Ber. d. Reinh.-Tüxen-Ges. 14, 145-160. Hannover 2002

Structure and dynamics of *Erica* forest at tropical-African treelines

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Abstract

Erica forests are the dominant vegetation types at afroalpine timberlines. They show a surprising floristic and physiognomic similarity between various isolated mountain regions in eastern Africa. The timberline climbs higher in valleys than on ridges and isolated *Erica* groves are found high above the present timberline. Soil temperature measurements on Mt. Elgon revealed that there is no thermal background for this pattern, instead evidence is presented here that the distribution of *Erica* forest has been altered by recurrent fires in most mountains of the region. Heather plants survive fire but regenerate much more slowly than afroalpine grassland so that they are replaced when fires recur. The status of the upper montane *Erica* forest as a possible replacement community of broad-leaved montane forests is discussed but no conclusion can be drawn until more detailed data on the regeneration ecology of eastern African *Erica* species are available.

1. Introduction

Tropical mountains are islands of cold and moist conditions in a warm and often dry matrix. They are of great importance as water catchment areas and they offer fertile soils, so the lower slopes are usually densely cultivated. This is particularly true for tropical Africa, where isolated volcanoes reach several thousand metres above the semi-humid to semiarid surroundings. Neither the regions above the timberline nor the upper montane forests of the isolated mountains had been in contact in the late Quaternary (HEDBERG 1986), so vegetation types rich in endemic species developed. Still, the physiognomy of vegetation types and the floristic structure is similar among eastern African mountain regions, and similar plant formations are found even in South America. A widely known example of this convergence is the presence of Giant Rosette Plants in Africa and South America. Another example is the physiognomy of the timberline ecotone.

Tropical forests reach commonly higher up in valleys than on ridges, thus showing a pattern inverse to mid-latitude mountain environments, where valleys are often devoid of forest vegetation because of frequent avalanches (TROLL 1959, 1973). Moreover, isolated forest groves are regularly found in tropico-alpine grasslands high above the line of closed forest (ELLENBERG 1975, MIEHE & MIEHE 1994a). The dominant trees at most eastern African mountain sites are several species of the genus *Erica*, with *E. excelsa* as the most widely spread tree heather in the region. This *Erica* is replaced in southern Ethiopia by tree-forming taxa within the *E. trimera* complex (MIEHE & MIEHE 1994b), while *E. arborea* is the dominant tree heather in northern Ethiopia (NIEVERGELT et al. 1998).

The upper limit of closed forests in eastern Africa is usually located between 3200 and 3500 m asl., but *E. excelsa* groves occur up to some 3800 m (WESCHE et al. 2000, HEMP & BECK 2001). The reasons for this peculiar pattern have been debated for decades (summarised by MIEHE 2000). A focus on thermal conditions is traditionally of great importance in timberline research, and thermal limits of tree growth are still the most likely candidate for a general explanation for tree-line formation. This was confirmed in recent reviews by KÖRNER (1998, 1999), who summarised and updated the available information. He clarified the discussion substantially by distinguishing between ultimate limits of tree growth (e.g. soil temperature thresholds) and various other factors that lower actual timberlines to altitudes below the physiological growth limit of trees.

Human-induced timberline depressions are widely accepted for mid-latitude forests, but the importance of the "human factor" in tropical timberline environments has been acknowledged only in the last few decades (HOFSTEDE et al. 1995, RAMSAY & OXLEY 1996, KESSLER 2000, MIEHE 2000). This is equally true for mountains in tropical Africa, although HEDBERG emphasised the importance of fires for the ericaceous vegetation ("ericaceous belt", HEDBERG 1951) near the timberline as early as 1951. Increased research activity in the last 20 years provided a sound database, which makes an analysis of the relative importance of climate and fires in "afroalpine environments" possible. Here I will describe similarities of *Erica* forest in eastern Africa and will briefly review detailed measurements from Mt. Elgon, that were carried out during a Ph.D thesis (WESCHE 2002). These are supplemented by recent observations from other mountains in the region.

2. Study sites and methodology

The geology of eastern Africa is dominated by the formation of the East African Rift Valley system, which caused tectonic orogenesis from the early Tertiary onwards (SCHLÜTER 1997). Consequently, the larger part of eastern Africa is constituted by highlands over 1000 m asl., which are overshadowed by several isolated mountains reaching well above 4000 m. Most of these mountains are volcanic in origin, and emerged within the last 5 Mio. years. One exception is Mt. Elgon, at the interstate boundary of Kenya and Uganda, which erupted more than 20 Mio. years ago. The Ruwenzori is unusual as well, because it is not a volcanic range but an ancient fault block that was lifted to afroalpine elevations as late as 2 Mio. years ago (WARD et al. 1989).

