

**by Dennis J. Herlocker
and Herman J. Dirschl**

**Vegetation of
the Ngorongoro
Conservation
Area, Tanzania**



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Cover photo by H. J. Dirschl.
Ngorongoro Crater as seen from the
conservation area headquarters. Crater
Highlands in background.

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Field camp in the Eastern Seregenti Plains during the vegetation survey. Left to right: H. J. Dirschl, P. ole Sayalel, D. J. Herlocker. Photo by H. J. Dirschl



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Perspective

The vegetation of an area represents an integrated picture of all environmental influences, past and present. A map showing the distribution of vegetation types enables one to recognize environmental differences in different parts of an area and determine the productive potentials of various land uses. The vegetation map at the back of this report, combined with an understanding of the processes that have contributed to the distribution of types, is thus a valuable tool for the integrated land use and management planning required for the Ngorongoro Conservation Area.

Abstract

This report presents and discusses a map of vegetation types in the Ngorongoro Conservation Area, Tanzania, East Africa, as a tool in land use planning.

Résumé

Cette étude présente et analyse une carte des familles de plantes des territoires de conservation du Ngorongoro, du Tanzania, de l'Afrique de l'Est comme un outil dans la planification des sols.

Zusammenfassung

Im Rahmen dieses Berichts wird eine Karte der Vegetationstypen im Ngorongoro-Naturschutzgebiet in Tansania (Ostafrika)

als nützlicher Beitrag zur Planung der Bodennutzung vorgelegt und erörtert.

Kumbukumbu

Taarifa hii inaonyesha na kueleza ramani ya mimea ya aina mbalimbali katika mboga za Eneo la Kuhi fadhiwa la Ngorongoro katika nchi ya Tanzania, Afrika ya Mashariki, kama mfano katika mipango ya matumizi ya ardhi.

Introduction

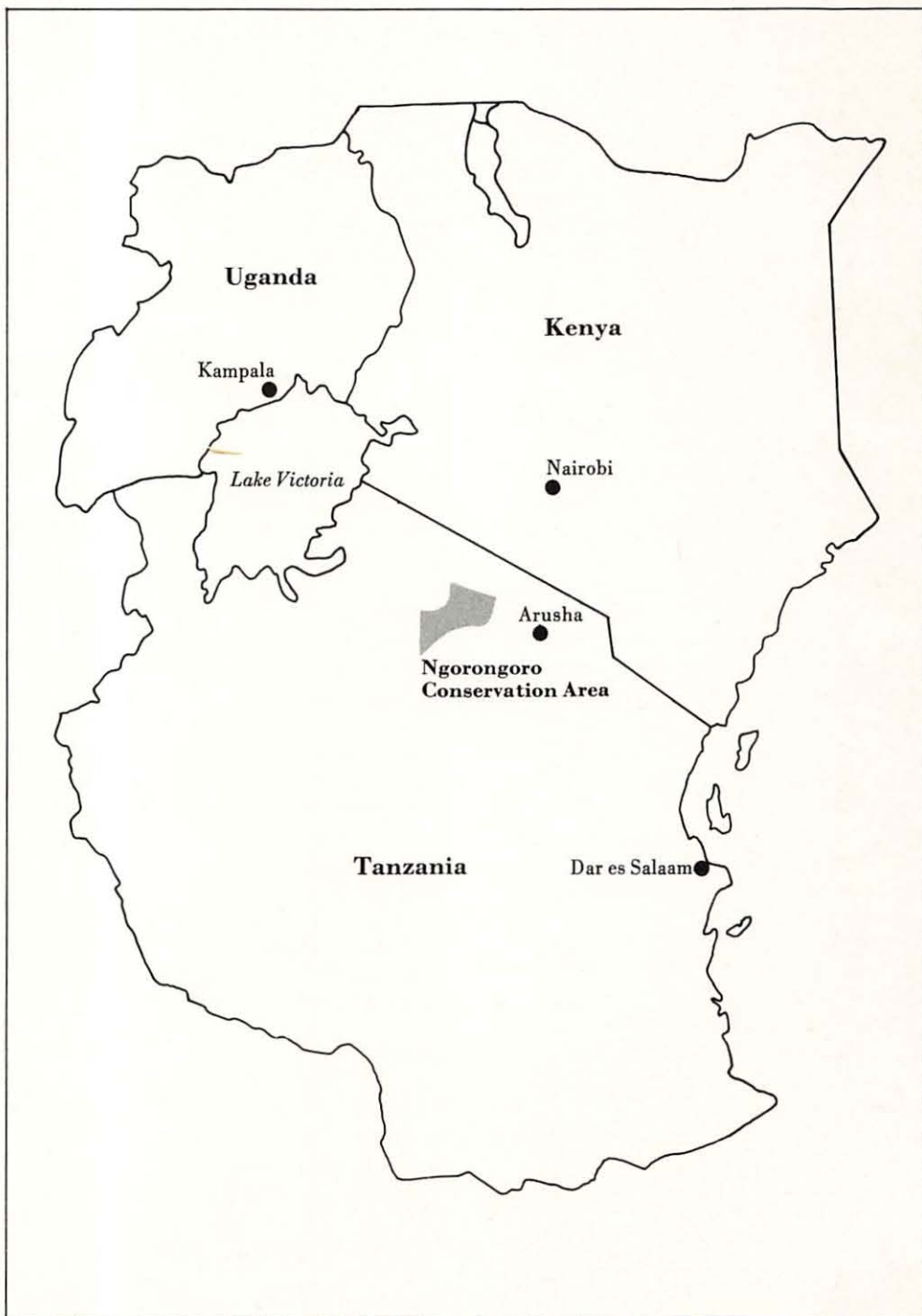
Figure 1. Geographic location of the Ngorongoro Conservation Area in East Africa

The Ngorongoro Conservation Area (Fig. 1) is the first land unit in East Africa, and one of very few in the world, which is administered for fully integrated development of various forms of land use—conservation of soils, natural vegetation and wildlife, protection of watersheds, production of livestock and cultivated crops, and tourism—in harmony with desirable social development of the Maasai and other resident peoples.

Rational development of natural resources on a multiple use basis requires that individual landscape units be allocated to the most suitable forms of use. The inherent biological productivity of the units and the relevant social and economic requirements (Dirschl, 1966) are important factors in allocating land use. An understanding of the main biophysical processes that operate within the area is thus a prerequisite for detailed land use planning and management.

The nature and distribution of the existing vegetation are useful clues to the prevailing biophysical influences and to the modifying effects of past and current human use, and provide an index to the productivity of the various landscape units. The vegetation map (inside back cover) and supporting descriptive detail presented here can thus serve as essential tools for the multiple land use planning and development of the Ngorongoro Conservation Area. It can also be valuable to future ecological studies of the area.

Figure 1



History of vegetation description in the Ngorongoro Conservation Area

Methods

The vegetation of the land included in the conservation area has been studied since the beginning of this century. Uhlig (1942) explored the geology of the Great Rift and described and photographed landscape features along the eastern edge of the area in 1907. Jaeger (1911, 1913) dealt with many facets of the natural history of the Crater Highlands, including broad features of the vegetation.

Descriptions of the montane forest vegetation on Olmoti Mountain and the Northern Highlands Forest Reserve are in the files, for 1930, of the Tanganyika Forest Department (H. R. Herring, *unpublished data*).

Gillman (1949) published a vegetation map of Tanganyika based essentially on physiognomic features, at a scale of 1:2,000,000.

Pearsall (1956) described the vegetation of Serengeti National Park, which then included the present Ngorongoro Conservation Area, for the Fauna Preservation Society of the United Kingdom. But he did not deal with the Kakesio-Endulen area which lay outside the national park. The Tanganyika Forest Department reported some observations on the distribution and status of *Juniperus procera* (African Pencil Cedar) forest in the Crater Highlands in 1958 (R. C. Steele, *unpublished data*). The Ngorongoro Conservation Authority (1960) included in its draft management plan a general description of the composition and distribution of woodland and forest communities, by J. Pollard. Anderson and Talbot (1965) examined soil-vegetation relationships of the Serengeti Plains grasslands.

Dirschl (1966) summarized pertinent data from these reports. Herlocker prepared the accompanying reconnaissance vegetation map at a scale of 1:250,000.

The information accumulated since 1907 was considerable but insufficient. We, therefore, carried out a systematic and comprehensive survey of the vegetation cover in the conservation area, from January 1966 to June 1967.

This vegetation study is essentially based on the concepts of Pratt, Greenway and Gwynne (1966) who regarded the physiognomic distinction between woody and graminoid vegetation as the most significant feature in classifying East African rangelands for land use purposes.

The vegetation classification is based on a combination of physiognomic and floristic criteria. We recognized five primary physiognomic vegetation classes: grassland, herbaceous swamp, bush, woodland and forest. Each was subdivided into two or more secondary classes according to height or density of the upper stratum, and these

were further divided into "species-types" (see Küchler, 1967:282) according to the dominant plants of the main strata. Table 1 lists the exact specifications used.

The laboratory and field procedures for preparing the vegetation map and the descriptive detail were as follows:

1. Aerial photographs were essential because the area was large (ca. 8,300 km² or 3,200 sq. miles) and inaccessible. The only available photographs had been taken in 1957-58 and ranged in scale from 1:40,000 to 1:50,000.

2. The mapping units were at first delineated through interpretation of stereo

Table 1.
Vegetation classification used for mapping and description

Primary physiognomic categories	Vegetation categories used for mapping	Specifications and definitions
Forest		Tree cover with closed canopy of one or more strata > 15 m (50 ft) tall; mainly evergreen
	Moist evergreen forest	Species-rich and structurally complex forest of highland slopes and plateaus
	Dry evergreen forest	Forest dominated by <i>Juniperus procera</i> ; now confined to steep upper slopes of the highest mountains
Woodland		Tree cover with one or, rarely, two discontinuous strata; minimum crown cover 21 per cent; usually deciduous
	High woodland	Tree > 9 m (30 ft) tall
	Low woodland	Trees < 9 m tall
Bushland		Upper stratum of woody plants of low stature with multiple stems. Minimum crown cover 21 per cent
	Deciduous bushland	Bushland, composed of mainly deciduous shrubs in dry locations
	Highland evergreen bushland	Secondary scrub resulting from disturbance by fire or grazing of moist evergreen forest
	Montane heath	Shrub vegetation above the tree line of the highest peaks, dominated by <i>Artemisia afra</i> and <i>Erica arborea</i>
Grassland		Continuous grass cover in which woody vegetation has a crown cover of ≤ 20 per cent
	Tall grassland	Grass cover > 150 cm (5 ft) tall
	Medium grassland	Grass cover 60-150 cm (2-5 ft) tall
	Short grassland	Grass cover < 60 cm (2 ft) tall
	Highland tussock grassland	Grassland dominated by the tussock-forming grass <i>Eleusine jaegeri</i> , and occurring on highland slopes and plateaus; probably favoured by frequent fires and heavy grazing
Herbaceous swamp		Herbaceous vegetation of depressional sites waterlogged at least part of the year
	Reed swamp	Vegetation dominated by emergent aquatics of permanently waterlogged locations
	Wet meadow	Graminoid vegetation of seasonally waterlogged locations

pairs of aerial photographs. Because of the small scale of the photos used, these units were broad and mainly reflected topographic positions and gross physiognomic differences between the vegetation of adjacent units.

3. Examples of all initial mapping units differing in tone, texture and stereo appearance were examined in the field. The units could then be divided into smaller, physiognomically and compositionally more homogeneous mapping units. Experience in the field indicated that the woody vegetation could be easily categorized into secondary physiognomic vegetation classes (Table 1) both on the ground and by photo interpretation. But grassland could be categorized from aerial photos into three height classes only after considerable field experience, when it could be accomplished indirectly by examining geographic and topographic positions.

4. The vegetation of a representative number of the final mapping units was then sampled to determine community structure and species composition.

Representative woodland and bush stands were sampled by the point-centred quarter method (Cottam and Curtis, 1956). A transect of 50 points was run in each community sampled and the nearest tree and shrub recorded in each quadrant of each point. By this means, the relative density of each woody stratum was determined and the two highest ranking species were listed as dominants.

5. Woody communities were further categorized according to three crown cover classes applied to the overstory: low (0–20 per cent), medium (21–60 per cent) and high (61–100 per cent). The cover determinations were made by using plastic overlays of crown closure scales¹ on aerial photographs.

¹These consist of a photographic print of 10 successive steps in crown closure for crown diameters of 10, 20, 30 and 40 feet at scales of 1:30,000 and 1:40,000. They were developed for Herlocker by R. C. Aldrich of the Pacific Southwest Forest and Range Experiment Station, U.S. Forest Service, Berkeley, California.

6. Vegetation formulae indicating structure (strata of different life forms), dominant species and the cover class of each stratum were subsequently constructed for each mapping unit.

7. The outlines of the mapping units were transferred from the aerial photographs to uncontrolled mosaics, at a scale of 1:50,000, and then traced. The map was then photographically reduced to 1:125,000 and colour coded.

Use of map colours and vegetation formulae

Individual units on the map accord with the colour scheme as provided in the legend with the appropriate vegetation formulae. Colours signify the physiognomy of the uppermost vegetation stratum which exceeds 20 per cent cover. The main montane vegetation categories are distinguished by colour from the more prevalent plains vegetation.

The following three examples explain the nature of the vegetation formulae.

Example 1: $\frac{At.}{\frac{Se, Je.}{Sm, Dma}}$

The map colour would signify that low woodland of medium cover density (..) is the life-form of the upper stratum. *Acacia tortilis* is the dominant species in the upper stratum; *Sansevieria ehrenbergiana* and *Justicia elliotii* are the dominant species in the bush stratum which falls into the low cover class (.); *Sporobolus marginatus* and *Digitaria macroblephara* are the dominant species in the grass layer.

Example 2: $\frac{Age.}{Ag, Pm}$

The map colour would signify medium grassland. *Acacia gerrardii*, with a crown cover of 20 per cent or less, occurs over medium grassland which is dominated by *Andropogon greenwayi* and *Pennisetum mezianum*.

Example 3: $\frac{Al.}{Li, L..}$

The map colour would signify high woodland. *Acacia lahai*, with a crown cover above 60 per cent (:), is the dominant tree species. *Lippia* spp. and *Lantana* spp. are the dominant shrubs in the lower vegetation stratum which falls into the medium cover class.

