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Authors: Wesche, Karsten, Miehe, Georg, and Kaeppeli, Meinhard

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Karsten Wesche, Georg Miehe and Meinhard Kaeppli

The Significance of Fire for Afroalpine Ericaceous Vegetation



This paper presents results from studies in 4 mountain regions in East Africa, 2 in Ethiopia (Simen Mountains, Bale Mountains), and 2 in Uganda (Rwenzori Mountains, Mount Elgon). The focus is on the ericaceous vegetation that

forms the (upper) treeline ecotone at all sites. There is little evidence for climatic control of the patchy appearance of this belt in all afroalpine environments. Since traces of former fires were observed in all ranges, repeated burning is most probably responsible for the present appearance of the ericaceous vegetation in East Africa. The fires observed were almost exclusively lit by local people, who utilize the afroalpine zone for poaching, livestock grazing, and honey hunting. Although these fires are man-made and not strictly natural, they help to maintain a structural and biologically diverse environment.

Keywords: Erica; fire ecology; tropical timberline; afroalpine environments; human impact; Uganda; Ethiopia.

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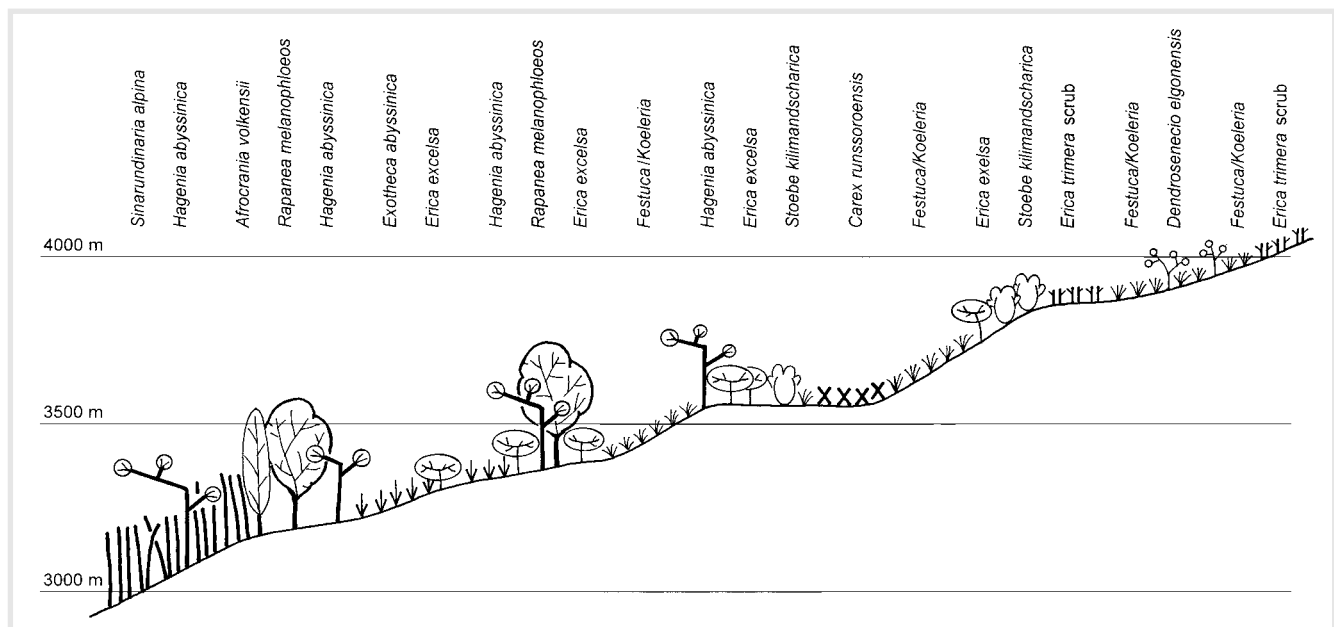
Introduction

Species of the family Ericaceae are common constituents of tropico-alpine vegetation world wide (Janzen 1973; van Royen 1980; Luteyn 1999). Members of the heather family attain dominance in high-altitude woodland and scrub in tropical Africa, and Hedberg has described the “ericaceous belt” as a characteristic feature of all mountains in the region (Hedberg 1951). The ericaceous belt forms the upper treeline ecotone and mediates between upper montane forest (usually dominated by *Hagenia abyssinica* and *Hypericum revolutum*) and lower afroalpine scrub (*Alchemilla* and *Helichrysum* spp). Ericaceous vegetation in tropical Africa consists mainly of species of the genus *Erica* itself, but several other microphyllous species are locally important as well.

