Journal of Vegetation Science 5: 87-98, 1994

Phytosociology and ecology of a humid Afromontane forest on the Central Plateau of Ethiopia

Tamrat Bekele

Department of Ecological Botany, Uppsala University, Villavägen 14, S-752 36 Uppsala, Sweden; Tel. +46 18 182850; Fax +46 18 553419; Permanent address (after March 1994): Department of Biology, Addis Abeba University, P.O. Box 1176, Addis Abeba, Ethiopia; Fax +251 1 552112

Abstract. This paper describes an analysis of the floristic composition and ecological relationships of the Jibat forest, a large remnant humid forest in western Shewa, Ethiopia. The description was based on cover-abundance data for both woody and understorey species. The environmental analysis included altitude, slope, aspect, and physical and chemical soil properties. The application of classification and ordination methods resulted in the recognition of eight community types, which could be arranged along an altitudinal gradient. Organic matter, cation exchange capacity, phosphorus, and silt are positively correlated, while clay, electrical conductance and magnesium are negatively correlated with altitude. A clearer result was obtained when Canonical Correspondence Analysis was applied only to the woody species composition.

Keywords: Canonical Correspondence Analysis; Classification; Discriminant analysis; Jibat; Optimal cluster level; Shewa; TABORD; TWINSPAN.

Nomenclature: Cufodontis (1953-1972); I. Hedberg & Edwards (1990); for grasses: Fröman & Persson (1974); for ferns: Johns (1991).

Introduction

At present, forests on the Central Plateau of Ethiopia occur only in a few isolated patches. They are probably remnants of forest vegetation that had a much wider extension in the past. There are no exact figures available on the original forest cover of the Central Plateau, because deforestation has occurred for thousands of years. According to an estimation of Sayer et al. (1992), montane forests do not cover more than 47 256 km^2 today, i.e. only 2.4 % of the total land area of the country.

Remnant forests are mainly found above 1800 m; they constitute part of the Afromontane floristic region of White (1983). Studies on the vegetation of Ethiopia on a national basis are scanty, and quantitative contributions to the understanding of the vegetation of the Central Plateau are few. The forests of Ethiopia have served and still serve as a source of food, fuel, construction material, farm implements, and medicine to the rural population. More than 88 % of the Ethiopian population live in rural areas (Anon. 1988). The ever increasing demand for forest products and forest land, together with the alarming rate of population growth (ca. 3 %/yr, Anon. 1988) has put the remaining patches of forests on the verge of extinction. A detailed quantitative and qualitative description of the remaining forests is necessary and timely as it will form the basis for future studies or plans to manage and restore these vanishing resources.

This study aims at: (1) describing the natural forest vegetation type of Jibat, the largest forest area left, and (2) understanding the ecological relationships between the vegetation and the physical environment, using multivariate methods. Special attention is paid to the problem of how to arrive at an effective classification and how to effectively describe vegetation-environment relations in an unknown and inaccessible area.

The study area

The Jibat forest is situated in western Shewa (37° 15' - 37° 30' E; 8° 35' - 8° 50' N), ca. 200 km west of Addis Abeba (Fig. 1). The forest covers an area of ca. 32 000 ha. The main part of the forest stretches between 2000 and 3000 m a.s.l. Towards the southwest the forest extends to lower altitudes over a wider area forming a mosaic of small woodlands and farmlands. According to Daniel (1977) the whole forest region belongs to the 'moist subhumid moisture region' with an average rainfall of 1000 - 1400 mm/yr. However, data over 14 years (1975 - 1989) from a station near the forest, at 2550 m, indicate an average rainfall of 1800 mm/yr. Rain occurs throughout the year, but there are two peaks, in March and August. The 'spring' peak is related to moist winds from the Indian Ocean, the 'summer' peak arises from warm winds from the southwest. Average monthly temperatures are between 14.4 - 16.2 °C with average minimum and maximum temperatures of 8.8 °C and 21.6 °C respectively.

Pre-Cambrian rocks underlie all superficial rock formations in Ethiopia, and basalts are the main rock type forming the substrate for the plateau soils. Soils on hillsides and steeper slopes are red to reddish-brown. Westphal (1975) classified these soils as alfisols with udalfs as the main suborder. The alfisols are characterized by a sub-soil horizon with an increased clay content, in which the base status increases with depth (Lathwell & Grove 1986). There is no record of the history of the forest and it is difficult to ascertain its degree of naturalness. The montane forest vegetation of most parts of tropical Africa is heavily influenced by man, so that secondary forests in various stages of regrowth prevail nowadays (Friis 1992). Since age determination of trees in the tropics is usually impossible, it is difficult to estimate the age of these forests. Human impact in the Jibat forest, notably forest clearing and tree felling, is evident at the edges and at some places in the interior of the forest. There is one sawmill which is not functioning any more; commercial exploitation is forbidden

Methods

Vegetation analysis

A reconnaissance survey of the Shewa Plateau was made in October-November 1988. The boundaries of the Jibat forest were derived from topographic maps [Series: ETH 4 (DOS 450), Sheet: 0837 A2, and 0837 A4, Edition: 1 EMA/DOS 1977] at scale 1:50 000, which appeared to be still actual (Fig. 1). Stands were selected as far away as possible from settlements and where human influence was apparently minimal. Tracks used by people who collect honey and leaves of wild *Rhamnus prinoides* shrubs (an important ingredient in locally brewed beverages) were followed to get reach remote areas. Logistics and security problems did not allow an analysis of the whole forest. The area traversed for this study amounts to ca. 80 % of the total forest. The Jibat forest is much dissected by rivers and their tributaries, and for the most part the terrain consists of alternating valleys and ridges. As a result, there is a considerable variation in habitat factors within short distances.

Representative stands were selected on the basis of homogeneity and visually checked for uniformity in floristic composition. In order to avoid heterogeneity of the floristic composition, the plot size was limited to 30 m × 30 m (cf. Westhoff & van der Maarel 1973; Hommel 1990). Where the topography and slope made this size impractical, the plots were smaller, but never less than 25 m × 20 m. A total of 77 sample plots from a wide range of altitudes, slopes and aspects were included. The field work was performed from November 1988 to January 1989 and December 1990 to February 1991.