Limitations of the survey

Time was limited. The Northern Highlands Forest Reserve remained entirely unmapped. Three parts of the conservation area were inadequately sampled: (1) the Naiobi Empakaai Crater-Kerimasi Mountain area in the northeastern corner, (2) the mountain peaks above approximately 2,600 m in elevation, and (3) the extreme southwestern portion of the area. Few field checks could be made in these three areas. Our field experience elsewhere enabled us to use aerial photos to delineate community types.

Conversely, we conducted an intensive survey of the grass, swamp and bush communities on the floor of the Ngorongoro Crater both because access was much easier and because we might facilitate the intensive use of that caldera for field research by various disciplines.

The information on the relative abundance and species composition of the ground stratum in the Kakesio-Olpiro area is liable to error because we visited it during the dry season only.

Finally, a photographic mosaic is a map made from numerous aerial photographs, each of which possesses some degree of distortion. We can correct the mosaic to eliminate these distortions if we know the exact horizontal distance between such points as mountain peaks, lakes and human settlements. Unfortunately, few exact distances were available. The distortions introduced into the vegetation map resulted in local gaps and changes in scale, particularly toward the edges of the mosaic coverage. The map may not be strictly accurate in shape, area and location of units and other features but it does give a meaningful picture of the relative location, distribution pattern and extent of the various vegetation types within the Ngorongoro Conservation Area.

Description of principal physiographic units and vegetation

We have divided the Ngorongoro Conservation Area into broad physiographic areas (Table 2) which are easily recognizable on the ground and within which such main environmental influences as climate, drainage and soils are fairly uniform. We shall now summarize the environmental factors for each area and discuss the major vegetation units. For grasslands, individual types are described; but for forest, woodland and bush areas, which tend to have a more complicated structure, a general account is given with emphasis on the broader aspects of the prevailing community types.

Dirschl (1966) provides additional information on the area's geology and drainage. Sayalel (1965) gives a good account of the movements of some of the resident Maasai graziers.

Western plains

The western plains—lying west of the Crater Highlands and north of the woodlands whose edge roughly parallels the Kakesio-Endulen automobile track—cover about 50 per cent of the conservation area. The plains comprise the Eastern Serengeti Plains, the Balbal Depression, Oldupai Gorge, the Sale Plain and the Doinyoogol Hills.

Eastern Serengeti Plains

The Eastern Serengeti Plains vary topographically from the level central portion around Oldupai Gorge, where elevations are 1,350–1,550 m (4,500–5,100 ft), to undulating hills in the north and a high plain in the south which rises gently to about 1,850 m (6,000 ft) in the Ildoinya Hills near Endulen.

The southern part of the area drains into Lake Eyasi. The extreme north drains north-east via the Sanjan River into Lake Natron or west through the Ngungu Stream into Serengeti National Park. The southern part of the Eastern Serengeti drains into Oldupai Gorge and then eastward into the Balbal Depression.

The geology, climate and soil-vegetation relationships have already been discussed

Table 2.

Physiographic divisions of the Ngorongoro Conservation Area

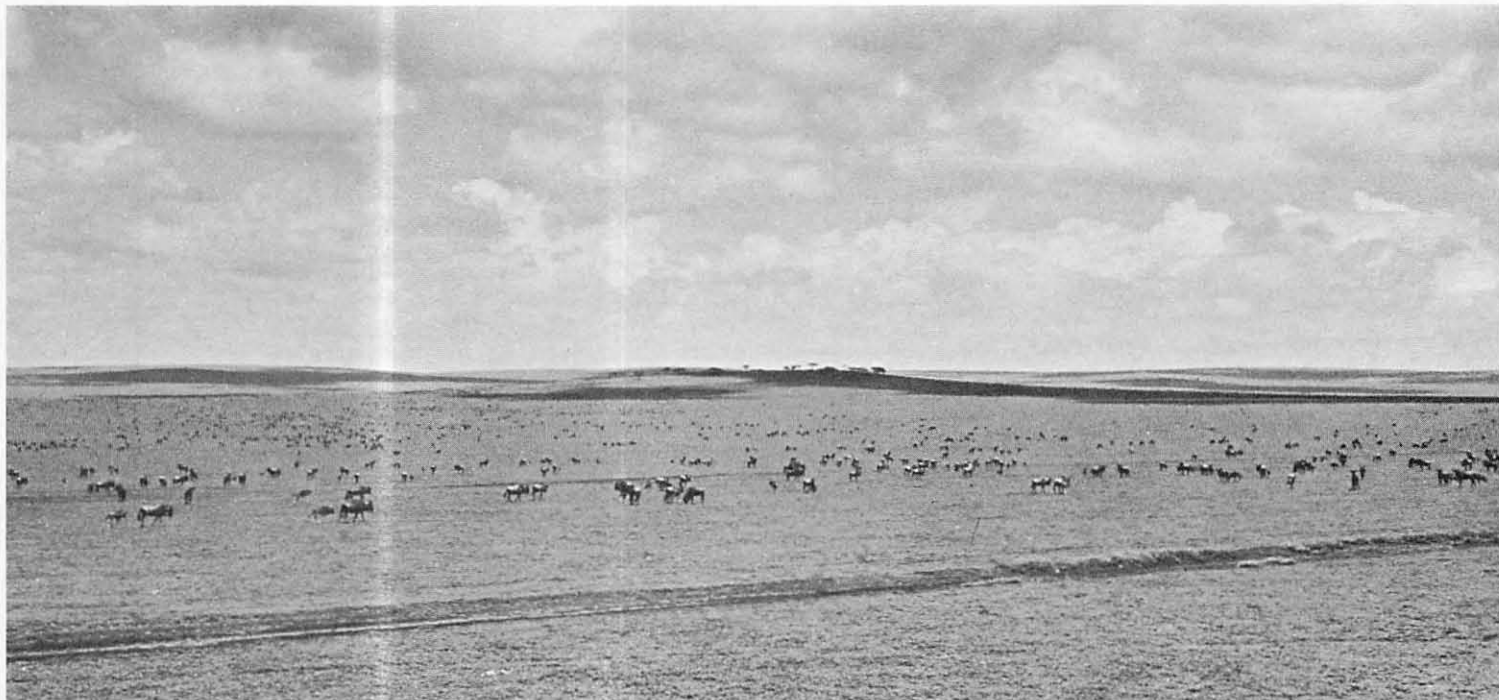
Major physiographic units	Minor physiographic units
Western plains	Eastern Serengeti Plains A1*
	Sale Plain A2
	Sand dunes north of Oldupai Gorge A3
	Balbal Depression A4
	Sand dunes north of the Balbal Depression A5
	Doinyoogol Hills A6
	Oldupai Gorge A7
Crater Highland massif	Western wall of the Crater Highlands B1
	Montane areas B2
	Highland plateau B3
Lake Eyasi-Kakesio area	Lake Eyasi flats C1
	Lake Eyasi Escarpment C2
	Misigio Escarpment C3
	Kakesio-Endulen area C4
Empakaai Crater D	
Ngorongoro Crater E	

*These units are designated on the map by letter or by letter-number combination.

by Anderson and Talbot (1965). They noted the presence of three main soil types: juvenile soils on volcanic ash, calcimorphic soils with hard pans, and vertisols of lithomorphous origin. The north and central sections of the Eastern Serengeti Plains consist of a shallow layer of fine volcanic dust over calcareous tuff which in turn overlies a hard pan (calcimorphic soils with hard pans). A high proportion of silt and fine sand and a high exchangeable sodium content render this soil very unstable and very subject to erosion. The higher land, south of the central plain, consists of vertisols of lithomorphous origin derived directly from calcareous tuff. Sand and silt fractions are lower and the soils much deeper than those further north. On the central plain immediately north of Oldupai Gorge there is an area of stabilized dunes composed of fine sand overlying calcareous tuff.

The Eastern Serengeti Plains is an area of high temperatures, high winds and variable rainfall. Precipitation data from

Part of the vast herds of wildebeest and zebra found on the Eastern Serengeti Plains (on *Sporobolus marginatus*-*Digitaria macroblephara* short grassland here) during the rainy season. Photo by H. J. Dirschl



Banagi in the west and Olalaa in the north show annual averages of 784 mm (30.90 inches) and 530 mm (20.88 inches), respectively. Data collected at Leakey's Camp at Oldupai Gorge in 1965, 1966 and 1967 show totals of 531 mm (20.94 inches), 378 mm (14.87 inches) and 331 mm (13.04 inches) of rain, respectively. These data substantiate the contention of Anderson and Talbot (1965) that rainfall is lower in the eastern than in the western part of the Serengeti Plains. High variability in rainfall, the high rate of transpiration and the hard pan layer near the surface possibly account for the dwarf forms of grasses which grow on the central plain.

Large concentrations of game graze the whole area for the duration of the rainy season.

Short grassland: *Sporobolus marginatus*-*Digitaria macroblephara*-*Kyllinga* spp. Short grass communities occupy the major part of the central and northern portions of the Eastern Serengeti Plains. Although

Digitaria macroblephara and *Kyllinga* spp. are locally dominant, *Sporobolus marginatus* is by far the most common of the approximately 20 grass species in this area. The sparse, perennial basal cover indicates soil instability particularly in the vicinity of Oldupai Gorge where heavy usage by wildlife and livestock has produced a deeply rutted, waffle-iron effect on the ground.

Short grassland: *Hypoestes forskalii* over *Sporobolus*-*Digitaria macroblephara*-*Kyllinga* spp.

This type grows along the lowlying drainage lines on either side of Lemuta Hill, in the Western Kiti Plain and along the eroded banks of Ngungu Stream. In the shrub layer, *Hypoestes forskalii* is dominant and *Justicia elliotii*, *Heliotropium eduardii* and *Indigofera basiflora* are common. The grass layer is identical with the above short grass type. The invasion of the grassland by these woody herbs may indicate heavy grazing (Anderson and Talbot, 1965:40).

Short grassland: *Digitaria scalarum*-*Digitaria milanjiana*

The short grasslands at the upper reaches of the Sanjan and Kerian streams contain a mixture of 13 grass species of which *Digitaria scalarum* and *D. milanjiana* are the most widespread. The western slopes directly below the Doinyoogol Hills contain moderate cover of herbaceous and small bush species.

The 1957-58 aerial photos show an apparently heavy cover of herbs or shrubs in the western part of this mapping unit but we could not trace this feature on the ground. The cover had disappeared, possibly because of changes in grazing pressures and rainfall.

Medium grassland: *Andropogon greenwayi*-

Pennisetum mezianum-*Chloris pycnothrix* This type occupies the higher land south of Oldupai Gorge. Of the 10 grass species found here, *Andropogon greenwayi*, *Pennisetum mezianum* and *Chloris pycnothrix* are the most common.

Justicia elliotii, *Indigofera basiflora* and *Solanum incanum* are shrubs occurring in moderate amounts throughout the type. *Hypoestes forskalii* is common on the higher hills in the southeast, especially around the small reservoirs there.

Achyranthes aspera, Cyperaceae and regeneration of *Acacia* spp. is common along the upper reaches of the Nenkutuk and Olgeju Nyiro drainage lines.

Short grassland: *Sporobolus marginatus*-*Sporobolus festivus*-*Andropogon greenwayi*
This type occupies an ecotonal position between the short grass of the central plain and the medium grass of the higher land to the south, and is found mainly on gentle to moderate slopes between these two secondary physiognomic types. Sixteen grass species are present in various mixtures. Step erosion is very common and some steps are as high as 60 cm (2 ft).

Low woodland: *Acacia drepanolobium*
This type is composed almost entirely of *Acacia drepanolobium*. It runs northwest along major drainage lines from the Nairbardad Hills to Oldupai Gorge and extends to the southwest of Lake Ndutu. Locally, low woodland approaches the thicket stage. The trees are of all age classes and average about 2 m in height. They are topped by scattered, tall *Acacia tortilis* and *Balanites aegyptica* trees. *Acacia seyal* and *A. xanthophloea* grow immediately adjacent to the drainage lines. The field layer consists of medium grassland dominated by *Pennisetum mezianum*, with *Indigofera basiflora* and *Justicia elliotii* shrubs present in small quantities. This woodland type seems to have expanded slightly since 1957-58 when the aerial photos were taken.

Low woodland: *Acacia tortilis*
This small area of woodland occupies the corner between Oldupai Gorge and the *Acacia drepanolobium* low woodland type and contains a mixture of age classes in the tree overstory and an underlying, medium grass cover of *Digitaria milaniana* and



Chloris pycnothrix. *Justicia elliotii* and *Indigofera basiflora* shrubs are moderately common.

Sale Plain

In this report, the Sale Plain is the land between the Carter Highlands in the east, the Doinyoogol Hills in the west, the Balbal Depression in the south and the conservation area boundary in the north. Actually, most of the plain lies north of the conservation area, in Loliondo District, west of Lake Natron and the Gregory Rift Wall.

The plain has an average elevation of about 1,250 m (4,100 ft) and slopes gently upward to the Doinyoogol Hills in the west and the Crater Highlands in the east. In the south, the level relief is broken by numerous, low sand dunes which continue farther south to the edge of the Balbal Depression.

Juvenile soils on volcanic ash are predominant. Their high porosity and low moisture retention, in combination with the generally low and unreliable rainfall,

nearly create an edaphic desert (Anderson and Talbot, 1965). Most of the area is covered with sand dunes, few of which are still mobile. Water drains from the Doinyoogol Hills and the Crater Highlands onto the Sale Plain and several large outwash fans have spread out along its edges.

Medium grassland: *Dactyloctenium* sp. nov.-*Sporobolus consimilis*

This type occupies the central part of the Sale Plain. The sand dunes are low in the north and higher in the south. *Dactyloctenium* sp. nov. is dominant and trees are rare on the dunes. Stands of the tall grass, *Sporobolus consimilis*, are dominant between the dunes.

The volcano Oldoinyo Lengai, which lies approximately 33 km (20 miles) to the east, erupted in 1966 and dumped ash over a large area along the boundary of the conservation area. As a result, the plant cover there is very low. Tall stands of *S. consimilis* have survived but seem heavily grazed. Much of the lower *Dactyloctenium* grass

Dactyloctenium sp. nov. and *Sporobolus consimilis* medium grassland on the Sale Plain. Photo by D. J. Herlocker

Low dunes, north of the Balbal Depression, which have been stabilized by a cover of *Cynodon plectostachyus* and *Dactyloctenium* medium grass and scattered *Acacia mellifera* and *Commiphora* trees. Photo by D. J. Herlocker



was covered with ash and is now beginning to regenerate.