The ericaceous belt consists of a wide variety of physiognomically different formations (Figure 1). Although the species concerned are usually similar, ericaceous vegetation may grow as a dense forest of single-stemmed trees, almost impenetrable bushland with multitemmed plants, or open high scrub merely 1 m tall. Ericaceous plants show an overall inverse relationship between height and altitude, but this general pattern exhibits considerable modifications. Remnant groves of *Erica* trees might occur high above the present timberline in afroalpine grassland (Figure 2), indicating other than a purely altitudinal control of plant growth.

While traditional phytogeography favored climatological control of the typical features of the tropical timberline (eg, Troll 1959, 1973), recent discussions have focused on the importance of fires for ericaceous

FIGURE 1 Simplified vegetation profile of the treeline ecotone in the tropical African mountains. Broad-leaved montane forest merges gradually into *Hagenia* forest. Tree heather becomes common in these forests above 3200 m, but pure stands are usually rare. Instead, remnant groves of *Erica* forest are found scattered throughout the afroalpine grassland.



vegetation in East Africa and tropical timberlines elsewhere (eg, Smith 1977; Laegaard 1992; Kessler 1995; Miehe and Miehe 1994a; Luteyn 1999). The present article will synthesize information currently available for parts of northeastern Africa.

Study areas

Observations are presented from 4 tropical mountains in East Africa, where the authors conducted studies in recent years.

The Simen Mountains are situated in northern Ethiopia (13°N, 38°E), and the Bale Mountains in the southeastern part of the country (ca. 6°45'N, 39°45'E). The equatorial zone of East Africa is represented by Mount Elgon at the border of Uganda and Kenya (1°N, 34°30'E) and by the Ugandan part of the Rwenzori Mountain Range (0°10'N, 30°E). While the latter is a Precambrian block that was lifted to its present elevation in the late Tertiary, the other ranges are a result of Tertiary volcanism. The mineralogical composition of the parent material differs among the mountains, but high-altitude soils show considerable similarities. The soils of the ericaceous and the lower afroalpine belts are rich in organic matter and are relatively acidic. Common soil types are Andosols, Gleysols, and Histosols, with well-developed profiles (Hurni 1978; Miehe and Miehe 1994b; Osmaston 1996; Wesche 2000). All ranges reach well above the present timberline at 3200–3500 m, so that the gradual transition of ericaceous vegetation to afroalpine grassland could be studied.

Impact of fires on the ericaceous belt

Evidence for fires comes from all afroalpine environments in the region. Postfire successions and charred

FIGURE 3 Comparison of high-altitude climatological conditions at the four study sites. All data are presented as the familiar Walter diagrams (Walter and Lieth 1960–1967). The data were compiled from various sources (Osmaston and Pasteur 1972; Hurni 1982; Hillman 1986; Wesche 2000). No long-term measurements of air temperature are available for the Rwenzori Range.

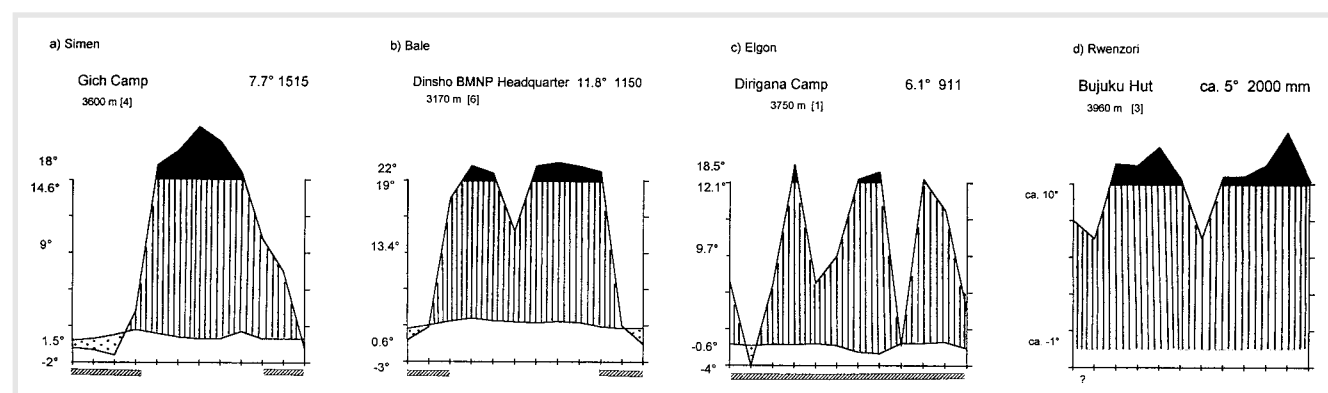


FIGURE 2 The upper timberline on the southern declivity of Mount Elgon at 3300 m. Remnant groves of *Erica excelsa* and occasionally *Hagenia abyssinica* grow in a matrix of lower afroalpine grassland with *Exothea abyssinica*. (Photo by K. Wesche, September 1997)