The vegetation description was based on the complete floristic composition of the plant communities following Braun-Blanquet (see Westhoff & van der Maarel 1973). Because uniformity of the canopy is easier to check over a larger area than uniformity of the field layer, some authors restricted their sampling to the trees or woody species only (Poore 1955b; Greig-Smith 1969a; Hall & Swaine 1981), or trees of certain diameter classes (e.g. Gentry 1988, see Hommel 1990). In the present work all trees and shrubs of DBH (diameter at breast height) ≥ 2 cm were measured as to height and DBH. Cover/abundance values were estimated for all tree and shrub species following the Braun-Blanquet scale as modified by van der Maarel (1979). Additional species occurring in the immediate vicinity of the plot (usually 10 m around) were recorded only as 'present'; they were not used in the subsequent data analysis. The field layer was analysed in a subplot which was selected after visual inspection. Considering the low herbaceous cover, poverty in species, and overall uniformity of the field layer, only one 2 m × 2 m subplot was located where the vegetation appeared representative. Cover/abundance values for all herbaceous species and the cover of litter were estimated. Additional species occurring outside the subplot but within the plot were recorded as 'present', but not included in further data analysis. Identification of plant species, apart from those readily identifiable in the field, was done at the National Herbarium, Addis Abeba University.

Site description and soil analysis

For each plot, altitude (m a.s.l.), slope (°), and aspect were determined. Aspect, linked to total solar energy, was codified according to Zerihun et al. (1989), with the following modifications: N = 0, E = 2, S = 4, W = 2.5, NE = 1, SE = 3, SW = 3.3, NW = 1.3, Ridge top = 4.

Soil samples were taken and prepared as follows. A composite sample was made from five different points (four at the corners and one in the middle of the plot; variation in microrelief was avoided. The samples were initially taken from the following depths: 0 - 10, 10 - 20, 20 - 30, 30 - 40, 40 - 50, 50 - 60 cm, or less for shallow soils. After mixing, a representative sample of 1 - 1.5 kg of each layer was collected. As it was not possible to obtain samples from all depths for all sites, only values from the top three layers were used in the subsequent data analysis.

Soil analyses were carried out at the Soil Laboratory of the Ministry of Agriculture, Addis Abeba, following standard procedures outlined in Allen (1989). The samples were analysed for texture (hydrometer method),

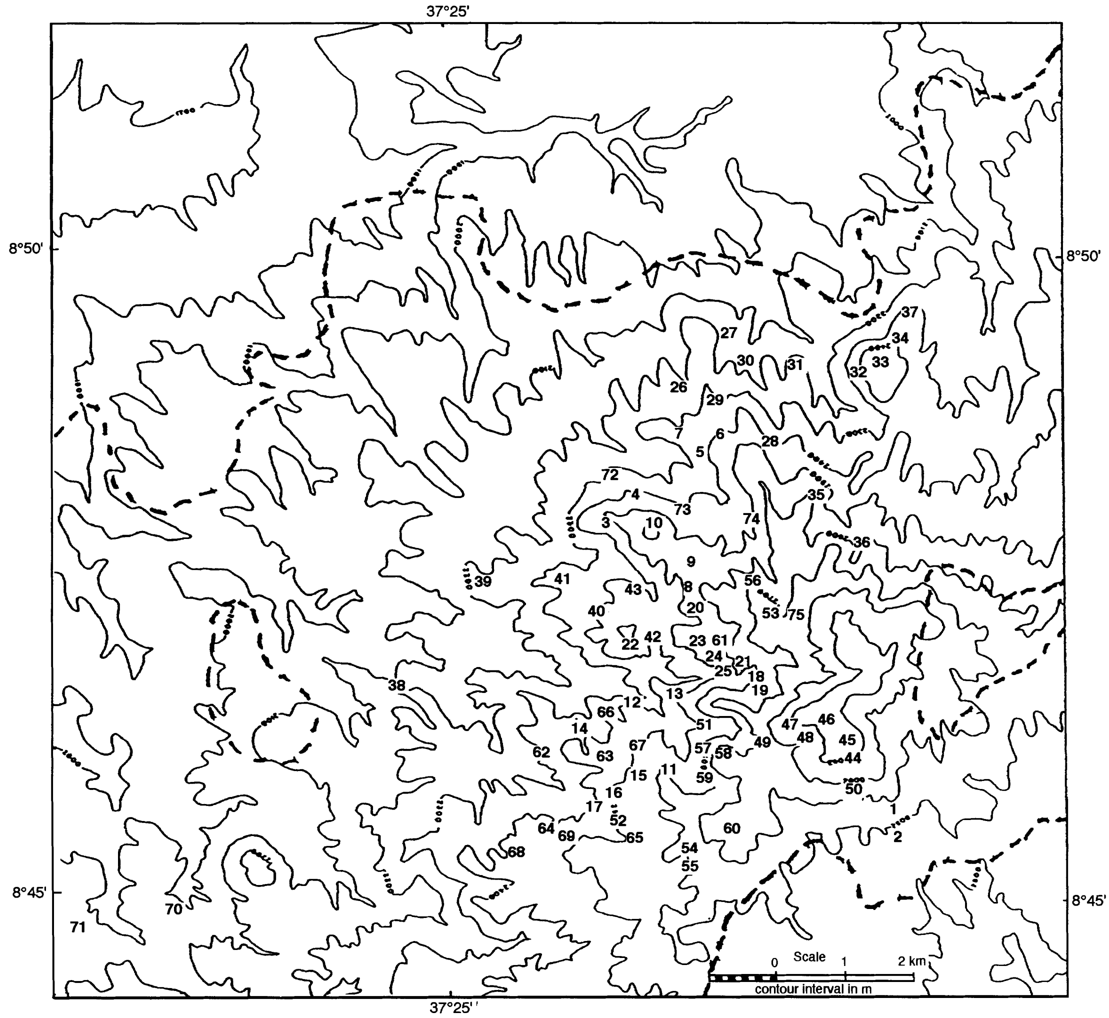

Fig. 1. Topographic map of the Jibat forest area showing the boundaries of the Chilimo forest and the location of the sample plots (two sample plots not shown).

with the categories sand, silt and clay (expressed as % weight); organic matter (Walkely-Black wet oxidation, % dry weight), pH and electrical conductivity (mmhos/l), both in 1:1 soil-water suspension; available phosphorus (Bray No. II method, ppm), total nitrogen (Kjeldahl method, meq./100g), calcium and magnesium (atomic absorption method), sodium and potassium (flame photometry), and cation exchange capacity (extraction with ammonium acetate at pH 7) (all in meq./100g).

Data analysis

In order to obtain an effective description of community types and their environmental relations, both classificatory and ordination techniques were employed. The relevés were grouped into clusters and arranged in an ordered table with the aid of TABORD (van der Maarel et al. 1978), an agglomerative clustering program with relocation of relevés, and TWINSPAN, the two-way indicator species analysis (Hill 1979) resulting in a hierarchical structure of relevés and species groups. 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. The resulting cluster structure was then arranged in an ordered phytosociological table using a frequency limit of 0.60 for characterizing species.