Detailed vegetation descriptions became available for almost every mountain in eastern Africa in the last years (e. g. REHDER et al. 1988, SCHMITT 1991, 1992, BUSSMANN & BECK 1995a, FISCHER 1996, HEMP & BECK 2001), but sound climatic measurements and long-term observations are very rare. Therefore measurements presented here come from a 15-months study on Mt. Elgon, where I recorded not only vegetation data, but also made climatological measurements (WESCHE 2002). Mount Elgon is not among the highest mountains in the region (4321 m), but still has one of the largest afroalpine belts. The afroalpine vegetation is dominated by tussock grasslands with *Festuca pilgeri* and *Carex* bogs in depressions.

The Aberdare Mts. are situated east of Mt. Elgon in Kenya. They are a high-altitude plateau 3000 to 3400 m in elevation with some summits reaching above 4000 m. Given that the plateau has a relatively low altitude, it is surprising that the vegetation there is mostly afroalpine tussock grassland and scrub, forests are largely missing (SCHMITT 1991). The slopes are, however, densely forested up to 3200 m. The Bale Mts. are also a high altitude plateau with some peaks above 4000 m. The plateau region is much higher than in the Aberdare Mts., being situated in some 3800 m asl. The vegetation of the afroalpine belt is *Alchemilla* and *Helichrysum* scrub, tussock grassland is rare (MENASSIE GASHAW & MASRESHA FETENE 1996). Forests grow mainly at the outer slopes up to 3500 m. The Ruwenzori Mts. in western Uganda are a deeply dissected range up to 5000 m high. Forests climb the steep slopes up to 3800 (-3900 m; SCHMITT 1996).

The Ruwenzori Mts. have a perhumid climate, where true dry season conditions occur in extreme years only (OSMASTON 1996). The other three ranges have a bimodal precipitation regime with at least one pronounced dry season. Rain might entirely miss for several weeks or even 1-3 months in extreme years, and conditions are humid in the remaining months (annual precipitation in the ericaceous belt >800 mm). All mountain ranges described here are protected as national parks, but the local population utilizes the upper montane or afroalpine belt in all of them. Poaching is particularly common on Mt. Elgon; whereas, the Ruwenzori Mts. have been a hiding place for rebel groups in the last years. The Bale Mts. are unusual for eastern Africa, because livestock is grazed on a permanent basis up to 3900 m asl. (fig. 1b), while human influence in the Aberdare Mts. is presumably small at present.

The data were collected with standard methods. Relevé sampling followed the method of the Zürich Montpellier school (MUELLER-DOMBOIS & ELLENBERG 1974). Climatic measurements were carried out with LI 1000 dataloggers connected to sensors for air temperature and relative humidity (LI 1400-14), global radiation (LI 200A pyranometer) and soil temperature (LI 1000-15). Air temperature and rel. humidity sensors were placed in white, ventilated screens that were fixed in 20 cm above ground. Soil temperatures were recorded with HOT-DOG DT1 dataloggers. All sensors were calibrated and checked against each other before fieldwork. Dataloggers stored hourly readings, which were used to calculate daily mean temperatures. Multivariate data analysis was performed with PC-ORD 3.15 (MCCUNE & MEFFORD 1997).

3. On the phytosociology of *Erica* forests at African treelines

HEDBERG (1951) noted that the vegetation of the various East African mountains is surprisingly similar, so that he was able to designate three main vegetation belts, which occur on all mountains. The treeline ecotone is formed by the ericaceous belt, which mediates between afromontane forest below 3000 m and the afroalpine belt above 3800 m. A wealth of phytosociological material became available in the last years (see above), so that direct comparisons are possible now. Table 1 demonstrates the similarities of upper montane *Erica* forests for various mountain ranges. I compiled the species lists from published phytosociological summary tables, resulting in some 300 species altogether. Presented here are only those species common enough in at least two study areas to consider them important. I included only the most typical *Erica* communities, omitting those from special edaphical situations like moist valleys and obviously secondary *E. excelsa* forests from the lower montane belt. Thus I concentrated on *E. excelsa* forests at the present timberline (usually together with *Hagenia abyssinica*) and remnant stands above. No published records were available for the Ruwenzori Mts., where the dominant tree heather is usually named *Erica johnstonii* (SCHMITT 1996). On Mt. Kenya, *Erica* forests appear to be rare (BUSSMANN & BECK 1995a, BUSSMANN 1997). The species set is different west of the Ruwenzori, so records from former Zaire were omitted (FISCHER 1996). *Erica excelsa* is also absent from the Bale Mts. in southern Ethiopia, where it is replaced by several undescribed species within the *E. trimera* complex. Nonetheless, the overall floristic similarity prompted me to include records from the Bale Mts. as well. This includes the *Hypericetum revoluti ericetosum excelsae*, described for the area by BUSSMANN (1997). Although I doubt that the description is valid because of the surprising identification of *E. excelsa* from the region, again the general species set nicely resembles the other communities.