plants were observed in Simen (Kaeppli 1998; Niev-ergelt et al 1998), and recurrent fires are held responsible for the physiognomy of the ericaceous belt in the Bale Mountains (Miehe and Miehe 1993, 1994b). Devastating fires were directly observed on Mount Elgon, where more than half of the ericaceous and afroalpine vegetation burned in 1997 and again in 1999 (Wesche 2000). Even in the humid Rwenzori Mountains, Miehe and Miehe observed charred trunks of *Erica trimera* at several locations in the ericaceous belt in 1997.

The 4 study areas have a generally moist climate (Figure 3). Annual precipitation generally exceeds 1000 mm, with distinct seasonal distribution. The Simen Mountains, as the northernmost site, display a unimodal precipitation regime with a marked dry season from December to March (Hurni 1982). The other ranges have a weakly bimodal precipitation pattern. The main dry season is usually concentrated from December to February, with a weakly pronounced second dry season.

As fires require relatively dry combustible matter, they occur during dry season conditions only. If the dry



FIGURE 4 The uppermost stands of *Erica arborea* in the Simen Mountains at Nebir Mekemacha at an altitude of ca 4000 m. (Photo by B. Nievergelt, 1967)



FIGURE 5 View of the location pictured in Figure 4, taken 30 years later. The dense ericaceous vegetation has moved up approximately 120 m. (Photo by M. Kaeppli, April 1997)

season is short in a given year, high-altitude soils can retain sufficient moisture to prevent burning. Thus, the severity of the dry season is crucial for the occurrence of high-altitude fires. On Mount Elgon, devastating fires in 1997 followed 8 entirely dry weeks in 1997 and 7 dry weeks in 1999. Under such conditions, ericaceous and afroalpine vegetation started to wilt and even *Erica trimera* plants in bogs showed clear signs of desiccation.

Partly dried plant matter burned rapidly in high-intensity fires under such conditions on Mount Elgon. While the climatic records suggest the regular occurrence of similar climatic conditions in the Ethiopian mountains (Figure 3), severe droughts are probably rare in the Rwenzori Mountains. This points up the importance of interannual variation in the East African climate. The region is notorious for major changes in conditions from year to year (Griffiths 1972; Nieuwohlt 1978). The dry season in 1997 was extremely pronounced, and long-term records from the footzone of Mount Elgon suggest intervals of 2–8 years for such droughts. Thus, at least for Mount Elgon, severe fires might be expected with a similar frequency; fire-induced changes in the ericaceous vegetation are a consequence.

Dynamics of ericaceous vegetation at the study sites

Simen Mountains

The Simen Mountains differ from the remaining study sites due to their northernmost position and unimodal precipitation regime. *Erica arborea*, the local *Erica* species, occurs all over Eastern Africa and the Mediterranean. It is the dominant woody species between 2900 and 3900 m in the Simen Mountains, occurring in any form from single-stemmed trees to low multistemmed dwarf shrub. The range's *Erica* forests show an uplift of up to 120 m and a thickening of the forests toward the upper timberline within the last 30 years (Figures 4, 5; Nievergelt et al 1998).

More favorable climatic conditions or reduced human and animal pressure could have induced these changes in forest distribution. In order to test the climatic hypothesis, long-term records of rainfall and temperature would be necessary to correlate rainfall, temperature, and growth increment, but unfortunately, only short-term records are presently available. For this reason, a dendroclimatological approach was recently tested in the Simen Mountains, but it yielded no meaningful results (Kaeppli 1998). The application of dendroclimatology was aggravated by the following circumstances: the lack of old *Erica arborea* trees (no extensive climatic records), eccentric growth of most individuals (many wedging rings), human impact (suppression or overlap of climatic signals in the wood), and occasionally more than one dry or rainy season (intraannual fluctuations in the wood structure). For these reasons, dendroclimatology with *Erica arborea* in the region is not very promising.