Short grassland: *Sporobolus marginatus*
Sporobolus marginatus short grassland occupies the Kiti Plain, the southern portion of the Sale Plain and the higher ground east and west of the *Dactyloctenium* sp. nov.—*S. consimilis* medium grassland type. The type then extends further south above a small northeast–southwest rift where it meets the *Sporobolus*–*Digitaria*–*Kyllinga* short grasslands west of the Balbal Depression. *S. marginatus* is dominant; *Digitaria macroblephara*, *S. spicatus* and *Dactyloctenium* sp. nov. are common.

During the short rains, game from the main Serengeti migration concentrate and graze on the higher, western slopes of the Sale Plain. Maasai cattle graze throughout the plain.

Sand dunes north of Oldupai Gorge

This is an extensive area of juvenile soils on volcanic ash and of low dunes, most of which have been stabilized by vegetation.

Low woodland: *Acacia mellifera*

On most dunes, *Acacia mellifera* is found with an undergrowth of *Maerua trichophylla*, *Lycium* spp., *Salvadora persica* and *Achyranthes aspera*. Some dunes are covered with *Dactyloctenium* sp. nov.—*Cynodon plectostachyus* short grass. *Digitaria macroblephara*–*Sporobolus marginatus* short grass is dominant on the more stable ground between the dunes. In some places, this grassland type extends eastward to the fault lines bordering the Balbal Depression and resembles the vegetation of the sand dunes north of that depression.

Low woodland: *Commiphora madagascariensis*–*Acacia mellifera*

This type occupies the vicinity of the small fault scarp which runs north from Makarut Mountain, past the mouth of Oldupai Gorge and along the eastern edge of the Doinyoogol Hills. The vegetation is mainly *Commiphora* and *Acacia* spp. in the overstory

with *Pennisetum stramineum*, *Enneapogon elegans* and *Dactyloctenium aegypticum* below. *Sansevieria ehrenbergiana*, *Salvadora persica*, *Cissus cactiformis*, *C. quadrangularis* and *Barleria eranthemoides* are locally abundant in the understory. *Balanites aegyptica*, *Acacia tortilis* and *Euphorbia metabelensis* also occur in the tree layer.

Balbal Depression

The Balbal Depression is about 26 km (16 miles) long and 8 km (5 miles) wide. It has gently sloping sides and a level floor of black cotton clay soil. The depression is bounded on the south by Makarut Mountain, on the east by the Crater Highlands, on the north by the sand dunes south of the Sale Plain, and on the west by a small fault scarp which crosses the mouth of Oldupai Gorge in a north-south direction. Lying at about 1,300 m (4,300 ft) above sea level, the depression is the base level for the streams which drain the central Serengeti Plains, the southern Doinyoogol Hills, the north-facing slopes of Makarut and the northwest slopes of Ngorongoro and Olmoti (Dirschl, 1966).

Medium grassland: *Pennisetum mezianum*
This community occupies the poorly drained southern half of the depression floor. *Pennisetum mezianum* is dominant. *Cynodon plectostachyus* and Cyperaceae are common.

Medium grassland: *Cynodon dactylon*
This type is found in the better-drained northern half of the depression. *Cynodon dactylon* is dominant. A number of other grasses are minor constituents in the grass layer. *Achyranthes aspera*, *Solanum* spp. and *Chenopodium* spp. are present, particularly along the northern edge where *Acacia xanthophloea* regeneration is abundant. *A. tortilis* regeneration is common throughout the area but retarded by annual grass fires.

Low woodland: *Acacia tortilis*
These woodland stands vary in degree of crown cover and height and grow on the well drained, gentle slopes that fringe the

floor of the Balbal Depression on the east, north and west.

Tree cover ranges from young, dense, even-aged stands with little ground vegetation to older, more open, even-aged stands with a heavy grass cover in which *Digitaria macroblephara* and *Sporobolus marginatus* predominate. *Lycium* spp., *Maerua trichophylla*, *Solanum incanum* and *Capparis elaeagnoides* bush species are found throughout.

Some *Acacia tortilis* regeneration occurs beneath very open *Acacia* stands and, locally, in grassland. In recent years, prolonged floods have killed a fringe of *A. tortilis* along the eastern edge of the depression.

Medium grassland: *Cynodon plectostachyus*–*Cynodon dactylon*

This type grows on the gentle slope in the southern portion of the Balbal Depression, in a band along the foot of Olmoti Mountain, and on the outwash fans of seasonal streams flowing off the Crater Highlands. Near the northern edge of this grassland type, cover is high and the grasses grow relatively tall; but toward the south, height and cover decrease and step erosion is locally present. Growth of *Indigofera basiflora* and *Hypoestes forskalii* shrubs and regeneration of *Acacia tortilis* occur locally.

Short grassland: *Sporobolus marginatus*–*Digitaria macroblephara*–*Kyllinga* spp.
This type occupies the first site in the Balbal to dry up after the rains—i.e., the southernmost part of the gentle rise between the Balbal floor and Makarut Mountain. The type is an extension of the larger short grass type which grows in the west above the fault.

High woodland: *Acacia xanthophloea*
This woodland has a light to moderate understory of unidentified bush and *Cynodon plectostachyus* medium grassland. The type is bordered by the Balbal Depression on the south and the sand dune area on the north. The land rolls gently—low, sandy ridges alternate with moist, loamy troughs. Generally, *Acacia xanthophloea* occupies the

ridges. Since 1957–58 when the aerial photos were taken, the death of large mature trees in the centre of this community has opened up a large area in the overstory. The death was probably due in part to the recent flooding of the Balbal.

A. xanthophloea stands are commonly considered “groundwater forest”. The presence of this relatively small and isolated stand, plus the existence of several moderately deep wells dug in the sand by Maasai, indicate that this small area may be a natural sump for the remainder of the Balbal Depression.

Sand dunes north of the Balbal Depression

This is an extensive area of predominantly low sand dunes between the Sale Plain and the Balbal Depression. Most of the dunes have been stabilized and are now covered with *Acacia mellifera* low woodland.

Tree and bush cover is moderately dense near the Balbal Depression in the southeast. Characteristic understory species are *Maerua trichophylla*, *Pavonia patens*, *Achyranthes aspera*, *Salvadora persica*, *Lycium* spp., *Barleria eranthemoides* and *Indigofera* spp. *Acacia tortilis* and *Euphorbia candellabrum* are minor constituents of the overstory. Most dunes have sparser cover than do the troughs between them.

Throughout the area *Cynodon plectostachyus* is fairly common in the short grass layer. *Dactyloctenium* sp. nov. and *Cenchrus ciliaris* are dominant on the dunes; *Sporobolus marginatus* and *Digitaria macroblephara* are dominant in the troughs.

C. plectostachyus and *C. dactylon* are codominant on the outwash fans at the mouths of seasonal streams which drain the Crater Highlands and the Doinyoogol Hills. During the dry season, the soil of these outwash fans appears to retain moisture longer than do other soils.

Doinyoogol Hills

The rugged topography of the Doinyoogol Hills forms a series of east-west ranges between the Serengeti and Sale plains. The hills present a steep face, 460–902 m (1,500–

Low woodland of *Commiphora madagascariensis* mixed with *Acacia drepanolobium* and *A. seyal*, common throughout the Doinyoogol Hills. Photo by D. J. Herlocker

3,000 ft) high, to the Sale Plain and rise to 300 m (1,000 ft) above the Serengeti Plains. The Kiti Plain is a long narrow strip of level grassland which cuts through the southern Doinyoogol Hills and connects the Serengeti Plains in the west with the Sale Plain in the east. The eastern face of the Doinyoogol is an old, eroded fault scarp (Pickering, 1960).

Generally, the soils are shallow and rocky but level tuff soils occur in some valleys. The underlying rock is composed largely of quartzite, gneisses and schists. It is always near the surface and often fully exposed.

Low woodland: *Commiphora madagascariensis*-*Acacia drepanolobium*

This type is the prevailing vegetation type in the Doinyoogol Hills. It grows in various densities on the steep slopes in most of the area and often on bare, exposed rock. *Acacia mellifera* is locally abundant in the north; *Euphorbia metabelensis* is often locally dominant in the south. Also *A. seyal*, *A. nilotica* and *A. tortilis* are found. *Euphorbia nyikae* is restricted to the steeper slopes. From a distance, this woodland community seems to be dominated by *A. tortilis*. It is taller and has a wider crown than the other tree species, but rarely contributes significantly to crown cover and density, except on the gentle slopes at the base of some hills. A light bush cover dominated by *Aspilia mossambicensis* exists throughout much of the area. Of the many grasses present, *Pennisetum stramineum*, *Themeda triandra* and *Dactyloctenium* spp. predominate. *Aristida adscensionis* is common.

Medium grassland: *Pennisetum stramineum* - *Themeda triandra* - *Dactyloctenium* spp.

This type grows at higher elevations in a large area of the northwestern Doinyoogol Hills. A smooth turf of this medium grassland, unbroken by trees or rocks, characterizes several of the small valleys and produces a distinct contrast to the rough topography of the hills. *Aristida adscensionis* is again common.



Oldupai Gorge

Oldupai Gorge divides the Eastern Serengeti Plains into northern and southern halves. The main canyon begins at Lake Ndutu at approximately 1,600 m (5,200 ft) and empties into the Balbal Depression at 1,300 m (4,300 ft). A tributary originates at about 1,580 m (6,000 ft) on the high ground immediately west of Makarut Mountain and enters the main gorge near its termination.

Oldupai Gorge can be divided into three physiographic parts. Westward from its mouth to its crossing with the Ngorongoro-Seronera road, the lower gorge is deep with steep, eroded walls and a narrow floor. The stream gradient is steep and runoff is rapid. Southwest from the road crossing to Lake Ndutu, the gorge is shallower with more gradually sloping sides. The stream gradient is gentler and water remains longer in or beneath the stream bed. The south fork of the gorge is much narrower and shallower than the main gorge and has a steep gradient in its upper reaches.

Western section of the gorge

From Lake Ndutu to roughly the crossing of the Ngorongoro-Seronera road, the vegetation is characterized by low woodland of *Commiphora madagascariensis*-*Acacia mellifera*-*A. tortilis*. Although *A. tortilis* is the least common of the three, it grows taller with a wider crown and thus predominates visually. The layer of bushy species ranges in density from low to moderate and consists typically of *Sansevieria ehrenbergiana*, *Cissus quadrangularis* and *C. cactiformis*. The grass layer is mostly *Digitaria macroblephara* and *Sporobolus marginatus* short grass. Such annuals as *Aristida adscensionis* are also common.

In the shallow canyon, the stream bed is covered with a dense layer of grasses of which the most common is *Sporobolus consimilis*. This tall grass grows among the shorter grasses, *Chloris gayana* and *Pennisetum mezianum*, in stands reaching 260 cm (8 ft) high. *Sporobolus spicatus*, *S. homblei* and *Odysea jaegeri* fringe the edges of this grassland mosaic and the lines of water

seepage where *Cyperus laevigatus* grows
(Anderson and Talbot, 1965).

Eastern section of the gorge

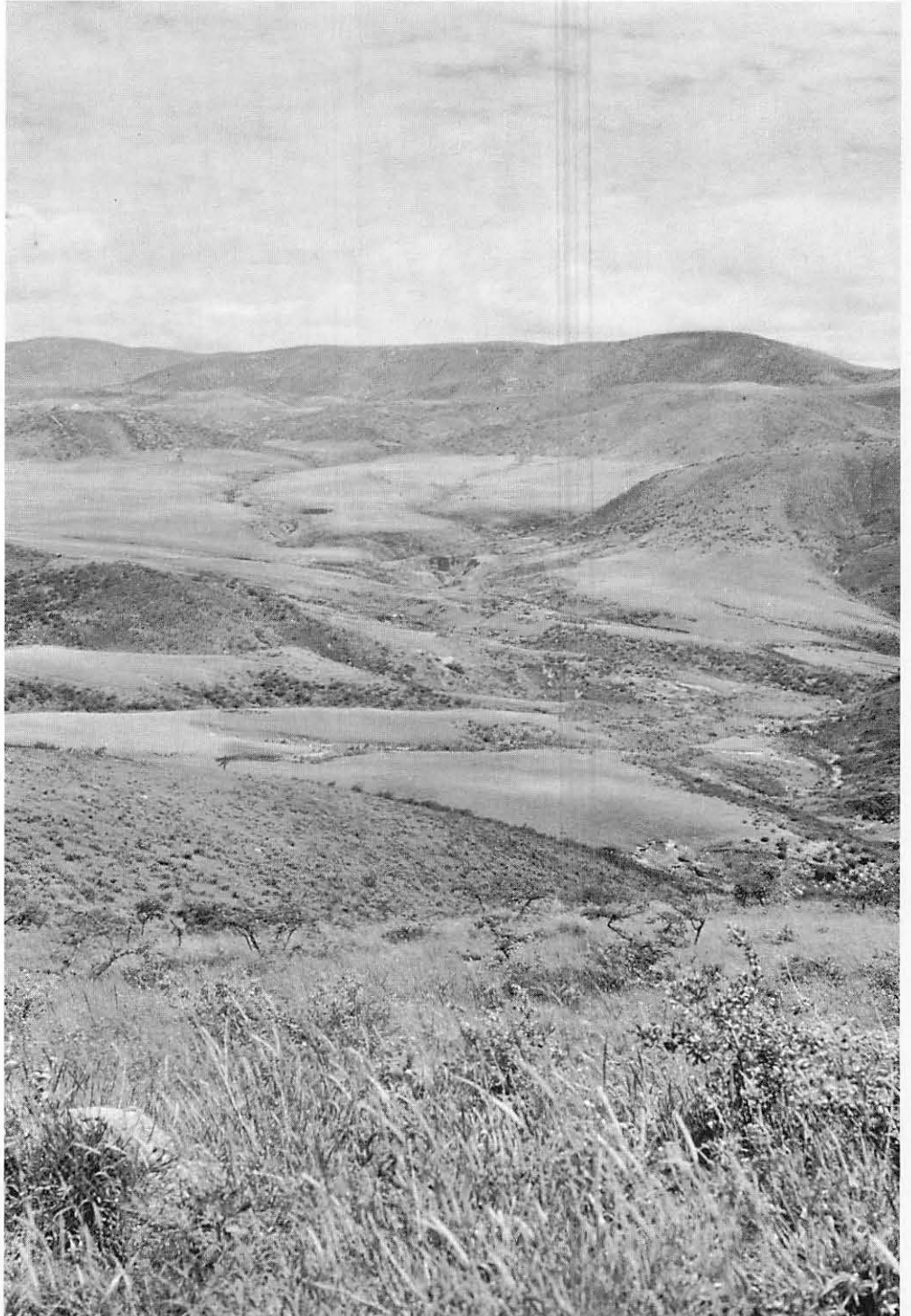
The vegetation here is somewhat more variable because of the steep, broken canyon walls. Low woodland over bush and grass is as common as it is in the western section, but tree cover is usually more open and the bush layer often reaches the thicket stage, especially along the margins of the stream bed. In some locations, vegetation cover is sparse and erosion severe: for example, at the junction of the main gorge and its south fork tributary near Leakey's Camp where Maasai cattle have removed much of the grass cover near the small water reservoirs provided by L. S. B. Leakey.