The following options were chosen in the TWINSPAN program: number of cut levels 9, minimum group size 2, maximum number of indicators per division 7, maximum division level 6, weights at different cut levels set to 1, indicator values at different cut levels set to 1. The cluster structures obtained with the two methods were compared and a final classification was based on a combination of the results. The resulting clusters were characterized as local plant communities. These were not placed in a hierarchical syntaxonomic classification system but in a network structure. A general formalized system of plant communities is not available for Ethiopia. Therefore, the clusters distinguished were described as 'types' and given provisional names after one or two dominating and/or characteristic species.

The classification results were further evaluated by relating the community composition to environmental variation with the program DISCRIM (ter Braak 1982). This is a modification of the TWINSPAN program which helps to construct simple discriminant functions and to classify attributes given a hierarchical classification of samples.

Canonical Correspondence Analysis (CCA) (ter Braak 1986), a variant of Reciprocal Averaging where axes are correlated with environmental variables and adjusted as to achieve maximal linear correlation, was performed including 13 soil variables (see above). Missing values in the environmental data were estimated and assigned by calculating the mean values of a particular variable within a cluster. CCA was performed with procedures in the program-package CANOCO (ter Braak 1988).

The community types obtained were subjected to an ANOVA based on environmental variables to find out whether there are significant variations between the groups. Pearson's product-moment correlation coefficient was calculated to evaluate the relationship between the environmental variables. Both the above analyses were calculated with the GLM (General Linear Model) procedure available in the SAS (Statistical Analysis Systems) package (Anon. 1990).

Results and Discussion

Classification

Out of 77 original relevés, two (28 and 73) were set aside. They were recognised as outlier relevés by TABORD; the former was subsequently described as a one-relevé cluster (see below). 53 tree and shrub species and 39 herbaceous species were identified. A total of 131 species of trees, shrubs and herbs were described from either within, or in the vicinity of, the sample plots. Seven community types were derived from the classification using TABORD. The decision on the number of clusters was based on results obtained with the CALCOM procedure (Noest & van der Maarel 1989), a program which computes the optimal level of clustering by comparing within- and between-cluster similarities. The seven community types were also distinguishable from TWINSPAN results at the 4-level of division, with slight modifications. Thus, from a floristic viewpoint, a seven-cluster solution was considered optimal. The clusters were then summarised by subjecting them to SYNOP (van der Maarel et al. 1987), a program that calculates a synoptic cover-abundance value, which is the product of frequency and cover-abundance. Synoptic cover-abundance values for the most important species are shown in Table 1. Cluster numbers in the tables correspond to numbers of the community types below.

1. *Arundinaria alpina* type

The tree species *Hagenia abyssinica* and *Rapanea simensis* occur scattered in this *Arundinaria* (bamboo) type. A shrub layer is absent; the field layer is composed mainly of the grass *Oplismenus compositus* and the sedge *Carex spicato-paniculata*. This type (Afromontane bamboo type *sensu* White 1983) grows most vigorously at the highest elevations in Jibat, between 2700 and 3000 m, but it can descend to lower elevations along valley slopes. The vegetation is open, partly because the bamboo is intensely used both for construction and fuel by local people. However, the leaves of the bamboo intermingle at the top, forming a dense canopy, which hardly allows any undergrowth. The stems are ca. 8 cm in diameter and generally attain a height of 9 - 12 m. A mean number of 9333 culms/ha was found.

2. *Ilex mitis-Rapanea simensis* type

The associated trees and shrubs include *Apodytes dimidiata*, *Galiniera coffeoides*, *Olinia aequipetala*, *Maytenus addat*, *Nuxia congesta*, *Olea hochstetteri* and *Psychotria orophila*. The field layer is dominated by *Oplismenus compositus* and *Carex spicato-paniculata*. The *Ilex mitis-Rapanea simensis* type is found in the interior of the forest and hence is the least disturbed type. It is generally found between 2500 and 2800 m; it is a high-altitude community; species like *Rapanea simensis* are mainly restricted to this range.

3. *Syzygium guineense-Psychotria orophila* type

Associated trees in this type include *Apodytes dimidiata*, *Galiniera coffeoides*, *Ilex mitis*, *Lepidotrichilia volkensii, Olea hochstetteri, Olinia aequipetala* and *Prunus africana*. *Dracaena afromontana* is a characteristic shrub. The field layer is dominated by *Oplismenus compositus* and *Hypoestes triflora*. Most of the individuals are of medium height and have very slender stems. There is a relatively high number of emergent trees (> 20 m tall) as compared to the very few individuals in type 2.

4. *Olea hochstetteri-Olinia aequipetala* type

Regarding its floristic composition, this community is similar to type 3. However, *Ilex mitis* and *Galiniera coffeoides* are very rare here. *Oplismenus compositus* is

Table 1. Cluster structure of the Jibat forest relevés with synoptic cover-abundance values for species reaching a value ≥ 1.0 in at least one cluster. The names of species used for the names of the community types based on the clusters are given in bold. Results of Tukey's multiple range test between environmental variables and clusters are shown at the bottom of the table; significant differences at $p < 0.05$ (if any) are indicated with different letter notations below each row.