There is evidence for recent climatic change in afroalpine environments from studies on glacial retreats (reviewed in Hastenrath et al 1997). However, given that neither climatological nor dendroecological information is available for the Simen Mountains, we

cannot evaluate the influence of climatic change on the upper limit of *Erica arborea*. Rising temperatures might have facilitated the obvious extension of ericaceous vegetation in the Simen Mountains since 1968 (Figure 4). This explanation is problematic since, even in 1968, single individuals of *Erica arborea* were found high above the timberline. It is not yet clear whether low temperatures at the timberline generally prevent stands from closing or if the treeline and the forest line are essentially the same (Körner 1998). Since management of the Simen Mountains National Park has become more effective in recent decades as well, reduced human impact caused by cattle grazing, wood cutting, or burning is another possible explanation for apparent change. Although Nievergelt et al (1998) observed increased regrowth and forest extension of *Erica arborea* after a widespread fire in the Simen Mountains, ericaceous vegetation normally benefits from reduced human impact (Kaeppli 1998). This question can only be resolved by permanent monitoring.

Bale Mountains

Miehe and Miehe studied the ericaceous vegetation of the Bale Mountains in some detail. They adopted a primarily phytosociological approach that was supplemented by short-term climatological measurements (1994b). The local taxa of *Erica trimera* show a gradual transition from single-stemmed trees to multistemmed shrubs over an altitudinal range between 3100 and 4200 m. Striking features of the vegetation pattern in the Bale Mountains include sharp borders between ericaceous forests and afroalpine dwarf-shrubland with *Helichrysum splendens*, remnant groves high above the closed forest line, and spherical *Erica trimera* plants with well-developed lignotubers (Figure 6). Short-term measurements suggested no climatological background for these features (Table 1). Soil temperatures were not lower above the upper limit of the ericaceous belt but higher as a result of more insolation in the open vegetation. Although soil temperatures of 5–7°C are usually considered critical for (tropical) timberline formation (Walter and Medina 1969; Winiger 1986; Körner 1998), this threshold appeared to be unimportant in the Bale Mountains. Afroalpine grasslands with no ericaceous vegetation nearby still showed subsoil temperatures of up to 9°C (Table 1).

Traces of former fires were common everywhere in the ericaceous belt. Trunks of *Erica trimera* plants were regularly charred and lignotubers must also be regarded as a result of recurrent injury. At some sites, the tree trunks were apparently killed by a severe fire and plants regenerated through suckers from the base of the plant. Even where groves survived, a patchy and heterogeneous vegetation structure hints at regular disturbances. The evidence from the Bale Mountains clearly



FIGURE 6 Lignotuber of repeatedly burned *Erica trimera* plant on Mount Elgon. The suckers are approximately 3–5 years old. (Photo by G. Miehe, February 1997)

revealed that the present physiognomy of ericaceous vegetation is a result of repeated burning. Fires altered the structure of the present stands of ericaceous vegetation, but more important, they triggered a large-scale replacement of *Erica trimera*-dominated communities by afroalpine grasslands and *Helichrysum* scrub (Miehe and

TABLE 1 Subsoil temperatures (–50 cm) near the upper limit of ericaceous vegetation in the Bale Mountains in 1989/1990. Temperatures ranged widely but were generally lower under ericaceous vegetation. Measurements of air temperature near the surface (+20 cm) did not reveal more beneficial temperatures in wooded vegetation (Miehe and Miehe 1994b).

Altitude (m)	Temperature (°C)	Season	Vegetation
3990	3.3	Rainy season	<i>Erica</i> scrub
3990	3.3	Rainy season	<i>Erica</i> scrub
4030	4.6	Dry season	<i>Erica</i> scrub
4030	4.0	Dry season	<i>Erica</i> scrub
4030	4.1	Rainy season	<i>Erica</i> scrub
4030	4.4	Rainy season	<i>Erica</i> scrub
4040	7.1	Dry season	<i>Erica</i> nearby
4030	9.0	Dry season	<i>Erica</i> nearby
4100	5.1	Rainy season	No <i>Erica</i> nearby
4120	6.0	Rainy season	No <i>Erica</i> nearby
4100	6.9	Dry season	No <i>Erica</i> nearby
4030	7.7	Rainy season	No <i>Erica</i> nearby

FIGURE 7 Young suckers of a 4-m high *Erica excelsa* tree on Mount Elgon 2 years after fire consumed all the foliage. The trunk is still mostly bereft of foliage and the *Erica* forest has recovered little of the structure it had prior to burning. (Photo by K. Wesche, March 1999)



Miede 1994b). Thus, the present timberline was lowered by several hundred meters due to the impact of fire in the Bale Mountains.