Within Oldupai Gorge, the woodland overstory is composed of *Commiphora madagascariensis* and *Acacia mellifera* and lesser amounts of *A. tortilis* and *C. merkeri*. Associated lower vegetation is *Sansevieria ehrenbergiana*, *Salvadora persica*, *Lycium* spp., *Cissus quadrangularis*, *C. cactiformis*, *Euphorbia schimperi* and *E. tirucalli*. *Grewia* spp., *Cordia* spp., *Pluchea ovalis* and *Justicia bentonica* also grow along the stream.

South fork tributary

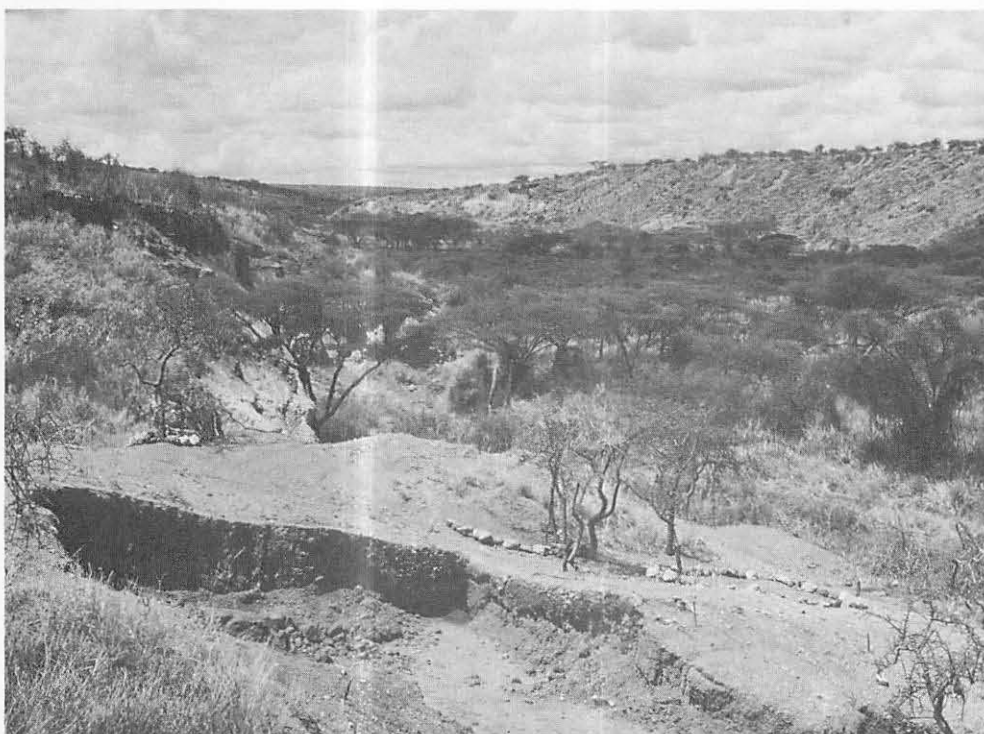
This section is characterized by bush and bush thicket of *Sansevieria ehrenbergiana*, *Salvadora persica* and *Cissus* spp. on the stream banks, paralleled by narrow strips of low woodland. *Commiphora madagascariensis*, *Acacia tortilis* and *A. mellifera* predominate in the overstory; *Sansevieria ehrenbergiana*, *Salvadora persica*, *Barleria eranthemoides*, *Digitaria macroblephara*, *Sporobolus marginatus* and *Kyllinga* spp. form the ground vegetation.

Over a large area of the headwaters, medium grass of *Pennisetum stramineum*, *Aristida adscensionis* and *Enneapogon elegans* grows beneath low woodland of *Commiphora-Acacia mellifera*. The upper reaches are covered with low woodland of *A. gerardii*, *A. drepanolobium* and *A. seyal* over medium grass of *Themeda triandra*, *Hyparrhenia* spp. and *Pennisetum mezianum*.



Typical vegetation on the gentle slopes of the western section of Oldupai Gorge—*Commiphora madagascariensis*–*Acacia mellifera* low woodland with an understory of *Sansevieria ehrenbergiana*. Photo by D. J. Herlocker

View of the eastern section of Oldupai Gorge near Leakey's Camp. The tree species growing in the bottom is *Acacia tortilis*. Photo by D. J. Herlocker



Crater Highlands massif

The Crater Highlands lie between the northeastern edge of Lake Eyasi and the extreme northeastern corner of the conservation area, and form a high plateau with an average elevation of 2,150–2,450 m (7,000–8,000 ft). Several extinct volcanoes rise above the plateau to elevations of more than 3,050 m (10,000 ft). Several calderas are sunk into the plateau.

The greatest rise occurs in the southwest where Oldeani Mountain climbs from Lake Eyasi at 1,000 m (3,250 ft) to an elevation of 3,050 m (10,000 ft). The 75-km-long (45 miles) western face of the highlands reaches 2,000 m (6,500 ft) above the adjacent Serengeti and Sale plains. It is anchored at its southwestern and northeastern ends by Makarut Mountain and Empakaai Crater, respectively, and at its mid point by Olmoti Mountain. All three peaks are over 3,000 m (9,750 ft) high. The outer face of the highlands then extends about 16 km (10 miles) southeast along the northern and northeastern flanks of Empakaai, merges with the Great Rift Escarpment and runs south to the eastern slopes of Lolmalasin Mountain which is over 3,350 m (11,000 ft) high. The wall leaves the Great Rift at this point, drops to about 2,300 m (7,500 ft) and runs southwest and west along the eastern and southern slopes of Ngorongoro Crater to Oldeani Mountain.

Exterior drainage is into Lake Eyasi in the south, the Balbal Depression in the west, and over the rift wall in the northern, western and southwestern portions of the conservation area.

Because of the abundance of craters and depressions in the highlands, there are several interior drainage systems of which Ngorongoro Crater is the largest. The contiguous area of highland grassland to the northeast drains into the Balbal Depression at the centre of a triangle formed by the Losirua, Lolmalasin, Olmoti and Empakaai mountains. Smaller drainage systems are those of Empakaai Crater in the extreme northeast, and of the Malanja Depression in the southwestern part of the Crater Highlands.

Commiphora madagascariensis low woodland over *Pennisetum stramineum*, *Aristida adscensionis* and *Enneapogon elegans* medium grassland on the lower western slopes of the Crater Highlands. Photo by D. J. Herlocker

The prevailing easterly winds strike the eastern slopes of the highlands, cool as they rise and deposit heavy amounts of precipitation over the slopes and over the highland plateau. No rainfall records are available for the eastern slopes but the average annual rainfall at Ngorongoro settlement is about 890 mm (35 inches). The Endulen area and the western slopes of Olmoti Mountain probably receive similar amounts of rain. Most of the rain falls from November to May. A dry season occurs between June and October, but there is considerable cloud cover over the eastern and southeastern parts of the highlands during the first three months of the dry season. Large temperature differences reflect the range of altitudes in the highlands. Temperatures as low as 2°C (35°F) have been recorded during July and August (Dirschl, 1966).

Western wall of the Crater Highlands

The western wall rises 1,200 m (3,900 ft) above the adjacent Serengeti and Sale plains. It stretches approximately 75 km (45 miles) northeast from Makarut Mountain to Jaeger Summit, the westernmost extension of Empakaai, and then 16 km (10 miles) east and southeast along the northern and northeastern flanks of Empakaai Crater almost to Kerimasi Mountain in the extreme northeast of the conservation area.

The western wall is the area on the western and northern sides of the Crater Highlands below 2,450 m (8,000 ft) in elevation. This contour line forms an approximate dividing line between *Acacia lahai* high woodland and montane forest. Vegetation at higher elevations is discussed in the section entitled "Montane areas".

Minor storms, which form over the main peaks along the western wall during the short rains, characteristically follow fairly regular routes over the wall and, for a short distance, over the plains beyond. Devotion to these routes is made evident by straight strips of green grass extending west from the highlands into the otherwise dry and brown plains.

There is a distinct altitudinal zonation of vegetation on the western wall, particularly



on the lower to middle slopes of the three main mountains. Here the zones comprising this pattern occur at lower elevations than on adjacent parts of the wall fronting the plateau. Consequently the lowermost belt of woody vegetation (*Commiphora* low woodland) is at its narrowest on these mountains. A washboard system of deep canyons breaks the zonation into a complex arrangement of small, horizontal vegetation communities cut at right angles by long and narrow canyon vegetation communities.

The soil tends to be shallow at lower elevations and slightly deeper at higher elevations. Soils are particularly shallow on the steep slopes of canyons with the underlying rock frequently exposed on the lower to middle slopes where livestock trails are in permanent use.

Major vegetation types of exposed slopes

Low woodland: *Commiphora madagascariensis*

A variety of low woodland communities occupy the lower band in the zonation pat-

tern. The band is narrowest—about 1.6 km (1 mile) wide—on the lower slopes of Olmoti. *Commiphora madagascariensis* is the dominant tree species throughout. *C. merkeri* is common; *Acacia tortilis*, *A. mellifera* and *A. senegal* occur in the lower portions of the band. *A. seyal*, *A. nilotica* and *A. drepanolobium* occur infrequently throughout the rest of the area. The understory is mostly *Pennisetum stramineum*–*Aristida adscensionis*–*Enneapogon elegans* medium grass south and southwest of Olmoti, *Themeda triandra*–*Hyparrhenia*–*Heteropogon contortus* medium grass on Olmoti's lower slopes, and *Digitaria macroblephara*–*Sporobolus marginatus* short grass, with a shrub layer of *Aspilia mossambicensis* and *Lippia* spp., at the wall's northeastern extremity just west of Empakaai.

Low woodland: *Acacia drepanolobium*

This type grows in a broad band above the *Commiphora* low woodland association on the slopes of Makarut Mountain and Ngorongoro Crater. The band reaches about



1,700 m (5,500 ft) in elevation where it is replaced, usually by grassland. Few tree species other than *Acacia drepanolobium* grow within this community type. The open spacing of stems and the small crown diameter result in an open physiognomy of the tree overstory. The understory is mainly *Andropogon greenwayi* medium grassland.

Low woodland: *Acacia gerrardii*

This type is found in two areas at the same elevational stratum as the *Acacia drepanolobium* low woodland: on the western slopes of Makarut Mountain, including the headwaters of the south fork of Oldupai Gorge; and on the southwestern slopes of Olmoti. To the west of Makarut Mountain, stands of *A. gerrardii* are mixed with those of *A. drepanolobium*. On Olmoti Mountain, *A. seyal* and *A. gerrardii* are codominant. Small numbers of *A. kirkii* occur throughout, particularly among streams. Medium grasses, *Themeda triandra*, *Seteria sphacelata* and *Hyparrhenia* spp. scattered with *Solanum incanum* make up the undergrowth.

High woodland: *Acacia seyal*

Acacia seyal high woodland grows on Olmoti Mountain, northeast of the *A. gerrardii* type. The zone is widest on Olmoti's northwestern flank and extends in a tapering and often broken band to the western slopes of Empakaai Crater. Elsewhere, *A. seyal* is often a minor component of low woodland communities, but here it reaches heights of 12–15 m (40–50 ft) and forms a single-layered stand of large-crowned mature trees. Little regeneration of *A. seyal* occurs beneath these stands of high woodland. The understory is mostly moderate to dense layers of *Lippia-Lantana-Solanum incanum* bush. In the northeast, below the Melinda Highlands and beyond, *Aspilia mossambicensis* replaces *Lantana* spp.

Several large stands of *A. seyal* occur near the conservation area boundary on the upper drainage of seasonal streams running over the rift wall from the eastern and northern flanks of Kerimasi Mountain and Empakaai Crater. An understory of bush probably consists of *Lippia-Lantana-*

Solanum incanum and, possibly, of *A. mossambicensis*; but this could not be verified by means of a ground survey.

Bush: *Lippia-Lantana-Solanum incanum*

This vegetation belt, of variable width, grows immediately above the *Acacia seyal* high woodland on Olmoti Mountain and tapers off to the northeast. Composed principally of *Lippia* spp., *Lantana* spp. and *Solanum incanum*, the shrubs are 370 cm (12 ft) high and often grow so dense as to be almost impenetrable. A few emergent trees, chiefly *A. seyal* at lower and *A. lahai* at higher elevations, are scattered throughout this type.

Bush of variable density covers most of the Naiobi-Enkopironi-Engamat area. Small patches of moist evergreen forest are found within the canyons here, whereas bush grows on the ridges above. A tall species of *Euphorbia*, similar to that found in the forested canyons on Ngorongoro Crater's south wall, is typical in these forest patches.

An area of ecotone between moist evergreen forest and *Acacia lahai* high woodland near Misigio. The forest is now restricted to fire-protected gullies, whereas the fire-resistant *Acacia lahai* occupies the exposed slopes. Photo by D. J. Herlocker



High woodland: *Acacia lahai*

This type occupies the next highest zone of vegetation, at an approximate elevation of 2,100–2,450 m (6,800–8,000 ft). It extends along almost the entire length of the western wall of the highlands (about 70 km or 42 miles). A particularly dense, pure stand covers 32 km² (12.5 sq. miles) on the southwestern slopes of Makarut Mountain. *A. lahai* seems to regenerate and grow in pure even-aged stands. Seedlings seem unable to compete with dense ground vegetation but often grow in thickets within open grassland or in gaps of senescent stands of the same species. In grassland, the growth of *A. lahai* is often retarded by annual grass fires. The characteristically dense and interlocked canopies of young- to medium-aged stands prevent dense herbaceous ground vegetation. When the stands become senescent, individual trees die and bushy and herbaceous understory plants become established in the openings.