This is not a phytosociological synopsis in the strict sense, because it is not based on the raw sample data, but suffices to demonstrate the main pattern. There is some scatter in the table and differences between ranges are apparent. However, the overall similarity is striking,

Table 1: Summary table of *Erica* forest (only those species with constancy >40% in one and >20% in another region)

	Elgon			Aberdare		Kilimanjaro			Bale			Bale
Unit	I.H	I.I	I.J	IIID	III.E	8	9	11	I.2	I.3	III.2.2	C.1b1
No. of Samples	6	22	7	20	25	12	18	6	28	28	3	2
Species of upper montane Erica forest												
Erica excelsa	V	V	V	V	V	III	V	V	.	.	.	2
Erica trimera 'A'	.	.	.	.	.	.	.	.	V	III	.	?
Erica trimera 'B1'/B2	.	.	.	.	.	.	.	.	I	V	3	.
Helichrysum nandense	V	IV	V	.	.	.	I	III	.	.	.	.
Helichrysum guilelmi	III	I	.	.	III	.	.	.	.	.	.	.
Cynoglossum amplifolium	.	I	.	.	.	III	II	I	IV	III	.	.
Species of montane broad-leaved forest												
Rapanea melanophloeos	V	I	I	I	I	V	III	II	V	III	.	2
Hypericum revolutum	II	.	I	III	I	III	IV	IV	V	IV	.	2
Clematis simensis	II	.	.	.	.	.	.	.	IV	I	.	.
Carduus afromontanus/nyassanus	II	.	.	.	.	IV	II	III	IV	I	.	.
Galium thunbergianum	II	I	.	.	.	.	.	.	II	III	.	2
Species of upper montane Hagenia forest												
Hagenia abyssinica	V	I	.	.	.	V	III	II	III	I	.	2
Rubus steudtneri	V	II	I	III	I	I	II	.	III	II	.	.
Polystichium fuscopaleaceum/wilsonii	V	II	.	III	.	V	III	V	IV	III	.	2
Carex simensis	III	I	.	.	III	.	.	.	II	III	.	.
Bromus leptoclados	V	I	.	II	.	.	.	.	V	II	.	2
Dryopteris inaequalis	IV	I	.	I	.	.	.	.	V	I	.	2
Stachys aculeolata	V	I	.	.	.	.	.	.	III	II	.	.
Prunus africana	III	I	.	.	.	V	I	.	.	.	.	.
Alchemilla fischeri	.	.	.	III	.	I	I	.	.	IV	.	.
Species of Hagenia forest and afroalpine scrub												
Helichrysum odoratissimum	V	V	V	II	I	.	.	.	.	.	.	.
Helichrysum formosissimum	II	III	III	.	.	I	II	II	II	III	.	.
Conyza vernonioides	V	II	.		.	III	III	IV	II	II	.	.
Peucedanum elgonense/linderi	I	II	I	.	.	III	II	.	.	.	.	.
Asplenium aethiopicum s.l.	I	II	.	.	.	III	II	.	V	III	.	2
Species of afroalpine scrub												
Erica arborea	IV	III	V	I	I	.	.	.	I	III	.	.
Stoebe kilimandscharica	V	V	V	I	I	.	.	.	.	.	.	.
Satureja biflora	I	V	V	I	I	.	.	.	.	.	.	.
Helichrysum forskahlii	.	IV	V	I	II	.	.	.	.	III	.	.
Swertia crassiuscula	I	II	II	I	III	.	.	.	.	.	.	.
Helichrysum globosum	II	III	II	.	.	.	.	.	II	III	.	.
Anthospermum usambarense	II	IV	V	.	.	.	I	IV	.	.	.	.
Myrica salicifolia	I	.	III	.	.	.	II	.	.	.	.	.
Bartsia decurva	.	IV	III	.	.	.	.	III	.	.	.	.
Species of afroalpine scrub and grassland												
Geranium kilimandscharicum	III	V	V	II	II	.	.	.	.	.	.	.
Cerastium indicum	V	IV	I	.	.	.	.	.	V	III	.	.
Hebenstretia angolensis/dentata	II	IV	.	.	I	.	II	II	II	.	.	.
Dendrosenecio johnstonii s.l.	IV	III	.	.	.	II	.	.	.	.	.	.
Anagallis serpens	I	I	II	I	III	.	.	.	.	.	.	.
Alchemilla elgonensis/argyrophylla	V	II	.	.	II	.	.	.	.	.	.	.
Species of afroalpine tussock grasslands												
Galium ruwenzoriense/simense	III	IV	IV	.	.	.	.	.	III	V	3	.
Kniphofia angolense/isoetifolia	III	V	II	I	I	II	II	V	II	II	.	.
Luzula abyssinica	III	V	V	II	I	.	II	I	.	I	.	.
Deschampsia flexuosa	II	III	.	IV	III	I	II	.	.	I	.	.
Poa schimperana	II	.	I	IV	I	.	.	.	IV	II	2	2
Pentaschistis borussica/chrysurus	.	III	III	I	II	.	III	III	.	.	.	.
Pimpinella oreophila	I	II	I	I	I	.	.	.	III	II	.	.
Festuca abyssinica s.l.	.	I	III	II	I	.	.	.	V	V	3	2
Agrostis gracilifolia	.	IV	II	.	II	.	.	.	.	.	.	.
Festuca pilgeri	.	IV	IV	IV	.	.	.	.	.	.	.	.
Crepis carbonaria	I	I	III	.	I	.	.	.	.	.	.	.
Huperzia saururus	I	.	.	.	III	.	.	V	.	.	.	.
Alchemilla johnstonii	.	I	I	.	V	.	I	II	.	.	.	.
Viola eminii	IV	III	III	.	.	III	IV	II	.	.	.	.
Galium aparinoides	IV	I	.	.	.	V	III	III	.	.	.	2
Cineraria deltoidea/abyssinica	I	III	II	.	.	III	II	II	III	II	2	.
Ardisiandra wettsteinii	I	.	.	.	.	I	IV	.	I	III	.	.
Cerastium afromontanum	.	III	III	.	.	III	II	.	.	.	.	.
Helichrysum meyeri-johannis	.	II	I	.	.	.	.	III	.	.	.	.
Oxalis corniculata	II	I	I	.	.	.	.	.	V	III	.	2
Geranium arabicum	.	.	.	III	.	II	III	V	V	III	.	.
Xiphopteris flabelliformis	.	.	.	.	.	V	IV	II	V	I	.	.