Mount Elgon

One of the authors had the opportunity to study fire successions in the lower afroalpine zone and the ericaceous belt of Mount Elgon (Wesche 2000; Wesche et al 1999). Dry season conditions at the time of the study were particularly pronounced. Eight weeks were completely dry from February 1997 and again from December 1999 onward. Long-term records from the footzone of Mount Elgon revealed that months with less than 10 mm total precipitation are unusual and occur only every 4–8 years (Tororo 1960–1999, MNR 1999). Extremely dry conditions in 1997 made burning experiments at 3600 m on Mount Elgon possible; later about two thirds of the afroalpine zone of the mountain were completely burned by poachers. Results of the experimental studies

TABLE 2 Microclimatic conditions near the surface (+20 cm) in the afroalpine belt of Mount Elgon. One year’s temperature records (1997) are compared for an open space in otherwise dense ericaceous scrub on a valley floor and for grassland on the adjacent slope (Wesche 2000). More extreme temperatures on the valley floor are a consequence of cold air ponding. Subsoil temperatures (–100 cm) were measured at the same sites.

	Altitude (m)	
	3670 m	3630 m
Annual mean	6.9°C	7.2°C
Variation of monthly means	2.2 K	2.6 K
Absolute minimum	–4.4°C	–5.7°C
No. of days with frost	135	202
Mean annual soil temperature	8.3°C	8.2°C

were confirmed by observations in these areas. A continuous stay of 14 months and a second visit 25 months after the fires allowed an assessment of secondary successions following the fires. Both individuals and plant communities on entire plots were monitored for this period.

The local heather species *Erica arborea*, *E. trimera*, and the tree heather *E. excelsa* burned fiercely when lit. As the plants contain high amounts of volatile oils, they literally exploded in high-intensity fires. Although combustion was complete for all twigs and leaves, plants usually survived the burning and produced new suckers within half a year’s time. The annual growth of the suckers was always well below 20 cm a year. Even tall *Erica excelsa* trunks were not capable of quicker recovery and were still largely denuded 2 years after the fire (Figure 7). The typical structure of a closed canopy forest had by no means recovered within the duration of the study period. Similarly, slow growth rates were observed for the accompanying ericaceous species (*Stoebe kili-mandscharica*, *Anthospermum usambarense*).

In sharp contrast to the ericaceous vegetation, afroalpine grasslands recovered almost completely within 9 months after burning, and 2 years after burning no traces hinted at a previous fire. Fires triggered change neither in the species composition of the burned tussock grasslands nor in the relative cover of the species concerned.

Given that charred trunks of *Erica* spp and *Dendrosenecio elgonensis* were common everywhere in the afroalpine zone of Mount Elgon and that grasslands recover faster than woody vegetation, the present physiognomy of the high-altitude vegetation must be considered as a fire pattern. Woody vegetation was largely replaced by grassland; tall ericaceous vegetation survived in remnant groves and only occasionally in deep valleys, around rocky outcrops, or on boulder streams (Figure 2). Again, temperature differences between sites were not responsible for this pattern. Temperatures in an ericaceous scrub on a valley bottom were more extreme than on the neighboring grassy slopes, where no *Erica trimera* grew (Table 2).

Rwenzori Range

Since working conditions are adverse in the area (wetness, political instability), only casual observations are available. When camping in the upper afroalpine zone in 1934, Syngé and his party accidentally lit a grassland fire (Syngé 1985). Langdale-Brown et al (1964) reported that ericaceous vegetation “will burn fiercely in dry weather, even on the Rwenzori in exceptional dry seasons.” Such an unusual dry season was experienced by Miede and Miede in February 1997, when no rain fell for at least 3 weeks. The mountain range was closed due to rebel activities shortly afterward, so neither the extent nor the occurrence of potential fires is known.

The authors observed no fires personally but were able to take phytosociological samples of the ericaceous vegetation on the Ugandan side of the range.

There is no doubt that the Rwenzori Mountains support the most intact ericaceous belt of all the mountain regions considered. Extended *Erica* forests are still found, and the epiphytic vegetation indicates that conditions are predominantly moist. Nevertheless, several sample plots of ericaceous vegetation showed a patchy vegetation structure, and bracken (*Pteridium aquilinum*), as a typical postfire successional species, covered large areas in the montane belt. Moreover, heather trees commonly had charred trunks, evidence that fires had definitely occurred recently. Although fires undoubtedly occur in the Rwenzori, they are small in scope by comparison with the vast and largely undisturbed remaining stand of *Erica* forest.

Other mountains in the region

The examples given so far are representative of the whole “afromontane archipelago” (White 1983). Fires are described for virtually all higher mountains in the region. The most important examples are the Aberdare Mountains (Bader 1976; Schmitt 1991) and Mount Kilimanjaro (Beck et al 1986). The latter area also experienced a severe dry season in 1997, resulting in the burning of large parts of the ericaceous forests (A. Hemp, personal communication). Any traveler can easily see traces of recent fires on Mount Kenya, where they are a part of land management. Although the smaller mountains have been scientifically neglected in recent decades, descriptions of fires are nonetheless available (eg, Thomas 1943; Snowden 1953; Jackson 1956; Maberley 1975).