Cluster no.	1	2	3	4	7	5	6
Cluster size	7	22	22	16	2	4	2
Arundinaria alpina	**9.0**	0.0	0.0	0.0	0.0	0.0	0.0
Hagenia abyssinica	1.1	0.4	0.1	0.0	0.0	0.0	0.0
Carex spicato-paniculata	4.8	1.6	0.0	0.1	0.0	2.1	8.0
Oplismenus compositus	4.8	5.3	1.7	7.1	0.5	3.4	4.5
Rapanea simensis	2.7	**5.7**	0.0	0.2	0.0	0.0	0.0
Ilex mitis	0.0	**6.0**	5.6	0.1	0.0	0.0	0.0
Maytenus addat	0.0	1.4	0.2	0.2	0.0	0.5	4.0
Nuxia congesta	0.0	1.1	0.0	0.0	0.0	0.0	0.0
Geranium arabicum	0.0	1.0	0.1	0.6	0.0	0.0	0.0
Galiniera coeffoides	0.0	3.8	4.3	0.6	6.5	0.1	0.0
Psychotria orophila	0.0	0.9	**5.9**	1.2	1.3	0.8	0.0
Dracaena afromontana	0.0	0.1	2.3	0.9	0.3	0.0	0.0
Olea hochstetteri	0.0	1.2	2.9	**6.0**	1.5	3.6	8.0
Olinia aequipetala	0.0	3.3	0.7	**2.9**	0.0	0.1	0.0
Lepidotrichilia volkensii	0.0	0.1	0.7	1.7	1.3	0.4	0.0
Apodytes dimidiata	0.0	0.5	2.7	4.0	0.3	0.3	4.0
Prunus africana	0.0	0.0	1.0	1.5	4.0	0.1	1.3
Syzygium guineense	0.0	0.1	**6.9**	3.2	**8.0**	3.2	0.0
Vepris dainellii	0.0	0.0	0.2	0.1	**1.5**	0.0	0.0
Impatiens aethiopica	0.0	0.0	0.0	0.0	9.0	0.0	0.0
Albizia sp.	0.0	0.0	0.0	0.1	3.5	4.5	1.0
Bersama abyssinica	0.0	0.2	0.4	0.3	0.5	1.3	0.3
Teclea nobilis	0.0	0.0	0.0	0.3	0.0	1.7	1.3
Ehretia cymosa	0.0	0.0	0.0	0.0	0.0	1.5	0.0
Ficus sur	0.0	0.0	0.0	0.0	0.0	**3.0**	0.0
Croton macrostachyus	0.0	0.0	0.0	0.0	0.3	**4.3**	0.3
Calpurnia aurea	0.0	0.0	0.0	0.1	0.0	1.7	4.0
Hypoestes triflora	0.0	0.5	0.9	0.4	0.0	5.5	5.0
Rytigynia neglecta	0.0	0.0	0.0	1.3	0.3	1.3	3.5
Olea welwitschii	0.0	0.0	0.0	0.2	1.0	0.8	**7.0**
Carissa edulis	0.0	0.0	0.0	0.0	0.0	0.0	**4.0**
Millettia ferruginea	0.0	0.0	0.0	0.0	2.0	0.0	4.0
Cassipourea malosana	0.0	0.0	0.0	0.2	0.0	0.4	1.5
Oxyanthus speciosus	0.0	0.0	0.0	0.0	0.3	0.4	1.0
Hippocratea sp.	0.0	0.0	0.0	0.0	0.0	0.0	1.3
Altitude (m.a.s.l.)	2833	2626	2459	2417	2050	2203	2195
	a	b	c	c	d	de	e
Organic matter (%)	19.8	15.1	11.7	11.2	7.4	10.4	9.0
	a	ab	bc	bc	c	bc	bc
C.E.C. (meq./100gm)	73.3	58.0	55.1	53.8	46.3	53.0	50.7
	a	b	b	b	b	b	b
P	14.2	4.8	1.1	2.2	0.0	1.6	3.0
	a	b	b	b	b	b	b
Silt (%)	85.7	85.4	82.7	78.0	70.4	71.3	81.0
	a	a	ab	abc	c	bc	abc
Clay (%)	7.2	8.8	11.8	16.3	26.0	19.7	14.0
	c	bc	bc	abc	a	ab	bc
Sand (%)	6.0	5.7	5.5	5.7	3.7	9.0	5.0
	ab	ab	ab	ab	b	a	ab
Electric conductivity	0.12	0.21	0.23	0.21	0.25	0.42	0.20
	b	ab	ab	ab	ab	a	b
pH	6.5	5.6	5.7	5.6	5.4	6.0	5.5
	a	b	b	b	b	ab	b
Na	0.41	0.9	0.16	0.49	0.0	0.50	0.55
K	0.90	1.16	1.49	1.23	0.75	1.48	1.95
Mg	3.1	3.4	3.8	5.2	4.6	6.4	5.7
N	0.7	0.6	0.4	0.5	0.4	0.6	0.6
Exposure	3.0	1.9	1.7	1.3	2.7	0.7	2.0
Slope	26.3	22.1	20.8	17.3	18.0	10.7	17.0
Ca	21.2	13.8	15.4	23.1	10.4	25.1	16.6

still the dominant grass, and *Geranium arabicum* is an associated herb. This type extends to altitudes lower down than those occupied by the previous group and has a general distribution between 2100 and 2600 m.

5. *Croton macrostachyus-Ficus sur* type

The shrub layer is well-defined and is represented by *Bersama abyssinica*, *Calpurnea aurea*, *Ehretia cymosa*, *Psychotria orophila*, *Rytigynia neglecta* and *Teclea nobilis*. Other species in the tree layer include *Albizia* sp., *Olea hochstetteri* and *Syzygium guineense*. The field layer is composed of *Carex spicato-paniculata*, *Hypoestes triflora* and *Oplismenus compositus*, This type is found along the forest edge at altitudes between 2100 and 2300 m.

6. *Olea welwitschii-Carissa edulis* type

Associated trees and shrubs in this type include *Apodytes dimidiata*, *Calpurnea aurea*, *Cassipourea malosana*, *Maytenus addat*, *Millettia ferruginea*, *Olea hochstetteri*, *Oxyanthus speciosus* and *Rytigynia neglecta*. *Carex spicato-paniculata*, *Hypoestes triflora* and *Oplismenus compositus* are the dominant herbaceous species. This type has a distribution similar to type 5. *Milettia ferruginea* and *Carissa edulis* are found mainly along streams. The trees in this group are medium in stature, but some emergent trees attain heights of > 20 m.

7. *Syzygium guineense-Vepris dainelli* type

Associated species in the tree and shrub layer include *Albizia* sp., *Galiniera coffeoides*, *Lepidotrichila volkensii*, *Millettia ferruginea, Olea hochstetteri*, *O. welwitschii*, *Prunus africana* and *Psychotria orophila*. A dominant herb here is *Impatiens aethiopica*. This community is situated along the lower western fringes of the forest at altitudes around 2000 m. Human interference is very pronounced here, and trees and shrubs, especially in the lowest height classes (2 - 6 m), are very few in number. Most of the farm utensils used by farmers are made from trees or shrubs in this height class. The field layer shows a characteristic composition which differs a great deal from the other types.

8. *Erica arborea* type

One individual plot (no. 28) is taken as a one-relevé cluster and described here separately. It is a stand situated on a very steep south-facing slope (49°) with an irregular surface with small rock outcrops. It is almost exclusively composed of *Erica arborea*, a shrub of 2 - 4 m height. *Myrsine africana* saplings occur in the undergrowth. There is a very thick moss cover on the ground. Very few trees are found in the stand, including *Rapanea simensis*, *Myrica salicifolia* and *Olinia aequipetala*. It is known that a fire burned the vegetation on the upper slope about 25 yr ago. There is hardly any soil cover except in rock crevices.

Sample plot 73 showed a very low similarity to all clusters formed; it is slightly similar to community type 7, both in distribution and floristic composition, the major difference being the absence of the herb *Impatiens aethiopica*. This relevé was assigned to type 7.