Extensive tall stands of *A. lahai* grow mainly on the southern slopes of Makarut

Mountain, on Olmoti Mountain and above the northern rim of Ngorongoro Crater. Although areas of regeneration are present, especially on Ngorongoro Crater's western rim and in the grasslands of the Misigio area, most of the *A. lahai* woodlands are characterized by open stands of mature trees with large crowns, and by an undergrowth of dense *Lippia-Lantana-Solanumincanum* bush and *Themeda triandra*, *Cynodon dactylon* and *Chloris gayana* medium grass.

Short grassland: *Digitaria milanijana*

This type grows on Jaeger Summit (Empakaai)—with a sparse overstory of *Commiphora madagascariensis* and *Aspilia mossambicensis* on the low to middle elevations of the western slopes and without bush or tree cover on the northwestern slopes—and in several smaller areas of the northern flank of Empakaai. *Pennisetum stramineum* and *Aristida adscensionis* are codominant with *Digitaria milanijana*.

The Nairobi–Enkopironi–Engamat area is used intensively by cultivators and by

Maasai graziers. A large area of land at Nairobi on the north slope of Empakaai was cultivated until a few years ago. Small subsistence farms are common on the ridges above the Rift Wall on the lower eastern slopes of Empakaai in the Enkopironi area.

Vegetation of canyons

The frequency and effect of grass fires are reduced within the canyons by their steep sides, rocky slopes and generally narrow mouths. These characteristics create a climate somewhat more mesic than on intervening ridge tops. In canyons on the slopes of the three larger mountains there is also surface or subsurface water from springs at higher elevations. Because of these factors the canyons generally carry vegetation of a greater density than occurs on exposed slopes. This density is especially apparent on the western slopes of Olmoti. Canyons near the bottom of the slope contain dense low woodlands, dominated by *Commiphora madagascariensis*, *Acacia mellifera* or *Albizia harveyi*, with an undergrowth of *Croton dichogamus*, *Cordia ovalis* and *Grewia* shrubs. This woodland type generally extends along the lower third of the canyons where it gradually changes to a thin ribbon of montane forest vegetation. Until it approaches the main, moist evergreen forest association at about 2,450 m (8,000 ft) elevation, the ribbon is restricted to the very bottom of the canyons.

In the middle reaches, the canyon walls are covered with a vegetation catena which typically follows this sequence. Along the very edge of the canyon, there is a band of *Combretum* woodland, as much as 100 m (330 ft) wide, containing *C. molle*, *Acacia hockii* and *Azanza garckeana*. These species change to *Euphorbia candelabrum* and *Acacia seyal* trees over *Lippia-Lantana* bush above the band; and to *Croton macrostachyus*, *Albizia gummifera* and *Calodendrum capense* trees over *Crotalaria imperialis*, *Pavonia irakuensis* and *Vernonia auriculifera* bush below the band.

Lippia spp. and *Lantana* spp. are the principal bushes in some canyons on the

Interior view of a stand of dry evergreen forest, dominated by tall cedars (*Juniperus procera*), in a canyon on the west side of Oldeani Mountain. Photo by D. J. Herlocker

northwestern slopes of Olmoti. Elsewhere, the vegetation inside and outside the canyons is less distinctly differentiated, except for *Juniperus procera* (discussed later).

Montane areas

Typical montane vegetation generally grows above the 2,450 m (8,000 ft) contour on the western wall of the Crater Highlands and on all slopes of the mountain peaks above the plateau. Montane vegetation occurs above 1,600 m (5,250 ft) on the moister eastern wall of the Crater Highlands, the area included in the Northern Highlands Forest Reserve. Remnants of montane vegetation also exist on the inner walls of the Ngorongoro and Empakaii calderas.

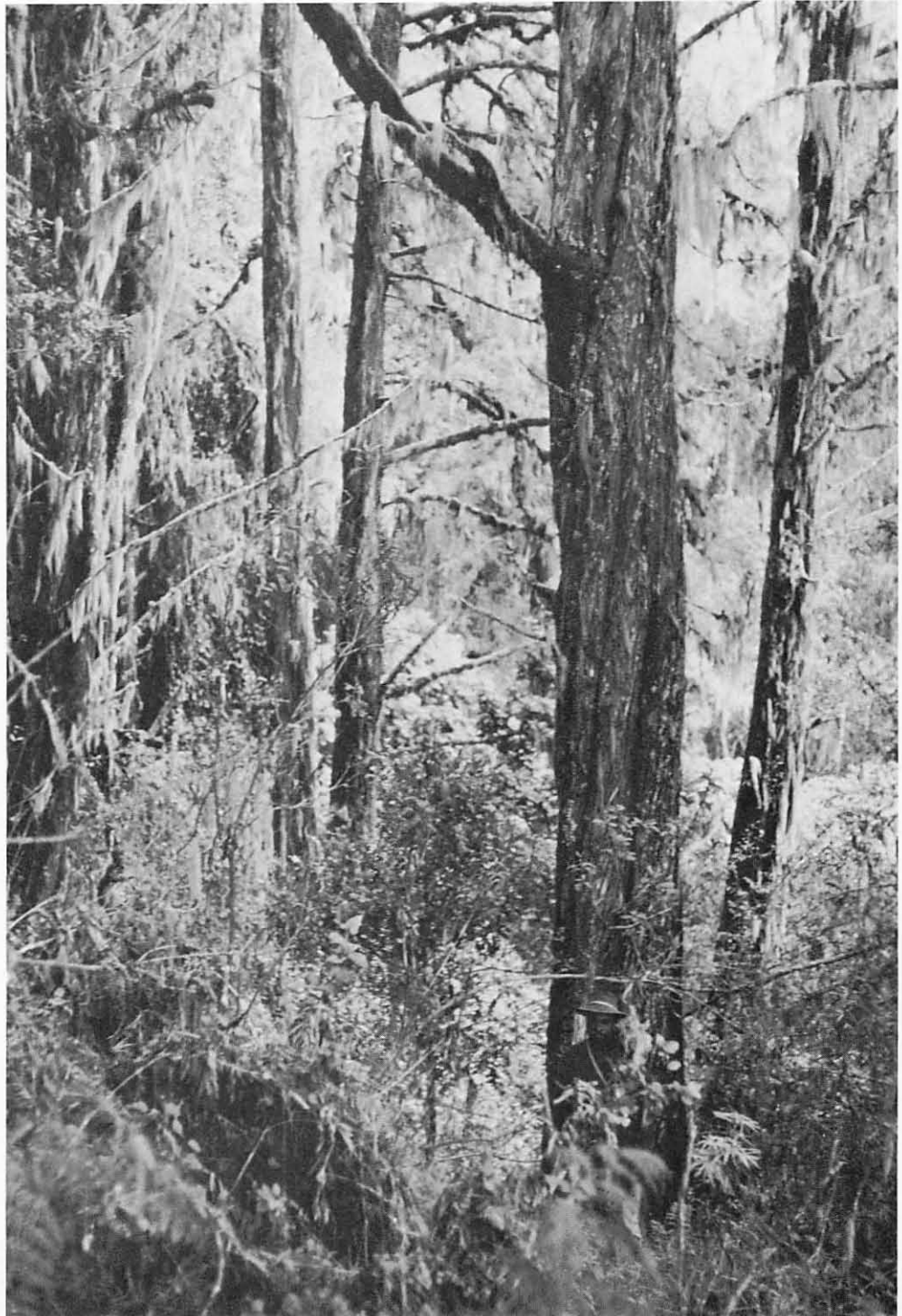
Large, isolated mountains rise from a high plateau to elevations exceeding 3,000 m (10,000 ft). The somewhat abrupt topography, the prevailing easterly winds, a dry season of 4–5 months, a wide range of climatic factors related to elevational differences, and the continual disturbance of vegetation by Maasai graziers create a complex environmental situation which is reflected in a complex distribution of plant communities.

Montane forest and bush communities are extensive in such areas of heavy rainfall as the eastern and southern slopes of the highlands and the western and southern slopes of Olmoti. The main central plateau area, whose eastern edge lies in the rain shadow of the higher mountains, is mostly grassland. The peaks are covered with mountain heath dominated by *Artemisia afra* and other shrubs.

Montane forest and bush vegetation

Moist evergreen forest

This forest vegetation can be divided, according to elevation, into lower and upper montane forest zones. However, the boundary is vague because the changes in the composition of this species-rich and structurally complex forest are extremely gradual along the elevational and other environmental gradients.



Moist evergreen forest near the eastern rim of Ngorongoro Crater. View shows an abrupt boundary with *Vernonia-Crotalaria* bushland. Photo by H. J. Dirschl

The largest stands of the lower montane forest zone form a discontinuous semi-circular band on Olmoti's western slopes. The band is bordered below by *Acacia lahai* high woodland, at an elevation of about 2,600 m, and above by *Vernonia-Crotalaria* bush. Smaller stands are found in the canyons on the eastern face of Makarut. Small relict patches and single trees are also scattered throughout the extensive area of *Vernonia-Crotalaria* bush on Olmoti and the eastern and northeastern slopes of Empakaai. Species characteristic of this zone are *Croton macrostachyus*, *Albizia gumifera*, *Calodendrum capense*, *Olea welwitschii*, *O. africana* and *O. hochstetteri*.

Where the forest has not been disturbed, the crowns of many tree species interlace to form a tight canopy permitting little light to enter from above. The forest floor is more typically covered by litter and herbaceous plants than by grass. Where the death of mature trees has opened up the canopy, herbaceous plants, especially vines and creepers, are dense, often covering smaller trees and severely stunting growth.

Tree species of the upper montane forest zone occur at higher elevations on the mountains and in a narrow belt on the southwest flank of Losirua. The zone is probably best characterized by *Lasiosiphon glaucus* and *Hagenia abyssinica*, but also contains many species found at lower elevations.

Dry evergreen forest: *Juniperus procera*
Isolated stands of *Juniperus procera* grow in steep canyons at elevations of 2,450–2,900 m (8,000–9,500 ft). The largest *J. procera* forests grow in canyons extending almost to the summits of Makarut and Empakaai and on every side of Makarut but the eastern. Small relict stands also exist on the western and northwestern slopes of Olmoti, on the southwestern flank of Losirua and in small, westward facing canyons extending northeast from Olmoti to Empakaai.

J. procera regeneration is more common in open grassland or in light bush areas on



the forest fringe than within the stands themselves. Seedlings are more easily destroyed by fire than are pole-sized or larger individuals. This characteristic explains the present distribution of cedar forests in deep canyons which fire rarely penetrates.

On Makarut, *J. procera* stands are relatively pure in composition. In other places, they are mixed with varying amounts of such broadleaved species as *Nuxia congesta* and *Olea africana*.

J. procera has been used both by the conservation unit and the Maasai for building materials. Large patches of dead trees high on the north face of Makarut Mountain and on the contiguous Laronya Ridge have been caused by fire.

Bush: *Vernonia-Crotalaria*

The west and southwest slopes of Olmoti and the eastern flanks of Empakaai are extensively covered with bush, predominantly *Vernonia auriculifera*, *Crotalaria imperialis*, *Pavonia irakuensis* and *Cutia abyssinica*.

Growth is dense and can reach 4.6 m (15 ft) high. A variety of vines, creepers and other herbaceous and woody species are also abundant.

Throughout this bush vegetation occur scattered patches and single tree relicts of moist evergreen forest, particularly *Nuxia congesta* or, at higher elevations, *Lasiosiphon glaucus*. On the edges of the patches, some tree regeneration is present; elsewhere, only scattered specimens of *Bersama abyssinica* are found. A retrogression to bushy grassland and thence to grassland is apparent on the southern and western slopes of Olmoti and probably results from persistent use of fire by Maasai graziers. A mosaic of *Vernonia-Crotalaria* bush and *Pennisetum schimperi-Eleusine jaegeri-Cynodon* grassland now exists, except where a complete change to grassland has already taken place. Thus, *Vernonia-Crotalaria* bush appears to be a seral stage in secondary succession to moist evergreen forest after severe disturbance.

Montane heath

The highest zone of vegetation in the conservation area occurs above 2,900 m (9,500 ft) and caps all the major mountain peaks. The principal shrub species is *Artemisia afra*. Other common shrubs are *Erica arborea*, *Stoebe kilimandscharica* and *Anthrospermum usambarensis*. Low trees of *Lasiosiphon* spp. and *Protea* spp. sometimes form small, open stands. *Eleusine jaegeri* and *Pennisetum schimperi* medium grasslands are found beneath the woody layer. Despite the elevation, grass fires are common during the dry season and are probably responsible for the downward extension of the montane heath's lower limits (Pearsall, 1956).

Juniperus procera stands are found within this bush vegetation in some deeper canyons on the northwestern and western slopes of Losirua and Lolmalasin mountains. Frequent cutting and fires have greatly deteriorated the *J. procera* stands on the northwestern slopes above the Bulbul Depression.

The extensive area of mountain heath on the Losirua and Lolmalasin mountains likely contains a more complex mosaic of vegetation, particularly in the grass layer.

Highland tussock grassland: *Eleusine jaegeri*-*Pennisetum schimperi*

The rest of Makarut and Empakaai mountains is covered with *Eleusine jaegeri* and *Pennisetum schimperi* medium grassland, typically on the ridges between the bush and forest-filled canyons and above the woodland types. This grassland extends to the mountain summits beneath an overstory of *Artemisia afra* bush.

Highland plateau

The highland plateau consists mainly of grasslands and is the area most heavily used by the Maasai. It can be divided into the Melinda and the Ngorongoro-Misigio-Endulen areas.

Melinda grasslands

The Melinda grasslands denote the area extending south from the lower limits of

mountain heath on Empakaai and Olmoti craters and Losirua and Lolmalasin mountains, to Lemala near the northeastern rim of Ngorongoro Crater and west and east to the upper limits of woodland or forest. The area includes the Bulbul Depression, the floor of Olmoti Crater and a long arm of grassland extending east and north on Losirua and Lolmalasin mountains, above the Northern Highlands Forest Reserve and below the mountain heath.

The topography ranges from the level floor of the Bulbul Depression to the moderate and steep slopes of the surrounding mountains. The Bulbul Depression is separated from the western wall of the highlands by two steep escarpments and a large bench which extends north from Nainokanoka to the southwest slopes of Empakaai Crater. South of Nainokanoka, the gently rolling land is cut by several streams draining Olmoti and Losirua.

Almost daily during the rainy and early dry season, dense fog is common on the grasslands, from the forest reserve and Ngorongoro Crater north to Nainokanoka and sometimes beyond. The land lies at about 2,300 m (7,500 ft) and is usually very cool. Rainfall was 1,120 mm (44 inches) in 1966, for the Lemala-Nainokanoka area, but is probably somewhat less north and northeast of Nainokanoka because of the rain shadow effect of Empakaai Crater and Losirua and Lolmalasin mountains.