The human dimension

We have discussed the climatic preconditions for high-altitude fires but not sources of ignition. Usually natural causes such as lightning or rockfalls (Killick 1979) are cited, although the predominance of man-made fires is widely acknowledged (Hedberg 1964; Beck et al 1986). We cannot rule out fires ignited by natural agents, but we know of no empirical evidence for this. None of the authors has ever observed a naturally ignited fire in an afroalpine environment; on Mount Elgon, virtually all fires were ignited by poachers. There is a strange imbalance between the general importance of fires in East African mountains and the complete lack of reports on naturally ignited fires. The same holds true for the Páramos, where apparently no reports of natural fires have been published so far (Luteyn 1999). We know of only one unpublished report of lightning causing fires in *Polylepis* woodland in Bolivia (Bode 1998). Thus, we hypothesize that the

overwhelming majority of fires in tropical mountains are man-made, with natural causes contributing at most a minor fraction.

The reasons for igniting a fire are manifold. In the Bale Mountains, cattle are kept even in the afroalpine zone. Since fires promote grasses and clear away the hiding places of hyenas, burning is an easy tool for improving grazing conditions. Cattle were grazed in the afroalpine zone on Mount Elgon up to the 1980s, so the situation was probably similar. Cattle grazing is unimportant today, but poaching has become a common source of income. Dense scrub and even high mature tussock grassland severely hamper hunting, so fires are an option. Moreover, bee hunters and forest-dwelling farmers make frequent use of fire that can easily spread from the montane forest into the ericaceous belt.

The central parts of the Rwenzori Mountains are so remote that even locals do not travel there. But traces of fires were found even in this remote and perhumid mountain region. Some settlements were established here during the Ugandan Civil War in the 1970s and 1980s, but these were restricted to the montane forest. When political conditions stabilized, they were largely abandoned, and only the lower montane zone is presently utilized.

The Simen Mountains outside the National Park are a densely populated area where fire might play an important role. However, the more important impacts on the *Erica* forests are the result of gradual forest degradation caused mainly by local farmers who use the area as a source of fuelwood and timber. Grazing of cattle is common in the afroalpine zone and in the ericaceous belt, whereas forest clearance for agriculture is the most important human impact on upper montane *Erica* forest in Simen. Although the Simen National Park was designated in 1969, buffer zones were not implemented until 1983.

Management considerations

All 4 study areas are currently national parks, so there is at least a theoretical possibility to control fires. It is doubtful, however, whether this would be sensible. Since fires are apparently rare in the Rwenzori, fire management is not an issue there. The situation is very different in the Bale Mountains and on Mount Elgon, where burning is definitely a major factor. If we accept that fires are almost exclusively man-made, the afroalpine and ericaceous belts in these ranges are by no means in a truly “natural” state. As a consequence, traditional nature conservation policy would suggest the use of law enforcement to patrol fires. While it is doubtful that park management authorities have the necessary capabilities, it is also possible to make several theoretical arguments against a zero-burning manage-

ment scheme. Observations of postfire successions on Mount Elgon revealed that biodiversity is generally maintained except when fires are extremely hot and when they do not occur every few years. Parts of the ericaceous belt of Mount Elgon have been burned at least since the middle of the last century (Dale 1940), but so far, no extinction of the vascular plant flora has been observed. One of the authors had no difficulty collecting specimens of all known afroalpine endemics on Mount Elgon. But fires may still cause severe soil erosion problems on steep slopes. This is a general land use problem, however, and of relatively minor importance in the gently sloping afroalpine zone of Mount Elgon and the Aberdare Mountains.

Without fires, ericaceous vegetation would undoubtedly replace large areas of today's afroalpine grasslands. Vast areas of impenetrable ericaceous forest and scrub are undesirable in terms of biodiversity and in relation to tourism in afroalpine environments. Moreover, if a zero-burning management scheme is adopted, biomass would accumulate with a danger of increasingly severe fires. As soon as fuel is abundantly available, even a single poacher can destroy large areas with one match. Such fires would not only be extensive but also relatively hot. Very hot fires on Mount Elgon even killed tussock grasses and apparently sterilized the

topsoil. Regeneration on such plots was extremely slow since few plants survived and almost no seedlings emerged. Even 2 years after a fire, vegetation was very scattered and the species set impoverished. Thus, occasional but controlled fires might be the better management option.