Relating the classification to environmental variation

In order to characterize the community types derived from those environmental variables which optimally predict the classification, program DISCRIM was applied to the results from the TWINSPAN classification. Note that the final cluster structure (Table 1) is not identical with the TWINSPAN result. As Table 2 shows, five TWINSPAN clusters are largely or wholly identical with five types, i.e. types 1, 2, 5, 6 and 7, one cluster includes two types, i.e. 3 and 4, and one cluster was not maintained in the final typology. In order to give the environmental factors equal weight values for these factors were transformed as follows: $y = 10\,(x - x_{min})\,/\,(x_{max} - x_{min}) - 1$, where the y-values were rounded off to the nearest integer. As a result the transformed values range from 0 to 9.

The first discrimination is on altitude, where first cluster 1 is separated at division level 1, and cluster 2 at level 2. Clusters 3, 4 and 7 are discriminated from clusters 5 and 6 by K and Mg at division level 3. At lower levels in the hierarchical classification, discrimination is only meaningful if both the species composition and the environmental variables are taken into account.

The cluster 3 + 4 is divided into two groups at the fourth level of the division with soil texture as discriminating factor. A similar within-cluster division can be noticed in the distribution of the herbs *Oplismenus compositus* and *Hypoestes triflora*. The former is found abundantly on clayey soils while the latter is found more on silty soils. The *Arundinaria alpina* type is split into two subtypes at the second level of the division based on differences both in species composition and environmental variation. Plot 38 includes the fern *Pteris catoptera*, and lacks the grass *Oplismenus compositus*, as different from the other plots within the cluster. This plot also deviates in nutrient status; it has relatively high values for Ca, K, Mg, and cation exchange capacity. Such a local variation may be accounted for by the history of the site. This plot occurs on a site where there are remains of old dwellings buried just below the subsoil. Gentry (1988) attributed the poor species composition of west-African forests to the alteration of the habitats by the native population in the past.

Zerihun & Backéus (1991) found a strong correlation between silt content and slope in the shrublands of the Central Plateau of Ethiopia, and attributed this to historical factors such as grazing and erosion. Local conditions such as soil parent material and topography may also affect the accumulation of certain nutrients and influence species distribution.

In addition, correlations of environmental variables among each other and with the community types were calculated with the Tukey test (Anon. 1990). The communities were significantly different from each other, mainly with respect to altitude and organic matter (Table 1). Community type 1 is significantly different from the other types (2 - 7) with respect to most environmental variables. Altitude, organic matter, silt, cation exchange capacity, N and P are strongly correlated (Table 3). Accumulation of organic matter at higher altitudes can be partly accounted for by the low rate of decomposition due to the low temperature. Nitrogen and phosphorus constitute important parts of the organic fraction, and hence are bound in higher quantities at higher elevations. The cation exchange capacity relates to both the soil solution and the colloid (humus and clay); its correlation with altitude can be explained, in part, by the high amount of organic matter as well.

The exchangeable bases, especially Ca and Mg, are correlated with pH. A high proportion of the exchange positions of soil colloids are saturated with cations at high pH values, and become replaced with H-ions at low pH values. Under rain forest conditions the bases are quickly discharged in the drainage water, thus rendering the soil acidic (Richards 1952). There is a strong correlation between silt and altitude whereas clay is negatively correlated with both variables.

The high organic matter content in soils at higher altitudes (Richards 1952) has been shown for various forests (e.g. Whitmore & Burnham 1969; Edwards & Grubb 1977), and African soils in general (Birch & Friend 1956). Bouxin (1976) observed a similar increased correlation between organic matter and slope for a forest in Uganda. Lower temperatures at high altitudes combined with the greater wetness in humid regions decrease the rate of mineralization of the organic matter and hence lead to the accumulation of organic matter. The other correlations between nutrients can be attributed to the parent material. The overriding importance of soil parent materials over climate in determining the distribution of forest types on tropical mountains has been pointed out by Grubb & Whitmore (1966).

Ordination

There is a general agreement between the ordination and classification results. The CCA of the woody species only and of all species together gave similar results, but omission of the herbaceous species improved the

Table 2. Results of the application of program DISCRIM to seven TWINSPAN clusters. Clusters 3 and 4 are combined. The cluster structure of variables and relevés are added in the usual output format of TWINSPAN.

Cluster	6	5	7		3 and 4	2	1	
Sample	2	22	223	66	1322235555555566641233311111	44111445624445 1	343343	
Plots	567	01	341	01	4002694234567892349152358967	723345461585780183292	719608	
Potassium	716	47	775	44	9661614502413843245670021183	231013305154124235034	212315	000
Clay	425	32	228	66	2264453011211339730222024111	002411321010100011431	110111	00100
Electrical conductivity	202	21	562	22	3222221101211321112215322320	021102401132010321011	010200	00101
Sodium	433	58	834	31	5537237513648525388733631377	100366005460068946455	221415	0011
Calcium	301	12	432	11	4590275100211421123330010204	110022102122123123013	321325	0100
Sand	111	12	494	01	2320920124412132324062233104	051126275202235022221	522601	010100
Silt	684	67	640	43	7736257987789650268867975998	988597767999899988579	779799	0101010
Nitrogen	632	55	500	58	0062069608630903566863225656	086399006520860908027	096069	0101011
Slope	122	23	220	33	3434336326535514576343023224	267234745445543405232	085079	01011
pH	423	34	556	23	6444527112625642246643440445	253043315255645843224	875969	011
Magnesium	333	55	662	21	5530230553570001227321125605	685356535992578658365	666269	100
Organic matter	221	11	111	00	2010110000000000000010001100	287000950017540222002	111111	101
Phosphorus	322	22	331	21	4510230534454531125222123371	667243445673537637335	776569	11000
Altitude	333	21	112	00	4314454343435443454444345545	667675576755668665556	987979	11001
Cation exchange capacity	221	11	320	00	2500112412323311013232321231	322213121452345322233	357459	1101
Exposure	000	11	100	00	2200112100000200000111002342	066220710126002231200	972978	1110
	000	00	000	00	0000000000000000000000000000	00000000000000000000	111111	
	000	00	000	00	0000000000000000000000000000	11111111111111111111	000001	
	000	00	000	11	1111111111111111111111111111	00000000000000111111	00001	
	000	11	111	00	0000000000000000001111111111	00000000001111000111	0111	
	011	00	111	00	1111111111111111110000001111	00011111110001001001	001	
	01	01	001	01	0001111111111111110111110011	011000000010110010010	01	

final result; the eigenvalue of axis 1 is increased. This may be due to the elimination of background noise arising from species with very rare occurrences (Greig-Smith 1969a). It has been pointed out that rare species often contribute little information to overall variation (Austin & Greig-Smith 1968). The eigenvalue for axis 1 of the woody species CCA is higher than that for the ordination of all species (0.57 against 0.44).