List of vegetation units

	upper montane		**lower afroalpine**
Mt. Elgon (Wesche in press-a)			
I.H	*Hagenia abyssinica-Erica excelsa* -community	I.I	*Erica excelsa-Luzula campestris* -commur
		I.J	*Erica excelsa-Myrica salicifolia* -communit
Aberdare Mts. (Schmitt 1991)			
III.D	*Erica excelsa-Rubus steudtneri* community	III.E	*Erica excelsa-Carex simensis* community
Kilimanjaro (Hemp & Beck 2001)			
8	Subalpine *Hagenia* forest	11	Middle subalpine *Erica excelsa* forest
9	Subalpine *Erica excelsa* forest		
Bale Mts. (Miehe & Miehe 1994b)			
I.2	*Erica* -dominated *Hagenia-Hypericum* forests	III.2.2	*Luzula johnstonii-Erica trimera* 'B2' forest
I.3	*Helichrysum formosissimum-Erica trimera* 'B1' communities		
Bale Mts. (Bussmann 1997)			
C.1b1	Hypericetum revoluti ericetosum excelsae (since *Erica excelsa* does not occur in the Bale region, tree layer probably *E. trimera* s.l.)		

virtually all regions have some species in common. Since a general synopsis of afroalpine and afromontane vegetation is not yet available, no conclusive statement on the status of the species listed can be made. Nonetheless, I formed species groups according to personal field experience and the published phytosociological tables. The apparent lack of true character species for the *Erica* forests is surprising. Even regional character species are rarely reported and, except for the tree heather itself, no true character species emerged. Instead, most communities comprise some afromontane forest species but a far greater number of species typical for the afroalpine belt. Hence, *Erica* forests are "subalpine" in the sense that they resemble afroalpine vegetation more strongly than montane forests.