Even in a landscape free of humans, the ericaceous belt would not have a homogenous structure. Edaphical and topographical conditions (eg, waterlogging) introduce some variation. More important, herbivores would be much more common in a natural landscape and also hamper the growth of woody plants. Buffalo herds are common on the well-protected eastern side of Mount Elgon, and damaged shrubs and giant groundels (*Dendrosenecio elgonensis*) were seen as high as 3800 m. This correlates with observations on Mount Kenya (Mulkey et al 1984).

We conclude that the present-day appearance of the ericaceous belt is largely a result of man-made fires. Nonetheless, the "natural" afroalpine vegetation will be patchy as well, given that edaphic conditions and notably large herbivores introduce some heterogeneity. As large herbivores will remain rare in the region's mountains in the near future, a prescribed burning scheme can be regarded as a sensible measure for conservation of nature.

AUTHORS

Karsten Wesche

Institute of Geobotany and Botanical Garden, Martin Luther University, D 06108 Halle (Saale), Germany.
wesche@botanik.uni-halle.de

Georg Miehe

Faculty of Geography, Philipps University, D-35032 Marburg, Germany.
miehe@mail.uni-marburg.de

Meinhard Kaeppli

Muottastrasse 7, CH-6440 Brunnen, Switzerland.
meinhard.kaeppli@freesurf.ch

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REFERENCES

- Bader FJW.** 1976. *Vegetationsgeographie-Ostafrika*, Afrika-Kartenwerk, Serie E, Beiheft zu Blatt 7. Berlin, Stuttgart: Borntraeger.
- Beck E, Scheibe R, Schulze ED.** 1986. Recovery from fire: observations in the alpine vegetation of western Mount Kilimanjaro (Tanzania). *Phytocoenologia* 14(1):55–77.
- Bode R.** 1998. *Anthropogener Einfluß auf die Bestandsstruktur von Polylepis-Relikten seit der Agrarreform—ausgewählte Beispiele aus dem Departamento Cochabamba in der Ostkordillere Boliviens* [diploma thesis (MSc)]. Marburg: Faculty of Geography, Philipps University.
- Dale IR.** 1940. The forest types of Mount Elgon. *Journal of the East African and Ugandan Natural History Society* 9:74–82.
- Griffiths JF.** 1972. Eastern Africa. In: Griffiths JF, editor. *Climates of Africa*. Amsterdam: Elsevier, pp 313–347.
- Hastenrath S, Greischar L, Rosto R, Hime W.** 1997. Variations of Mount Kenya's glaciers in the 20th century. *Zeitschrift für Gletscherkunde und Glazialgeologie* 33(2):169–172.
- Hedberg O.** 1951. Vegetation belts of the East African mountains. *Svensk Botanisk Tidskrift* 45(1):141–196.
- Hedberg O.** 1964. Features of afro-alpine plant ecology. *Acta Phytogeographica Suecica* 49:1–144.
- Hillman JC.** 1986. *Bale Mountains National Park—Management Plan*. Addis Abeba: Ethiopian Wildlife Conservation Organization.
- Hurni H.** 1978. Soil erosion forms in the Simen Mountains—Ethiopia (with a map 1:25 000). In: Messerli B, Hurni H, editors. *Cartography and Its Application for Geographical and Ecological Problems—Simen Mountains—Ethiopia*, Volume I. Geographica Bernensia G 8. Berne, Switzerland: Geographisches Institut der Universität Bern, pp 93–100.
- Hurni H.** 1982. *Klima und Dynamik der Höhenstufung von der letzten Kaltzeit bis zur Gegenwart. Hochgebirge von Semien—Äthiopien*, Volume II. Geographica Bernensia G 13. Berne, Switzerland: Geographisches Institut der Universität Bern.