The following trends can be observed (Fig. 2a). Altitude, organic matter, P, and cation exchange are the most important variables determining variation in species composition along axis 1. Soil texture (clay and silt), Mg, slope, electrical conductivity, and to a lesser extent Na and K, also contribute to this variation. Calcium, pH and sand are the most significant variables along axis 2. Along axis 1, type 1, *Arundinaria alpina*, with a high content of organic matter and P, is differentiated from the other types. This type is found at higher altitudes and on steeper slopes. The silt content of the soils of the *Arundinaria* type is significantly higher than in the types at lower altitudes, while the clay content shows the opposite trend. Also electrical conductivity is lower at higher altitudes, reflecting a low base saturation.

As seen in Fig. 2a, clusters 3 and 4 are clumped because of the masking effect of the dominating factor altitude. Further environmental variation may be displayed when the ordination is applied after removing the outlier group (cf. Haeck et al. 1982; Zerihun & Backéus 1991), i.e. the *Arundinaria alpina* type. Along axis 1, altitude is still the main variable determining variation in species composition (Fig. 2b), while N and slope are the most important variables along axis 2. Communities at high altitudes are found on steeper slopes and on soils with a high N content, which is related to the accumulation of organic matter at high elevations.

Human impact

The long history of human impact on the vegetation may obscure the differences between the effects between natural and man-made processes. As a result, it is difficult to say whether a species appears in a particular vegetation because it is a natural part of it, or whether it is related to human influence (Friis 1992). There is no palynological evidence for vegetation changes in this area. Upper Quaternary pollen diagram studies from the Danka valley, SE Ethiopia, (at 3830 m), indicate signs of human disturbance about 8000 yr ago (Hamilton 1982). Similar evidence from ca. 1850 B.P. has been obtained from pollen core studies on Mt. Badda (4040 m) on the western escarpment of the SE Highlands. A major vegetation change during this period, the widespread destruction of *Podocarpus* forest, has been attributed to the increased density of settlements (Hamilton 1982).

Much of the original forest of Jibat disappeared relatively early. Traces of what are believed to be remnants of a refuge of an Ethiopian king in the 15th century are still visible on the top of the mountain, which is now

Table 3. 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	pH	Org	Sand	Silt	Clay	Cond	Na	K	Ca	Mg	CEC	N	P
Altitude	-															
Slope	0.23 ns	-														
Exposure	0.06 ns	0.39 **	-													
pH	0.32 **	0.23 ns	0.03 ns	-												
Organic matter	0.64 ***	0.37 **	–0.01 ns	0.35 **	-											
Sand	0.10 ns	–0.11 ns	–0.01 ns	0.14 ns	–0.04 ns	-										
Silt	0.49 ***	0.19 ns	0.09 ns	0.21 ns	0.58 ***	–0.26 ns	-									
Clay	–0.55 ***	–0.18 ns	–0.09 ns	–0.28 ns	–0.60 ***	–0.05 ns	–0.95 ***	-								
Electrical conductivity	–0.35 **	–0.13 ns	0.03 ns	0.12 ns	–0.32 ns	0.14 ns	–0.09 ns	0.06 ns	-							
Na	0.23 ns	0.27 ns	0.15 ns	0.07 ns	0.22 ns	0.08 ns	0.17 -0.20 ns	0.05 ns	- ns							
K	–0.11 ns	–0.01 ns	–0.13 ns	0.31 ns	–0.06 ns	–0.09 ns	0.13 ns	–0.10 ns	0.19 ns	–0.45 ***	-					
Ca	–0.09 ns	0.10 ns	0.20 ns	0.44 ***	0.01 ***	0.07 ns	–0.08 ns	0.06 ns	0.27 ns	–0.09 ns	0.24 ns	-				
Mg	–0.39 **	–0.01 ns	–0.07 ns	0.35 ***	0.01 **	0.12 ns	–0.16 ns	0.14 ns	0.28 ns	–0.04 ns	0.36 **	0.52 ***	-			
Cation exchange capacity	0.55 ***	0.39 ns	0.03 ns	0.45 ***	0.72 ***	–0.05 ns	0.59 ***	–0.61 ***	–0.24 ns	–0.02 ns	0.08 ns	0.12 ns	–0.03 ns	-		
N	0.37 **	0.25 ns	0.04 ns	0.07 ns	0.62 ***	0.06 ns	0.45 ***	–0.50 ***	–0.12 ns	0.19 ns	0.00 ns	0.13 ns	–0.05 ns	0.54 ***	-	
P	0.61 ***	0.24 ns	–0.09 ns	0.48 ***	0.49 ***	0.04 ns	0.26 *	–0.31 *	–0.05 ns	0.41 ***	–0.27 ns	0.09 ns	–0.08 ns	0.44 ***	0.22 ns	-

completely overgrown by the bamboo forest. At various altitudes in the forest, pieces of charcoal were found in soil profiles at depths of 60 - 80 cm, and at one place a piece of clay, probably a pottery fragment, was recovered from the same depth.

The historical migration of the pastoralist Oromo people in the 16th century from southern Ethiopia to western Shewa did not lead to changes in the vegetation (Zerihun & Backéus 1991). The underlying reasons for the present-day ecological crisis in Ethiopia were traced back to changes in the land ownership systems of the 17th century (Tewolde 1989).

Phytogeographical comparison

The relevé data from the Jibat forest do not provide a complete species list, but they suffice to enable a regional comparison with other forests. Two forests in Ethiopia and two from East Africa were included (Table 4). The sizes of the compared floras are different and the lists may not be complete, but the figures give some indications. Within Ethiopia, the Jibat forest is more similar to the SW Plateau forests than to the Central Plateau forests. The Belette forest is situated in the same climate region as the Jibat forest. Wadera is a dry Afromontane forest with *Juniperus procera* and *Podocarpus gracilior* as the dominant trees. The forests on Mt. Mulanje are situated at lower altitudes, and hence exposed to different temperature and moisture conditions. Almost all the species present in the Jibat forest are characteristic Afromontane elements (Tamrat 1993). There is a distinctly defined high-mountain *Arundinaria alpina* zone in Jibat; at lower altitudes it occurs only in certain local habitats (e.g. valley bottoms). The bamboo zone is considered to be a natural component of the

Table 4. Floristic similarities between the Jibat forest and some related montane forests. N = number of species; N_c = number of species in common; QS = Sørensen's Quotient of Similarity.