4. Physiognomy and site conditions of *Erica* forest near the timberline

The timberline in most study areas shows the features described in the introduction. Valleys are often densely forested, while the ridges are covered by open afroalpine vegetation (fig. 1a,c). Boundaries are relatively sharp except in the Ruwenzori, where the transition to afroalpine vegetation is gradual (fig. 1d). The present timberline in the other mountains lies at some 3200 to 3400 m asl., while remnant groves of tree heather are found up to an altitude of 3750 to 3800 m. *Erica* forests at or below the present timberline are usually accompanied by the trees *Rapanea melanophloeos* and *Hagenia abyssinica*, while both are absent from groves above 3500 m. Such high-altitude groves grow usually in the shelter of large rocks or boulder streams (fig. 1b) and have a relatively patchy interior with various species from afroalpine scrub and grassland constituting the shrub and tree layer. *Erica excelsa* forms up to 25 m tall single-stemmed trees in the forest belt, but is at most 10 m high and often multistemmed above 3200 m.

Few long-term measurements are available to test, if these forests grow under thermally favourable conditions. The exception is Mt. Elgon, where I operated temperature and humidity dataloggers at various sites in all altitudinal belts. Table 2 gives the altitudinal extent of vegetation types and the corresponding soil temperature beneath open grassland. The present upper limit of closed *Erica* - *Hagenia* forest corresponds to a soil temperature of some 10°C on the western side of Mt. Elgon. These forests are largely replaced by patchy ericaceous bushland and scrub on the eastern declivity. This is not a consequence of thermally unfavourable conditions, since soil temperatures (at the same altitude) are clearly higher on the eastern side. However, if the uppermost *Erica* outposts are taken as indicators of the forest's maximum extent, then the upper limit of forest vegetation on Mt. Elgon would correspond to a mean annual air temperature (+ 20 cm) of 6.1°C and a mean soil temperature in 20 cm depth of 8.1°C (under open ground, both sides).