Highland tussock grassland: *Eleusine jaegeri*

This is the most extensive grassland community in the Melinda highlands. It occupies the entire tract from just north of Nainokanoka southward to Lemala near Ngorongoro Crater's northeastern rim, and includes part of the floor of Olmoti Crater and the grassland extension south and east of Losirua and Lolmalasin mountains. A band of *Eleusine jaegeri* also extends from Jaeger Summit to the east side of the Bulbul Depression.

E. jaegeri is dominant throughout, except locally when other species, as *Pennisetum schimperi*, are sometimes dominant. *E.*

jaegeri grows in large tussocks reaching 180 cm (6 ft) in height and 30–60 cm (1–2 ft) in diameter; *P. schimperi* is slightly smaller in stature. The low mat below consists of such species as *Andropogon greenwayi*, *Cynodon dactylon*, *Digitaria scalarum*, *Sporobolus* spp. and *Eragrostis* spp. *E. jaegeri* and *P. schimperi* are unpalatable to grazing stock and are eaten only when they are young or after all other grasses have been consumed. Thus, grazing pressure is confined to the underlying mat of palatable grasses. These are kept low by constant usage. *E. jaegeri* is also resistant to trampling and may even be spread by it. Glover (1961) suggested that restriction of grazing would allow other grasses to succeed *E. jaegeri*.

A dense population of the mole rat (*Tachyorettes daemon*) causes frequent patches of bare soil.

Medium grassland: *Pennisetum schimperi*-*P. clandestinum*-*Cynodon dactylon*

This type forms a large semicircle around the western, northern and eastern edges of the Bulbul Depression. *Pennisetum schimperi* is dominant throughout. *P. clandestinum* and *C. dactylon* alternate as codominants.

Along the outer face of the high ridge from Olmoti northeast to Jaeger Summit, the shrub *Hypoestes verticillaris* forms many small islands of bushy grassland. *Digitaria scalarum* and *Andropogon greenwayi* are other common grasses.

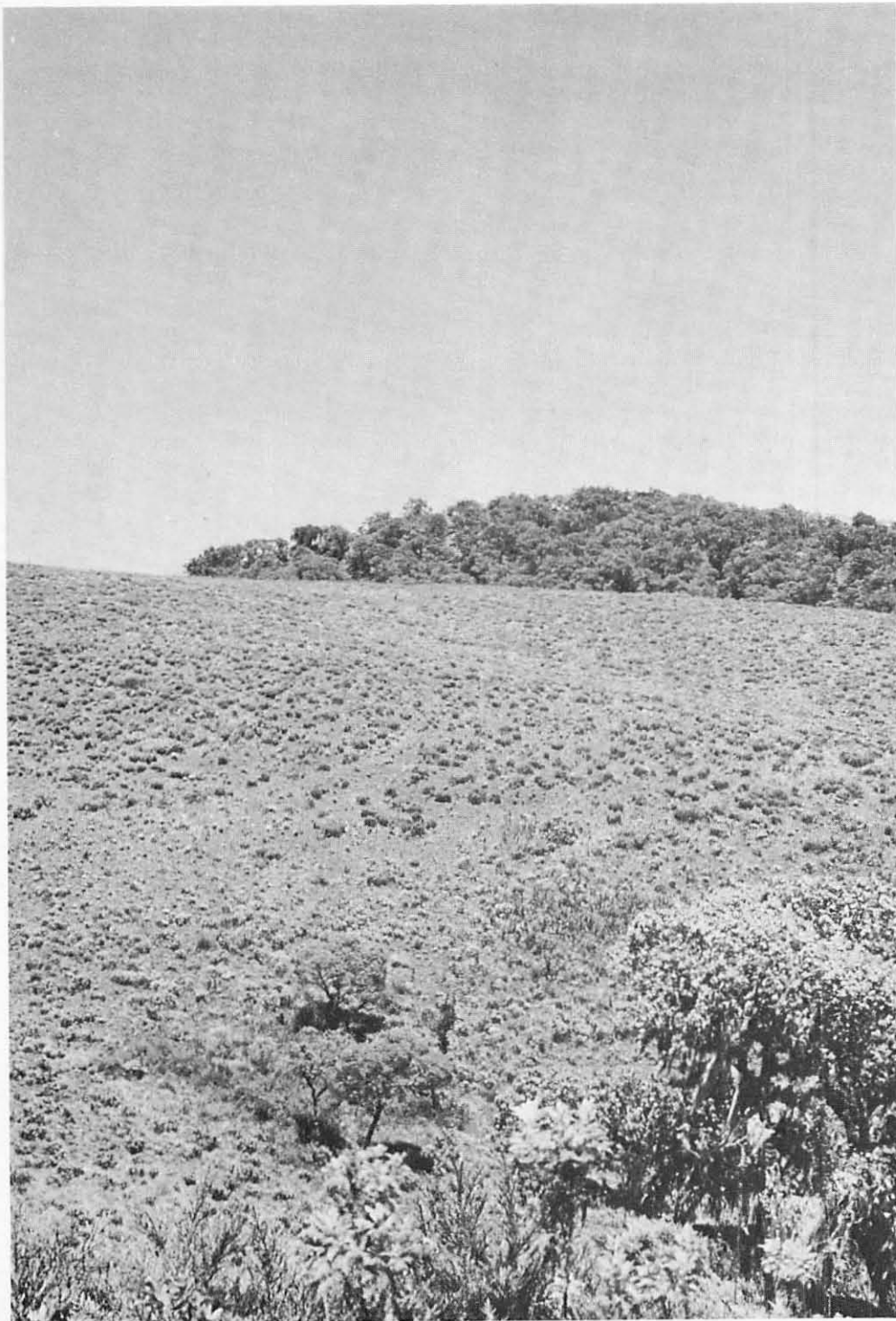
Short grassland: *Pennisetum clandestinum*-*Cynodon dactylon*-*Chenopodium* sp.

This type occupies the bench directly west and a small area east of the Bulbul Depression. It is characterized by the ground disturbance of a persistently high population of mole rats and by the dominant, herbaceous *Chenopodium* sp. Mole rats are common throughout the Melinda highlands but especially so here and on the floor of the Bulbul Depression.

Bush: Unidentified shrub

This type adjoins the Bulbul Depression

Mountain heath dominated by *Artemisia afra*, at approximately 2,850 m (9,500 ft) above sea level, on Makarut Mountain. The moist evergreen forest beyond is principally composed of *Hagenia abyssinica*. Photo by D. J. Herlocker



on the east and north. Sparse shrub cover is associated with a field layer dominated by *Cynodon dactylon*.

A similar community covers the floor of the Bulbul Depression where the field layer is dominated by *Pennisetum clandestinum* in association with *C. dactylon* and *Eragrostis tenuifolia*. Ground cover is significantly reduced by a dense population of mole rats.

Short grassland: *Andropogon greenwayi*
Andropogon greenwayi is the principal species on the steep, east-facing wall between the Bulbul Depression and the large saddle immediately to the west. Associated species are *Chloris pycnothrix* and *Cynodon dactylon*. The soil is quite thin. Locally, the underlying rock has been exposed. The type also seems to occur on the lower slopes of Losirua Mountain to the south of the depression.

Medium grassland: *Themeda triandra*–*Pennisetum schimperi*–*Andropogon greenwayi*
This type is common on the ridges of the western slope of the long saddle connecting Olmoti Mountain with Jaeger Summit. *Lippia*–*Lantana* bush and small stands of *Juniperus procera* forest grow in the canyons.

Ngorongoro–Misigio–Endulen grasslands
A belt of highland grasslands runs southwest and west from Ngorongoro Crater's southwest rim, along a large bench on the south flank of Makarut Mountain to the vicinity of the agricultural settlement at Endulen.

Here, it joins with the *Andropogon*–*Pennisetum*–*Chloris* medium grasslands at the headwaters of the south fork of Oldupai Gorge. The topography of the area is principally that of a large bench extending along the southern flank of Makarut Mountain and descending in elevation from Ngorongoro to Endulen. Rainfall is fairly high in the east and less in the west. During the early dry season, additional precipitation is derived from fog, which often

blankets the area between the south rim of Ngorongoro Crater and the saddle of Oldeani Mountain's northwest flank.

Medium grassland: *Pennisetum schimperi*
Pennisetum schimperi predominates in the area between Ngorongoro Crater's southwest rim and the saddle on Oldeani Mountain's northwest flank. The type occurs at about 2,400 m (7,900 ft) elevation, and its boundary conforms approximately with the farthest extension of daily fog during the early dry season. *Eleusine jaegeri*, *Digitaria scalarum*, *Cynodon dactylon* and *P. clandestinum* are also found. Along the drainage lines and in scattered small round depressions, there is a low mat of *C. dactylon*, *D. scalarum*, *P. clandestinum*, *Trifolium* spp. and Cyperaceae. Because *E. jaegeri* grows in large tussocks, it appears to be more abundant than it actually is. Inside the western and northern edges of the type, *Acacia lahai* regeneration occurs.

Several small tracts of *E. jaegeri* are scattered throughout the *P. schimperi* grassland.

Medium grassland: *Themeda triandra*–*Hyparrhenia* spp.

This type covers the remainder of the Ngorongoro–Misigio–Endulen part of the highland plateau. Around Endulen, the type exists as low wooded grassland with *Acacia gerrardii* and *Croton macrostachyus* in the overstory. The westernmost extension is found in the headwaters of the south fork of Oldupai Gorge. Between Endulen and Misigio, the grassland grows beneath a thin cover of *Acacia lahai*. Farther east, there are local thickets of *A. lahai* regeneration. *Themeda triandra* and *Hyparrhenia* spp. are codominant. Scattered shrubs including *Leonotis* spp., *Pluchea ovalis* and *Justicia elliotii*, are present.

Medium grassland: *Themeda triandra*–*Hyparrhenia* spp.–*Pennisetum schimperi*–*Seteria sphacelata*

Two separate communities, each containing a different mixture of these species, occur on the slopes east of the Malanja Depres-

sion and along the western rim of Ngorongoro Crater.

Medium grassland: *Andropogon greenwayi*

This type adjoins the Malanja Depression on the west, and is an extension of the grassland type occurring beneath *Acacia drepanolobium* low woodland along the western wall of the Crater Highlands. It has all the characteristics of that type but lacks tree cover.

Short grassland: *Cynodon dactylon*

The flat, seasonally waterlogged floor of the Malanja Depression is covered entirely with this short grassland community, dominated by *C. dactylon*. *Andropogon greenwayi* and *Digitaria scalarum* are lesser constituents of this community.

Lake Eyasi–Kakesio area

The Lake Eyasi–Kakesio area includes the flats north of Lake Eyasi in the Olpiro–Endamaga area, the adjacent escarpment on the north, the Eyasi Rift wall along the west side of the lake and, above the Eyasi Rift, a large area of low woodland and grassland extending southwest from Endulen to beyond Kakesio.

Soils are shallow. Some of the many seasonal streams, flowing into Lake Eyasi, have formed deep canyons in the northern section of the escarpment. Two permanent streams exist: one flows from the southwestern slopes of Makarut through Endulen into Lake Eyasi at Olpiro; the other flows from Oldeani Crater and enters the lake at Endamaga. Both streams are used for irrigation at Olpiro and Endamaga. The climate is semi-arid and hot, particularly in the flats north of Lake Eyasi. The precipitation pattern is irregular. Total annual rainfall at Kakesio above the rift wall was 170 mm and 460 mm (6.60 and 18.06 inches) for 1965 and 1966, respectively.

Lake Eyasi flats

This physiographic area contains all the land between Lake Eyasi and the escarpments in the north and west.

Tall grassland: *Sporobolus consimilis*
Seasonal fluctuations in the level of Lake Eyasi alternately expose and cover extensive mud flats. Along the edge of the lake's farthest advance, a narrow strip of mixed vegetation consists of *Sporobolus consimilis* tussocks, up to 260 cm (8 ft) high, within a low mat of Cyperaceae (probably *Cyperus laevigatus*). *Odyssea jaegeri* colonizes the outermost edge of this type.

High woodland: *Hyphaene ventricosa*–*Acacia tortilis*

A strip of woodland containing *Acacia tortilis* trees and tall, emergent *Hyphaene ventricosa* (doum palm) over *Maerua trichophylla* and *Cordia rothii* bush, adjoins the tall grass vegetation north of the lake. The type also occurs on outwash fans of small streams below the Eyasi Rift to the west of the lake. The rest of the land between the lake and the rift wall in the west is very sandy or gravelly, and supports only scattered vegetation of *H. ventricosa*, *A. tortilis* and *A. nubica*. Varying combinations and densities of *Acacia*–*Commiphora* low woodland, dominated by *A. tortilis*, *A. nubica*, *A. mellifera* and *Commiphora madagascariensis*, characterize the remainder of the flats on the north side of the lake.

Since we visited this area during the dry season only, we could not always positively identify the grass species. But the flats probably contain *Themeda triandra* and *Hyparrhenia* spp. These are also noted in several locations along the Endamaga–Olpiro settlements. Local cattle graze the flats north of the lake throughout the year. Maasai cattle graze the long, thin strip of grassland west of the lake during the wet season.

Lake Eyasi Escarpment

The Lake Eyasi Escarpment parallels the western shore of Lake Eyasi and is mainly covered with a mixture of low woodland and bush thicket. The steep slope is cut by many narrow, deep canyons through which seasonal streams descend from the plateau. Vegetation consists typically of *Croton*

Maerua trichophylla and *Cordia rothii* shrubs on gravelly outwash on the Lake Eyasi flats. Makarut Mountain is in the background. Photo by H. J. Dirschl

Oldeani Mountain seen from the Lake Eyasi flats. The vegetation is composed of *Euphorbia candelebrum* trees and *Maerua trichophylla*-*Cordia rothii* bush. Photo by H. J. Dirschl



dichogamus, *Stigmatorhynchus umbelliferus*, *Cissus* spp. and *Euphorbia tirucalli* bush thickets and an overstory of *Acacia mellifera*, *A. tortilis* and *Commiphora madagascariensis* trees. Scattered, single *Adansonia digitata* (baobab) trees and stands of *Euphorbia nyikae* also characterize the escarpment.

Misigio Escarpment

The rise of Oldeani and Makarut mountains forms a steep escarpment from the Eyasi Flats at about 1,050 m (3,500 ft) to the Misigio grasslands at about 2,000 m (6,500 ft). The steeply sloping ground is cut by many deep canyons containing dense thickets unlike those found on the ridges and high ground. The soil is usually shallow and often strewn with rocks. Large boulders protrude through the soil on the higher ridge tops.