Forest	Altitude (m)	*N*	*Nc*	*QS (%)*
Belette (SW Plateau)[1]	2700	92	18	14
Mt. Elgon (Uganda)[2]	2000 - 3000	66	15	13
Wadera (SE Plateau)[3]	2100 - 2650	75	14	12
Mt. Mulanje (Malawi)[1]	950 - 1950	205	18	10

[1]Fries et al. (1982); [2]Hamilton & Perrot (1981); [3]Dosett-Lemaire (1988)

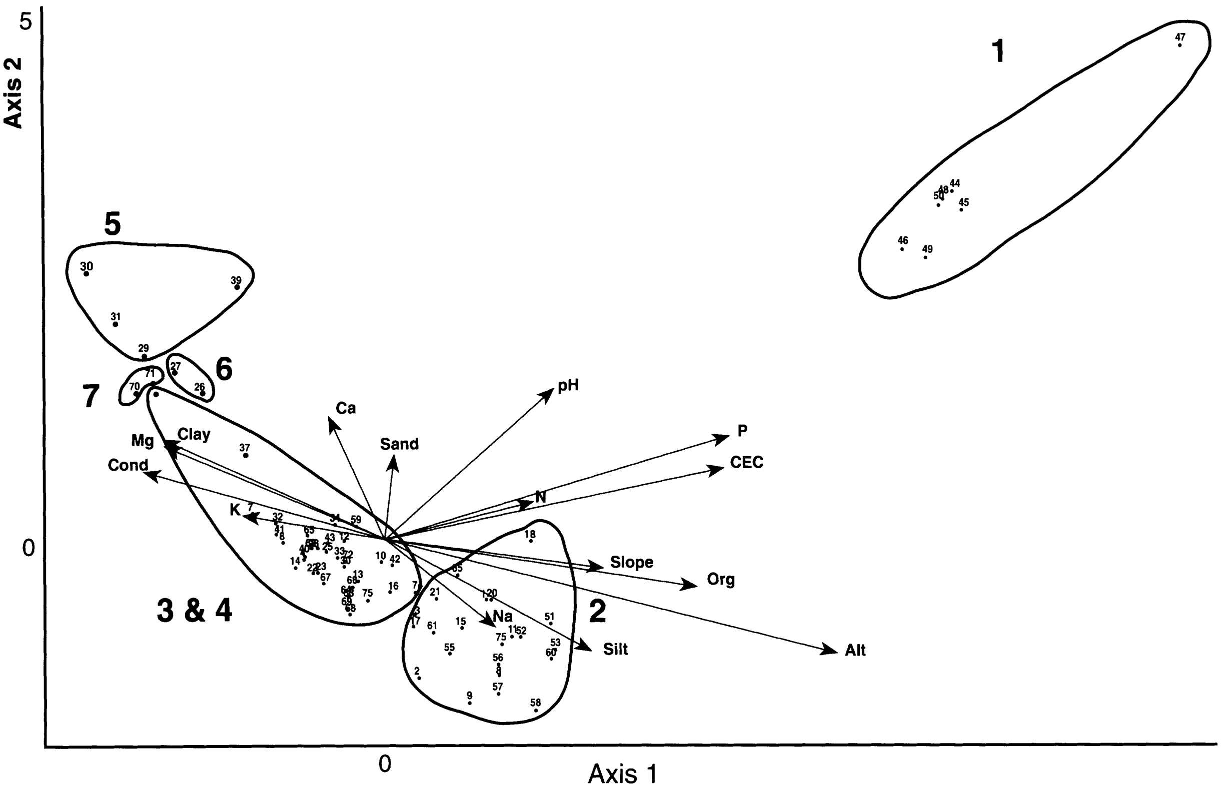

Fig. 2a. Ordination diagram with axes 1 and 2 of a Canonical Correspondence Analysis of all relevés of the Jibat forest. Boundaries of the community types are indicated; note the isolated position of Type 1. Environmental vectors (for abbreviations, see Table 4) are enlarged with a factor 3.

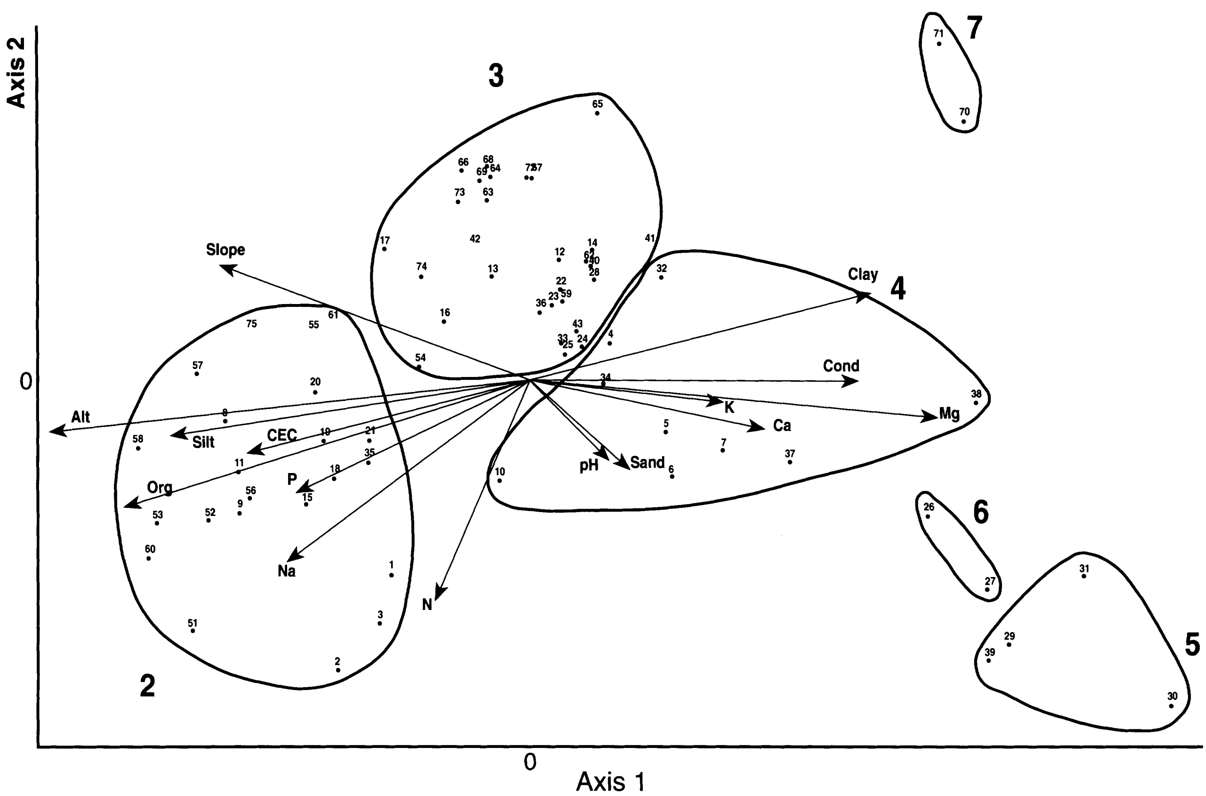

Fig. 2b. As Fig. 2a, but relevés from Type 1 were excluded. Environmental vectors are enlarged with a factor 3 (except the vector altitude, which is enlarged with a factor 2.3).

moist montane forest in East Africa (O. Hedberg 1951). Elsewhere in Ethiopia, *Arundinaria alpina* has been reported from scattered stands, e.g. in the forests of Wadera (Friis 1992), but the extensive stand in Jibat may be the only one on the Central Plateau of Ethiopia. Hamilton & Perrott (1981) suggested that bamboo forest is a colonizing stage in montane forest regeneration in drier areas, and a natural feature of moist montane forest vegetation.