- Jackson JK.** 1956. The vegetation of the Imatong Mountains, Sudan. *Journal of Ecology* 44:341–374.
- Janzen DH.** 1973. Rate of regeneration after a tropical high elevation fire. *Biotropica* 5(2):117–122.
- Kaeppli M.** 1998. *Regeneration and Age Structure of Relict Ericaceous Forests* [MSc thesis]. Berne: Institute of Geography, University of Berne.
- Kessler M.** 1995. *Polylepis-Wälder Boliviens: Taxa, Ökologie, Verbreitung und Geschichte*. Berlin, Stuttgart: J Cramer.
- Killick DJB.** 1979. African mountain heathlands. In: Specht RL, editor. *Heathlands and Related Shrublands. Descriptive Studies*. Amsterdam: Elsevier, pp 97–116.
- Körner C.** 1998. A re-assessment of high elevation treeline positions and their explanation. *Oecologia* 115:445–449.
- Laegaard S.** 1992. Influence of fire in the grass páramo vegetation of Ecuador. In: Balslev H, Luteyn JL, editors. *Páramo: An Andean Ecosystem Under Human Influence*. London: Academic, pp 151–169.
- Langdale-Brown I, Osmaston HA, Wilson JG.** 1964. *The Vegetation of Uganda*. Entebbe: The Government Printer.
- Luteyn L.** 1999. *Páramos: A Checklist of Plant Diversity, Geographical Distribution and Botanical Literature*. New York: New York Botanical Garden.
- Mabberley DJ.** 1975. Notes on the vegetation of the Cherangani Hills, NW Kenya. *Journal of the East African Natural History Society and National Museum* 15:1–11.
- Miehe G, Miehe S.** 1993. On the physiognomic and floristic differentiation of ericaceous vegetation in the Bale Mountains, SE Ethiopia. *Opera Botanica* 121:85–112.
- Miehe G, Miehe S.** 1994a. Zur oberen Waldgrenze in tropischen Gebirgen. *Phytocoenologia* 24:43–110.
- Miehe G, Miehe S.** 1994b. *Ericaceous Forests and Heathlands in the Bale Mountains of South Ethiopia—Ecology and Man's Impact*. Hamburg: Stiftung Walderhaltung in Afrika.
- Ministry of Natural Resources (MNR) 1999.** Meteorological data from Tororo Station, Tororo District, Uganda. Kampala.
- Mulkey SS, Smith AP, Young TP.** 1984. Predation by elephants on *Senecio keniodendron* (Compositae) in the alpine zone of Mount Kenya. *Biotropica* 16(3):246–248.
- Nieuwohlt S.** 1978. Rainfall variability and drought frequencies in East Africa. *Erdkunde* 32(2):81–88.
- Nievergelt B, Good T, Güttinger R.** 1998. A survey of the flora and fauna of the Simen Mountains National Park. *Walia*(special issue):1–109.
- Osmaston H.** 1996. Glaciations, landscape and ecology. In: Osmaston H, Basalirwa C, Nyakaany J, editors. *The Rwenzori Mountains National Park, Uganda*. Kampala: Makerere University, pp 49–65.
- Osmaston HA, Pasteur D.** 1972. *Guide to the Rwenzori*. Kampala: Mountain Club of Uganda.
- Schmitt K.** 1991. *The Vegetation of the Aberdare National Park Kenya*. Innsbruck: Wagner.
- Smith JMB.** 1977. An ecological comparison of two tropical high mountains. *The Journal of Tropical Geography* 44:71–80.
- Snowden JD.** 1953. *The Grass Communities and Mountain Vegetation of Uganda*. London: Government of Uganda.
- Synge PM.** 1985. *Mountains of the Moon*. London: [First Edition 1937] Waterstone.
- Thomas AS.** 1943. The vegetation of the Karamoja District, Uganda. *Journal of Ecology* 3:149–177.
- Troll C.** 1959. Die tropischen Gebirge. *Bonner Geographische Abhandlungen* 25:1–93.
- Troll C.** 1973. The upper timberlines in different climatic zones. *Arctic and Alpine Research* 5(3):3–18.
- van Royen P.** 1980. *The Alpine Flora of New Guinea, Volume 1, General Part*. Vaduz: J. Cramer.
- Walter H, Lieth H.** 1960–1967. *Klimadiagramm Weltatlas*. Jena: G. Fischer.
- Walter H, Medina E.** 1969. Die Bodentemperatur als ausschlaggebender Faktor für die Gliederung der subalpinen und alpinen Stufe in den Anden Venezuelas (vorläufige Mitteilung). *Berichte der Deutschen Botanischen Gesellschaft* 82(3/4):275–281.
- Wesche K.** 2000. *The High-Altitude Environment of Mount Elgon (Uganda/Kenya)—Climate, Vegetation and the Impact of Fire* [PhD thesis]. Marburg: Faculty of Geography, Philipps University.
- Wesche K, Clausnitzer V, Miehe S, Miehe G.** 1999. Habitat conditions in afroalpine communities—examples from East Africa. In: Breckle S-W, Schweizer B, Arndt U, editors. *Results of Worldwide Ecological Studies: Proceedings of the 1st Symposium*. Stuttgart: G. Heimbach.
- White F.** 1983. *The Vegetation of Africa. A Descriptive Memoir to Accompany the UNESCO/AETFAT/UNSO Vegetation Map of Africa*. Paris: UNESCO.
- Winiger M.** 1986. *Causes and Effects of the Thermo-Hygric Differentiation of Mount Kenya*. African Studies Series A1. Berne, Switzerland: Geographica Bernensia, pp 19–29.