Vegetation of exposed slopes

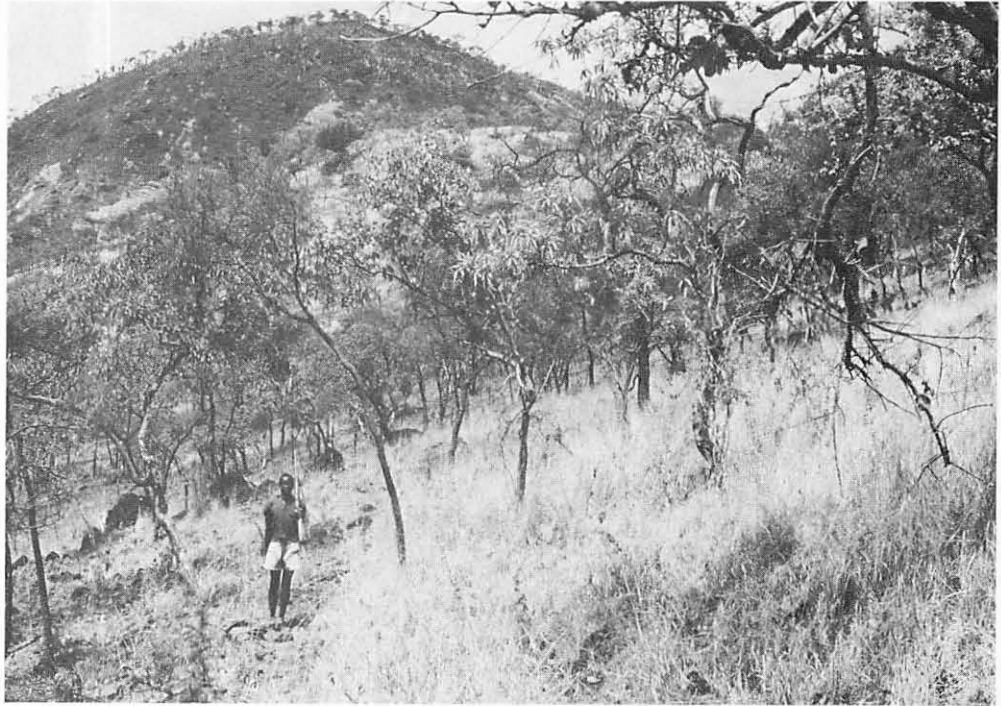
Low woodland, dominated by *Combretum* spp., is common on higher ground above the canyons. Bush is rare. The medium grass layer beneath the canopy is composed of *Themeda triandra* and *Hyparrhenia* spp. The major tree and bush species appear to be distributed along an altitudinal gradient as follows.

1,100–1,150 m (3,600–3,800 ft): *Acacia senegal*, *A. tortilis*, *Commiphora* spp., *Markhamia acuminata*, *Adansonia digitata* and *Terminalia brownii*.

1,150–1,300 m (3,800–4,300 ft): Marked changes in the association. Of the species in the lower zone, only *Commiphora* spp. continue. *Combretum apiculatum*, *Azanza garckeana* and *Sclerocarya birrea* var. *multifoliata* appear as new species.

1,300–1,500 m (4,300–5,000 ft): Only *Combretum apiculatum* continues. *Heeria reticulata*, *Acacia hockii*, *Combretum molle* and *Sterculia stenocarpa* appear as new species.

Above 1,500 m (5,000 ft): The species complement of the previous zone is enriched by *Erythrina abyssinica*, *Dombeya rotundifolia* and *Gardenia lutea*.



Vegetation of canyons

The vegetation of the canyons differs in structure and species composition from that of the exposed slopes. Vegetation associated with moist evergreen forest is commonly found in a narrow ribbon along the edge of stream beds, at the middle and upper elevations of the escarpment. *Calodendrum capense* is a typical tree species. *Euphorbia candelabrum*, *Cussonia* spp. and *Acacia seyal* are common on the steep slopes of the upper canyons. *Albizia petersiana*, *Premna holstii*, *Englerina heckmanniana*, *Tinnea aethiopica* and *Tarenna graveolans* form dense thickets of shrubs and small trees in the drainage lines above the canyons.

Terminalia brownii, *Markhamia acuminata*, *Acalpha fruticosa*, *Grewia* spp. and *Cordia* spp. are common species at lower elevations.

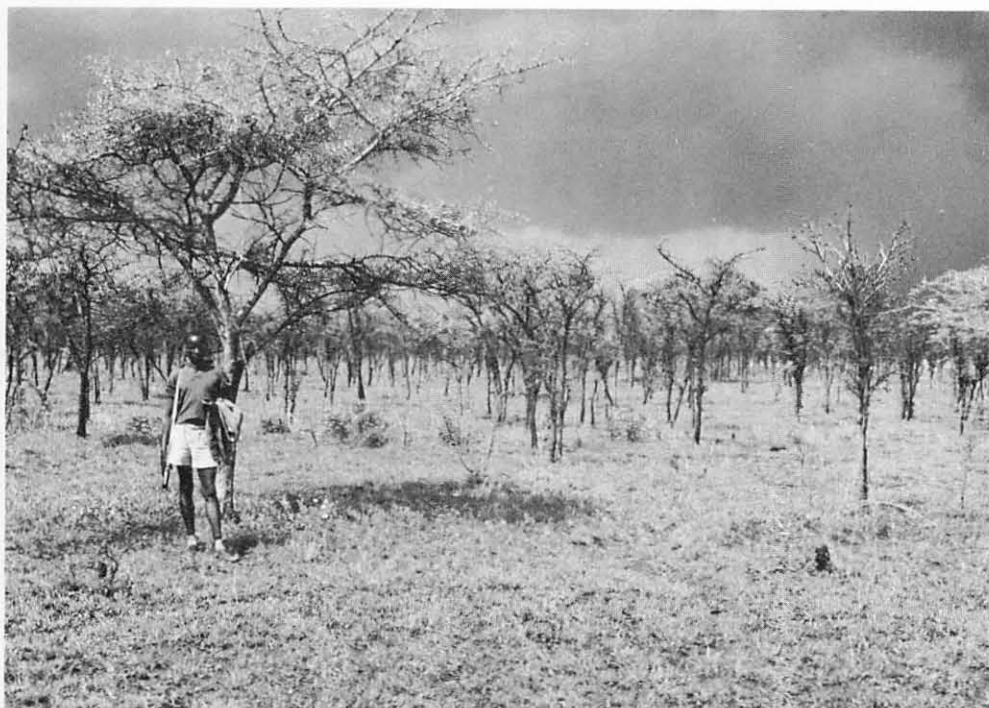
Kakesio-Endulen area

Westward, above the Lake Eyasi Escarpment, there is a gradual upward slope

toward Kakesio. The ground surface is dissected by many small drainage lines. Those lines draining southwest of Kakesio flow directly into Lake Eyasi; the remainder form part of the Engarusi stream drainage.

Low woodland: *Commiphora madagascariensis*-*Acacia drepanolobium*

This type covers most of the area of shallow rocky soils southwest of the Engarusi stream. Shrubs are rare. The understory consists of a mixture of grasses in which *Pennisetum stramineum*, *Cenchrus ciliaris* and *Cynodon dactylon* predominate. Annual grasses are also abundant. *Albizia harveyi* and *Acacia tortilis* trees are scattered throughout. Thickets of bush and woodland species grow on rock outcrops throughout. At higher elevations, granitic inselbergs are surrounded by a variety of tree and bush species not found elsewhere in the area: typically, *Sterculia stenocarpa*, *Sclerocarya birrea* var. *multifoliata*, *Cussonia* spp. and *Crassocephalum mannii*.



Low woodland: *Commiphora madagascariensis*–*Euphorbia metabelensis*–*Acacia senegal*

This type covers the area south and east of the Kakesio–Endulen track. Thickets of *Euphorbia metabelensis* are common in the canyon bottoms. A mixture of the three dominant species, *Acacia mellifera*, *A. drepanolobium* and scattered large *Adansonia digitata* occurs farther to the north-east, above the escarpment.

Near Endulen in the north, such low woodland species as *Combretum molle* and *Acacia hockii* are common. *A. drepanolobium* also grows in extensive stands of pure or mixed composition on gently sloped ridge tops.

The seasonal stream beds support dense *Salvadora persica* and *Maerua trichophylla* bush thickets and *Cordia*, *Grewia*, *Aloe* and *Cissus* shrubs. Tall *Euphorbia candelabrum* trees rise here and there above the shrubs.

Ribbons of *Acacia xanthophloea* high woodland, including *Ficus* spp. and *Vangueria acutiloba*, are found along the banks

and tributaries of an unnamed permanent stream flowing southeast through this area.

The major grasses are medium *Pennisetum stramineum*, *Cenchrus ciliaris* and *Themeda triandra*. The last seems dominant on the high ground in the north.

Low woodland: *Acacia tortilis*–*A. drepanolobium*–*Commiphora madagascariensis*
This heterogeneous type covers the middle to upper reaches of several seasonal streams originating in the Ildoinya and Nasiusu Hills west of Endulen and flowing south over the Lake Eyasi scarp.

The southern portion of this area also contains *Andropogon*–*Pennisetum*–*Chloris* medium grasslands. These are separated from the Serengeti Plains by the Engarusi and Magein streams. A large area of *Commiphora*–*Acacia* low woodland, similar to that near Kakesio, lies to the east. The broad beds of the Engarusi and Magein streams support low woodland of *Acacia tortilis* over a shrub stratum of *Grewia* spp., *Cordia* spp. and *Maerua trichophylla*. *Cyno-*

don dactylon, *Chloris gayana* and *Themeda triandra* predominate in the grass stratum.

Narrow bands of eroded, light-textured soil parallel the stream beds and support little vegetation. *Acacia xanthophloea* high woodland grows in the middle reaches of the Engarusi stream bed. Mono-dominant and mixed stands of *A. drepanolobium* and *A. tortilis* low woodland cover the rest of the headwaters of both streams.

Empakaai Crater

The entire vegetation described below is situated within the rim of Empakaai Crater. A large lake occupies most of the caldera floor, approximately 450–600 m (1,500–2,000 ft) below the rim. The walls are very steep. In the western portion, the land rises gradually from the lake to the foot of the wall. Elsewhere, the wall rises almost from the lakeshore and there are cliffs on the south wall.

Vegetation of the crater walls

Moist evergreen forest, with *Hagenia abyssinica* predominant, occupies the upper western and northwestern portions of the crater wall. Relict stands of *Juniperus procera* grow on the steep rocky cliffs of the south wall. Unidentified dry scrub covers the rest of the wall.

Vegetation of the crater floor

Bush covers most of the crater floor outside the lake. Near base level, *Lantana* and *Lippia* spp. dominate. *Leonotis mollissima* is common. Further up on the lower walls, the cover changes to *Vernonia auriculifera*–*Crotalaria imperialis* bush which shows an affinity to moist evergreen forest. Northwest of the lake, bush surrounds small relict stands of moist evergreen forest.

The extensive areas of bush on the floor and the lower walls and the reduction in forest cover probably resulted from intensive use of the caldera by the Maasai.

Ngorongoro Crater

We made a more intensive survey of the vegetation in Ngorongoro Crater than else-

Ngorongoro Crater viewed from the lower slope toward the western wall. *Acacia xanthophloea* high woodland is in the centre of the photo. Photo by H. J. Dirschl

Cynodon-Digitaria grassland on the central portion of Ngorongoro Crater during the rainy season. Photo by H. J. Dirschl

where in the conservation area because of its ease of access and its high ecological value as permanent habitat for large concentrations of big game.

Ngorongoro Crater is more properly called a caldera. It covers an area of about 300 km² (120 sq. miles), of which 250 km² (97 sq. miles) comprises the floor and 50 km² (20 sq. miles) the steep sloping walls.

The central plain is very flat. Small hills of scoria rise above the floor in the northern and eastern sections, which otherwise slope moderately (5–10°). The crater walls are steep (45–70°), except in the northeast where a gentle 15° slope confuses the division between floor and wall.

Physical environment

Water flows into the crater from the north-east through the Lonyokie and Munge streams, from a series of springs high on the south wall and at the base of the eastern and western walls, and from such seasonal streams with small watersheds as the Lainai Stream in the north. Drainage is internal and terminates in a large soda lake, Lake Makat, and a series of permanent and seasonal swamps which, with the exception of one to the northwest of Kitati Hill, are interconnected and affiliated with the lake.

The level of Lake Makat varies widely from year to year. During its most recent high point, in 1964, the lake covered approximately 18 km² (7 sq. miles). It has also dried up completely during droughts.

Colluvial deposits, derived from basalts, tuffs and scoria, cover most of the southern, eastern and northern portions of the floor. Yellow pumiceous and red-brown earthy tuffs overlie the west-central region. Step erosion is common between the western wall and Lake Makat. Lacustrine deposits surround Lake Makat. A mound field has formed from lahar at the foot of the south-western wall. Streams, bringing silt and clay from the northeast flank of Oldeani Mountain, have built up coalescent fans on the caldera floor (Pickering, 1960; 1961).

The Crater Highlands, of which Ngorongoro Crater is a part, generally have cool



and cloudy weather during the rainy season and part of the dry season. During the long rains, precipitation engulfs the entire crater, and fog and mist frequently lie low around its rims. During the early dry season, mists hang heavily almost daily on the south and east rims of the caldera while the rest of the crater usually lacks cloud cover. During the short rains, small local storms form daily in the north and northeast over Olmoti, Losirua and Lolmalasin mountains, and move southwestward in a regular sequence across the crater. Usually, the precipitation ceases before the clouds reach the crater's southern rim.

Personal observation and sketchy rainfall records indicate that there may be two zones of rainfall on the caldera floor. The central western section, including Lake Makat, probably averages 300–380 mm (12–15 inches) of rain per year, the remainder averages 510–760 mm (20–30 inches) per year. Rainfall at Ngorongoro meteorological station averaged 907 mm (35.73 inches) per year up to 1966 (Dirschl, 1966). The presence of heavy fog on the southern and eastern rims for most of the year undoubtedly adds considerable precipitation through condensation and drip.

Vegetation

Grassland

Grasslands occupy most of the caldera floor. They may be conveniently grouped into short and medium grasslands.

Short grasslands

Short grasslands cover the west-central portion of the crater floor, including most of the land adjacent to Lake Makat.