Hagenia and *Rapanea* species are characteristic of the highest altitude forest zone (O. Hedberg 1951; Langdale-Brown et al. 1964); they are both well developed in the Jibat forest. *Rapanea* has been reported as common in Ethiopian bamboo forest (Lundgren 1971). *Juniperus procera* is a characteristic tree of dry Afromontane forests, while *Aningeria adolfi-friederici*, *Olea welwitschii* and *Prunus africana* are more typical of lower altitude moist montane forests in Kenya and Uganda (Lind & Morrison 1974). The former tree is atypical but the latter three species form a well-developed association at lower altitudes in the Jibat forest. At forest edges where human influence is pronounced, forest pioneer species such as *Bersama abyssinica* and *Clausena anisata* are frequent. Along river courses at lower altitudes, lowland Guineo-Congolian floral elements may penetrate into the forest (e.g. *Ficus* spp.).

In his outline of Ethiopian forest types, Friis (1992) placed the Jibat forest in the 'Undifferentiated Afromontane forest' category. The two prominent tree species here are *Juniperus procera* and *Podocarpus gracilior*. However, these species are not well-represented in the Jibat forest. This may be explained by the relatively wet climate in this area. On the other hand, the 'Broad-leaved Afromontane rain forests' of Friis (1992) have many species in common with the Jibat forest, but the proposed geographical range of these forests does not extend as far north as to include the Jibat forest. The species composition of the 'Afromontane rain forest' (*sensu* White 1983) is completely different from that of the Jibat forest. Although they share some broad-leaved trees, most of the species listed as characteristic Afromontane elements are virtually lacking in the Jibat forest. This may be due to the high elevation. White (1983) confirmed that most of the Afromontane rain forest species are rather similar to the Guineo-Congolian species and have their closest relatives in the lowland tropics rather than in the highlands.

In a phytogeographical analysis of East Africa, Coetzee (1978) recognized two types of montane forest, the Moist Montane and Dry Montane Forests. The Moist Montane Forest contains the largest group of Afromontane endemics, and most of the species in Coetzee's list occur widely in the Jibat forest. However, characteristic species of the Dry Montane forests, including *Juniperus procera*, *Podocarpus gracilior* and *Olea europaea*, are virtually absent from the Jibat forest.

The 'Undifferentiated Afromontane forest' and 'Afromontane rain forest' *sensu* Friis (1992) are characterized by a mean annual rainfall of 700 - 1100 mm and 700 - 1500 mm, respectively. Daniel (1977) estimated a mean annual rainfall between 1000 - 1400 mm for western Shewa. White's (1983) 'Afromontane rain forest' occurs at an annual precipitation range of 1250 - 2500 mm. The mean annual rainfall estimates by Daniel (1977) and Friis (1992) are much lower than the actual mean annual precipitation of 1800 mm at Jibat. The climatic inferences made for different geographical regions in Ethiopia suffer from the lack of detailed data and several generalizations appear to be oversimplified . The relatively few stations generating field data, and the irregular topography of the country result in locally uncertain situations as to rainfall (Liljequist 1986). The present distribution data are still very schematic. The floristic data and the annual precipitation data indicate that the Jibat forest is more related to the forest vegetation described by Friis (1992) as the Afromontane rain forest' regime .

Conclusions

The phytosociological-ecological approach followed in this study has proven to be effective in the description of vegetation types and vegetation-environment relationships in a hitherto unknown area of Afromontane forest. The combination of a network classification (TABORD) and CCA ordination has been effective. Considering its efficiency and versatility as compared to other classificatory methods (e.g. Poore 1955a,b; Moore 1962; Moore et al. 1970; Werger 1974), the phytosociological approach could be more widely used in the study of Afromontane vegetation.

This should be seen in the light of the general scepticism about the effectiveness of the phytosociological approach in the study of tropical vegetation (e.g. van Steenis 1958; Werger 1974; Hommel 1990). The central argument is the high species richness of the forests which requires a very large plot size for sampling, which in its turn implies an uncertainty as to how to delimit the stand. This makes the approach impracticable. However, Greig-Smith (1969b), making a distinction between African rain forests and other tropical rain forests, pointed out that African forests are species-poor and amenable to traditional approaches of classification. There is further evidence indicating that certain African forests are relatively poor in species (Hamilton 1976), while the woody Afromontane floras of Ethiopia and West Africa are mentioned as particularly species-poor (White 1978).

The sampling scheme followed in the present study, has proven to be efficient. The comparison presented in this study suggests that the overall pattern of ordination of the stands reflects the environmental variation in an effective way (e.g. Table 1). It has been shown that more meaningful interpretations of ecological variation can be made by considering only the woody species (i.e. trees and shrubs), and by eliminating herbaceous species from the ordinations. In environments where taxonomic knowledge of the local flora is limited, satisfactory classification and ordination results may be obtained by dealing only with the relatively well-known and readily identifiable woody species and avoiding the less conspicuous and rare herbaceous species.

Another important aspect of vegetation that is often neglected in the study of plant communities, is the investigation of the structure. The importance of structure as a possible indicator of environmental factors (e.g. Barkman 1979; Lawesson 1990), and a criterion for delimiting plant communities (Barkman 1979) has already been stressed. In addition, as the study region is situated in the transition zone between the moist southwest Highlands and the relatively dry Afromontane region of the north, studies into the moisture relations of the plants may shed more light on the nature of the distribution of plants in general. In addition, the dynamical status should be studied in order to add a time dimension to the integral description of forest plant communities and their ecology. Tamrat (1993) has started with this approach in the Afromontane forests of Shewa.

Acknowledgements. I am grateful to Prof. Eddy van der Maarel for his guidance and critical comments; Ingvar Backéus and Jonas Lawesson for constructive discussions, to three referees for useful remarks, to Tsedale Bayou for drawing Fig. 1, and the staff of the Soil Laboratory of the Ministry of Agriculture, Addis Abeba, for assistance. Financial support from the Swedish Agency for Research Cooperation with Developing Countries (SAREC) is gratefully acknowledged.

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Received 30 March 1993;
Revision received 12 October 1993;
Accepted 20 October 1993.