lepidotrichilia volkensii	t
Turraea holstii	s

Melianthaceae	
Bersama abyssinica	sp
Menispermaceae	
Cissampelos sp.	cl
Stephania abyssinica	cl
Moraceae	
Ficus sur	t
Myricaceae	
Myrica salicifolia	t
Myrsinaceae	
Embelia schimperi	s
Maesa lanceolata	tp
Myrsine africana	s
Rapanea simensis	t
Myrtaceae	
Syzygium guineense	t
Oleaceae	
Jasminum abyssinicum	s
J. stans	s
Olea europaea	t
O. hochstetteri	t
O. welwitschii	t
Oliniaceae	
Olinia aequipetala	t
Orchidaceae	
Aerangis sp.	h
Polystachya fuscopalaeum	h
Piperaceae	
Peperomia abyssinica	h
Pittosporaceae	
Pittosporum mannii	t
P. viridiflorum	t
Plantaginaceae	
Plantago palmata	h
Plantago sp.	h
Poaceae	
Andropogon abyssinicus	g
Arundinaria alpina	g/b
Ehrharta erecta	g
Eragrostis tenuifolia	g
Oplismenus compositus	g
Panicum repentallum	g
Pennisetum sp.	g
Sporobulus africanus	g
Strebochaete longifolium	g
Podocarpaceae	
Podocarpus gracilior	t
Polygalaceae	
Polygala steudneri	h
Polygonaceae	
Phytolacca dodecandra	s
Polypodiaceae	
Pleopeltis macrocarpa	f
Proteaceae	
Protea gaguedii	s
Pteridaceae	
Pteris catoptera	f
P. cretica	f
Ranunculaceae	
Thalictrum sp.	h
Rhamnaceae	
Rhamnus prinoides	s
R. staddo	s
Rhizophoraceae	
Cassipourea malosana	t
Rosaceae	
Alchemilla abyssinica	h
Alchemilla sp.	h
Hagenia abyssinica	t
Prunus africana	t
Rosa abyssinica	s
Rubus apetalus	s
Rubiaceae	
Canthium oligocarpum	s
Galiniera coffeoides	t
G. saxifraga	t
Oldenlandia monanthos	h
Oxyanthus speciosus	s
Pavetta abyssinica	s
Psychotria orophila	s
Rytigynia neglecta	t
Rutaceae	
Clausena anisata	sp
Teclea nobilis	t
Vepris dainellii	t
Santalaceae	
Osyris lanceolata	h
Sapindaceae	
Allophylus abyssinicus	t
Sapotaceae	
Aningeria adolfi-friederici	t
Sideroxylon gillettii	t
Spiniluma oxyacantha	t
Scrophulariaceae	
Halleria lucida	s
Selaginellaceae	
Selaginella abyssinicum	h
Simaroubiaceae	
Brucea antidysenterica	s
Smilacaceae	
Smilax goetzeana	cl
Solanaceae	
Discopodium penninervium	s
Solanum indicum	s
Sterculiaceae	
Dombeya burgessiae	s
Thymelaeaceae	
Gnidia glauca	s
Ulmaceae	
Celtis africana	t
Trema orientalis	sp
Urticaceae	
Droguetia iners	h
Urera hypselodendron	s
Verbenaceae	
Lippia sp.	s
Violaceae	
Viola abyssinica	h

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