Odyssea jaegeri and *O. paucinervis* short grassland colonizes the saline-alkaline soils on the intermittently flooded flats around Lake Makat.

Sporobolus-Cynodon short grassland occupies a large portion of the floor northwest of Lake Makat. The major dominants are *Sporobolus marginatus*, *S. spicatus* and *Cynodon dactylon*. *Digitaria scalarum* is locally dominant. *S. spicatus* dominates on the



more saline areas next to the lake, and the herb *Tribulus terrestris* is abundant on the eroded steps.

A small area of short grass also grows on the small rocky mounds on the crater floor, southwest of Lera Forest. *D. scalarum* and *Eustachys paspaloides* are dominant. *Ficus* trees and *Commiphora*, *Ziziphus*, and *Lippia* shrubs are also present on this dry site.

Medium grasslands

Grassland dominated by *Sporobolus* spp. grows around the perimeter of the *Odyssea* short grassland. North from the lake to the Munge Swamp, *Sporobolus marginatus*, *Cynodon dactylon* and *Digitaria milaniana* are dominant. *S. spicatus* predominates to the east and south of the lake, and shares dominance with *S. marginatus* immediately southwest of the lake.

Along the lake edge, low-lying soda pans and finger-like extensions of exposed lake bed are scattered throughout the *Sporobolus* grassland. *S. marginatus*, *C. dactylon* and *D. milaniana* occupy the higher and drier

ground whereas *S. spicatus* and *Odyssea* spp. colonize the exposed mud flats formed by retreating lake waters. Along the southern and eastern edges of Munge Swamp, where the soil is usually moister, *Chloris gayana*, *Pennisetum salifex*, *Panicum repens* and various Cyperaceae are common.

Cynodon-Digitaria grassland occupies about 45 per cent of the crater floor, specifically the central plain. *C. dactylon* and *D. scalarum* are found throughout. *D. milaniana* shares dominance on the central plain. *Chloris gayana* is dominant where the soil is moister.

Pennisetum-Andropogon grassland is found on "black cotton" clay in two neighbouring areas, one within the *Cynodon-Digitaria* type, the other on the southeastern edge. This clay soil is characteristically both poorly drained and high in sodium salts. *P. mezianum* and *Andropogon greenwayi* are the dominant species; *D. scalarum* is also abundant.

Andropogon-Digitaria grassland forms a crescent-shaped band 500–1,500 m wide,



on the moderately sloping northwest, north and northeast boundary of the caldera's central plain. A small area of this grassland type is also found on the outer slopes of Kitati Hill. A number of species predominate locally, but *A. greenwayi* and *D. scalarum* are the leading dominants.

Themeda triandra grassland is most common on the higher, better drained land within the crater, particularly on the lower slopes of the wall northeast of Koitoktok Swamp and the high, exposed western rim near Seneto (Windy Gap). *T. triandra* and its usual codominants, *P. stramineum* and *A. greenwayi* are the most common grassland species beneath the sparse cover of bush or woodland.

Herbaceous swamp

Wet meadows dominated by *Panicum repens* occupy three areas of the crater floor. They adjoin permanent swamps, dominated by emergent aquatic plants, and receive their overflow during the rainy season. *Sporobolus spicatus* and *Cyperus laevigatus* are abun-

dant along the edges of the wet meadows, whose physiognomy resembles that of medium grassland.

Two large areas of reed swamp exist on the caldera floor. Koitoktok Swamp is in the southeastern part of the caldera, where the dominant species is *Cyperus immensus*. The swamp receives fresh water from perennial springs along its eastern edge. Emergent stands of *Diplachne fusca* in the water and of *S. spicatus*, *S. homblei* and *S. consimilis* on the adjacent dry land indicate that the southern and western portion of the swamp are alkaline-saline.

Other Cyperaceae are common. The herb *Aeschynomene schimperi* occurs sparsely. *Phragmites mauritianus* covers a large area on the southern side of the swamp, *Cyperus papyrus* an adjacent, smaller site.

Munge Swamp is in the northern part of the crater. This swamp receives its water from the Munge Stream, which originates in Olmoti Crater, and is apparently alkaline-saline. The dominant *A. schimperi* forms a dense thicket throughout. *Leersia hexandra*,

P. repens and *D. fusca* are also found in standing water. *S. spicatus* and *C. laevigatus* predominate on the drier parts along the edges of the swamp. In 1965, an accidental fire removed about 40 cm (16 inches) of accumulated, undecomposed organic matter and enhanced the dominance of *Aeschynomene*.

There is also a small area of reed swamp at Seneto Springs in the western part of the crater. Common emergents are *Typha latifolia*, *Cyperus* spp. and *Scirpus* spp. *P. repens* and *D. fusca* predominate along the edges.

Woodland

A broad band of *Acacia lahai* high woodland occurs on the northeastern and northern walls of Ngorongoro Crater and extends for a short distance onto the caldera floor. *A. abyssinica* is occasionally found in association with *A. lahai*. The understory usually consists of *Lippia-Lantana-Solanum* over a *Cynodon dactylon* grass layer.

A. lahai high woodland has degenerated into bush and grass communities in several locations on the northern wall and the crater floor, apparently because many large trees died from old age, fire and elephant damage, and from subsequent suppression of *A. lahai* regeneration by annual grass fires.

Two high woodland communities, dominated by *A. xanthophloea*, exist in Ngorongoro Crater: Koitoktok in the east and Leraï in the south. This vegetation type is commonly referred to as "groundwater forest" because its existence depends on a high water table. Perennial springs provide water for both Koitoktok and Leraï Forests. Those supplying Leraï Forest are high on the crater's southern rim. A portion of this forest was destroyed by high water levels of Lake Makat during the period 1963-66.

A. xanthophloea forms a fairly dense canopy, about 16 m (50 ft) high. *A. albida* is found occasionally throughout the woodland. *Rauwolfia caffra* trees and *Cyperus immensus* reeds grow in the wetter locations. Where large trees in the overstory have

Scattered *Euphorbia nyikae* trees on the arid western wall of Ngorongoro Crater near the Seneto descent road. Photo by H. J. Dirschl



died, permitting more light to reach the forest floor, a thick bush of *Pluchea ovalis*, *Achyranthes aspera*, *Abutilon longicuspe* and *Justicia bentonica* grows. There is little apparent regeneration of *A. xanthophloea*, and most of the few seedlings which reach pole size are pushed over by elephants.

Low woodland exists on drier sites in the crater in three small areas, each different in composition of tree species. *Erythrina abyssinica* low woodland is located on the eastern part of the crater floor. It grows over *Themeda triandra* grassland and its regeneration is limited by grass fires. *A. hockii*-*Commiphora* low woodland occupies two small contiguous promontories on the southern and northern crater walls. It grows over *Lippia* bush and *Themeda* grassland.

Moist evergreen forest

Moist evergreen forest covers the eastern wall of Ngorongoro Crater and is also found in canyons on the southern wall and in the Munge and Lonyokie canyons on the northeastern wall. On the eastern and southeastern walls, recurring grass fires have swept up from the caldera floor so the lower limit of the forest is higher up the wall and, in some places, almost at the top of the rim.

Bush communities

Bush covers an extensive area within the caldera. A variety of species occurs in diverse combinations and densities with grassland, woodland and forest. We have mapped 13 types of bush within the caldera, but for convenience we shall discuss them in three broad categories, based on differences in species composition and site conditions.

Bush communities typified by *Crotalaria imperialis* and *Vernonia auriculifera* are closely associated with moist evergreen forest on the upper caldera walls, and probably form a seral stage in secondary forest succession.

Bush, dominated by *Lippia*, *Lantana* and *Aspilia* species, completely rings the

outer edge of the caldera floor. This type is restricted to the crater walls, except in the east and north where it also occupies part of the adjacent crater floor. These shrubs are also principal understory components of the *Acacia lahai* high woodland on the northern and northeastern walls. *Cynodon dactylon* and *Themeda triandra* are the principal grass species associated with this bush type. *Solanum incanum*, another common shrub, often occurs with *Lippia-Lantana* and is also found on the central plain.

Aspilia mossambicensis is the most common bush on the drier west and southwestern walls. It grows with *Lippia* bush and *Pennisetum stramineum* and *T. triandra* grassland beneath an open low woodland of *Euphorbia nyikae*, *Cussonia* spp. and *Acacia hockii*.

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Appendix

List of common species encountered during the survey

Trees

Acacia abyssinica Hochst. and Benth.
A. albidia Del.
A. drepanolobium Harms ex Sjöstedt
A. gerrardii Benth.
A. hockii De Wild.
A. kirkii Oliv.
A. lahai Steud and Hochst. ex Benth.
A. mellifera (Vahl) Benth. subsp. *mellifera*
A. nilotica (L.) Del.
A. nubica Benth.
A. senegal (L.) Willd.
A. seyal Del.
A. tortilis (Forsk.) Hayne
A. xanthophloea Benth.
Adansonia digitata L.
Albizia gummifera (J. F. Gmel.) C. A. Sm.
A. harveyi Fourn.
A. petersiana (Bolle) Oliv.
Azanza garrckeana (F. Hoffm.) Exell and Hillcoat
Balanites aegyptica (L.) Del.
Bersama abyssinica Fresen.
Calodendrum capense (L. f.) Thunb.
Cassipourea malosana (Baker) Alston
Combretum molle R. Br. ex G. Don
Commiphora madagascariensis Haecq.
C. merkeri Engl.
Croton macrostachyus Hochst. ex Del.
Cussonia holstii Harms ex Engl.
C. spicata Thunb.
Dombeya rotundifolia (Hochst.) Planch.
Ekebergia rueppeliana (Fresen.) A. Rich.
Erica arborea L.
Erythrina abyssinica Lam. ex DC.
Euclea divinorum Hiern subsp. *keniensis* de Wit.
Euphorbia candelabrum (Trem. et Kotschy)
E. metabelensis Pax.
E. nyikae Pax.
Ficus spp.
Gardenia lutea Fres.
Hagenia abyssinica (Bruce) J. F. Gmel.
Heeria reticulata (Bak. f.) Engl.
Hyphaene ventricosa Kirk
Juniperus procera Hochst. ex Endl.
Lasiosiphon glaucus Fresen.
Markhamia acuminata K. Schum.
Nuxia congesta R. Br. ex Fresen.
Olea africana Mill.
O. hochstetteri Baker
O. welwitschii (Knohl.) Gilg and Schellenb.
Protea spp.
Rauvolfia caffra Sond.

Sclerocarya birrea var. *multifoliata* Engl.
Sterculia stenocarpa H. Winkler
Teclea nobilis Del.
Terminalia brownii Fresen.
Vangueria acutiloba Robyns
Ziziphus spp.

Shrubs and herbs

Abutilon longicuspe Hochst.
Acalpha fruticosa (L.) Del.
Achyranthes aspera L.
Aeschynomene schimperii Bak.
Aloe spp.
Anthrospermum usambarense K. Schum.
Artemisia afra Willd.
Asparagus spp.
Aspilia mossambicensis (Oliv.) Wild
Barleria eranthemoides R. Br. ex C. B. Cl.
Cadaba farinosa Forsk.
Capparis elaeagnoides Gilg
Cissus cactiformis Gilg
C. quadrangularis L.
Cutia abyssinica Jaub. and Spach.
Combretum apiculatum Sond.
Cordia ovalis R. Br.
C. rothii Roem. and Schultes
Crassocephalum mannii (Hook. f.) Milne-Redhead
Crotalaria imperialis Taub.
Croton dichogamus Pax.
Englerina heckmanniana (Engl.) Balle
Euphorbia tirucalli L.
E. schimperii Presl.
Grewia spp.
Helichrysum splendidum (Thunb.) Less.
Heliotropium eduardii Martelli
H. steudneri Nathe
Heteromorpha trifoliata (Wendl.) Eckl. and Zeyh.
Hypoestes forskalii (Vahl) R. Br.
H. verticillaris (L. f.) R. Br.
Indigofera basiflora Gillett
Justicia bentonica L.
J. elliotii S. Moore
Kalenchoe spp.
Lantana trifolia L.
L. viburnoides (Forsk.) Vahl
L. triphylla L.
Leersia hexandra Sw.
Leonotis mollissima Gürke
Lippia javanica (Burn. f.) Spring
L. ukambensis Vatke
Lycium spp.
Maerua trichophylla Gilg
Pavonia irakuensis Ulbr.
P. patens (Andr.) Chiov.
Pluchea ovalis DC.
Premna holstii Gürke
Salvadora persica L.
Sansevieria ehrenbergiana Schweinf.
Solanum incanum L.
Stigmatorhynchus umbelliferus (K. Schum.) Schltr.
Stoebe kilimandscharica O. Hoffm.

Tarenna graveolans (S. Moore) Brem.
Tinneo aethiopica Kotschy and Peyr.
Tribulus terrestris L.
Trifolium spp.
Vernonia auriculifera Hiern

Grasses and sedges

Andropogon greenwayi Napper
Aristida adscensionis L.
Cenchrus ciliaris L.
Chenopodium spp.
Chloris gayana Kunth
C. pycnothrix Trin.
Cymbopogon spp.
Cynodon dactylon (L.) Pers.
C. plectostachyus (K. Schum.) Pilg.
Cyperus immensus C. B. Cl.
C. laevigatus (L.) C. B. Cl.
C. papyrus (L.)
Dactyloctenium aegypticum (L.) Beauv.
Digitaria macroblephara (Hack.) Stapf.
D. milaniana (Rendle) Stapf.
D. scalarum (Schweinf.) Chiov.
Diplachne fusca (L.) Beauv.
Eleusine jaegeri Pilg.
Enneapogon elegans (Nees) Stapf.
Eragrostis tenuifolia (A. Rich.) Steud
Eustachys paspaloides (Vahl) Lanza and Mattei
Harpachne schimperii (A. Rich.)
Heteropogon contortus
Hyparrhenia spp.
Kyllinga spp.
Odyssea jaegeri (Pilg.) Robyns and Tournay
O. paucinervis Stapf.
Panicum repens L.
Pennisetum clandestinum Chiov.
P. mezianum Leeke
P. salifex Stapf. and C. E. Hubb.
P. schimperii A. Rich
P. stramineum Peter
Phragmites mauritanus Kunth
Scirpus spp.
Seteria sphacelata Stapf. and C. E. Hubb.
Sporobolus consimilis Fres. (= *S. robustus* Kunth)
S. fimbriatus
S. homblei De Wild.
S. marginatus A. Rich.
S. spicatus (Vahl) Kunth
Themeda triandra Forsk.
Typha latifolia L.

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