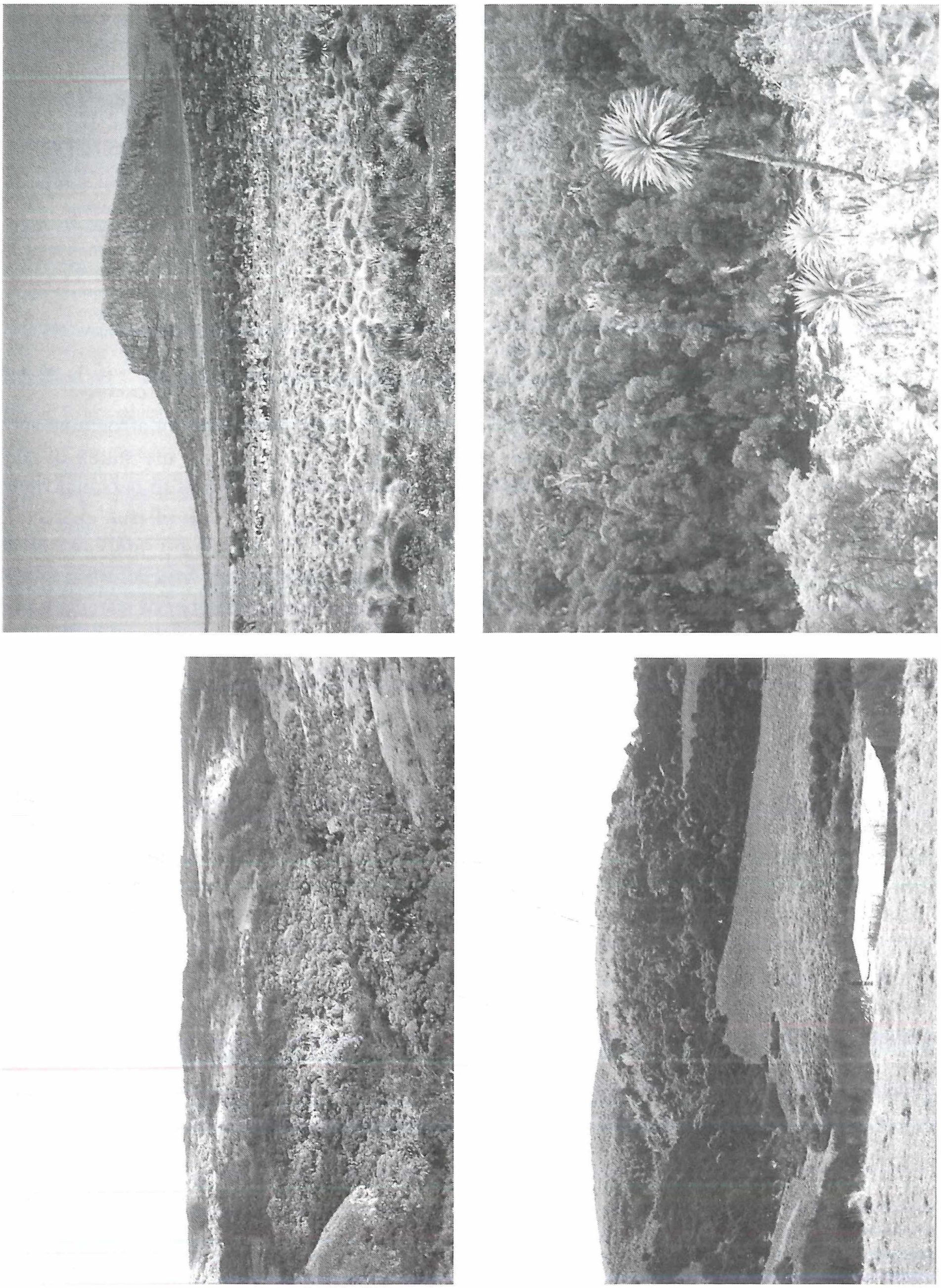

Fig. 1: Physiognomy of upper montane *Erica* forest in the four study areas.

1a: Upper timberline at the northern declivity of Mt. Elgon, ca. 3300 m, with *Erica excelsa* and *Hagenia abyssinica* (Sept. 1997). 1b: *Erica trimera* dwarf forest in a boulder stream on the Central Sanetti Plateau, Bale Mts., ca. 3900 m. Grazing by goats and cattle is common all over the plateau but boulder streams are avoided (March 2000). 1c: Dense *Erica excelsa* forest in steep valleys in the southern Aberdare Mts., ca. 3200 m. Ridges in between are covered by tussock grassland (March 2001).

1d: Dense *Erica* spp. forest in a steep valley in the Ruwenzori densely covered with epiphytes (Bujuku Valley, ca. 3200 m).

Western declivity	**(Uganda)**			**Eastern declivity**	**(Kenya)**		
Vegetation	Range (m asl.)	Temp. (°C)	Elev. (m)	Vegetation	Range (m asl.)	Temp. (°C)	Elev. (m)
Agriculture	< 2500	18.2	2250	Agriculture	< 2250		2250
Moist montane forest	2500 – 2900	17.4	2500	Dry montane forest	2250- 2900	17.5	2500
		13.6	2750			15.2	2750
Bamboo forest	2800 – 3150	11.8	3000	Bamboo forest	2800 – 3050	13.4	3000
Hagenia forest	3100 – 3300	10.1	3250	Mosaics of ericaceous vegetation	3050 – 3550	11.7	3250
Afroalpine grassland	3300 – 4100	9.0	3500			10.1	3500
Remnant *Erica* groves	3300 – 3750	8.7	3750	Afroalpine grassland	3200 – 4050	8.6	3750
		8.1	4000			8.0	4000
Rocky outcrop vegetation	3500 - 4300	7.5	4190	Rocky outcrop vegetation	3500 -4300		4190

Tab. 2: Altitudinal distribution of vegetation belts at the eastern and western site of Mt. Elgon. Mean annual soil temperatures (-20 cm) are given for every 500 vertical metres, indicating possible thermal limits of altitudinal belts.

Small-scale differences were analysed in some detail in the vicinity of our camp. Detailed climatic data are available for an afroalpine valley that was covered by *Erica excelsa* groves at the bottom and afroalpine tussock grassland at the shoulder (fig. 2). I operated two data-loggers at both sites (open vegetation) for more than a year, so the conditions near the soil surface could be compared. The monthly mean temperatures are relatively similar at both sites, corresponding to the small vertical distance. The difference is of the same order of magnitude as the possible instrumental error. Differences between valley bottom and shoulder are more

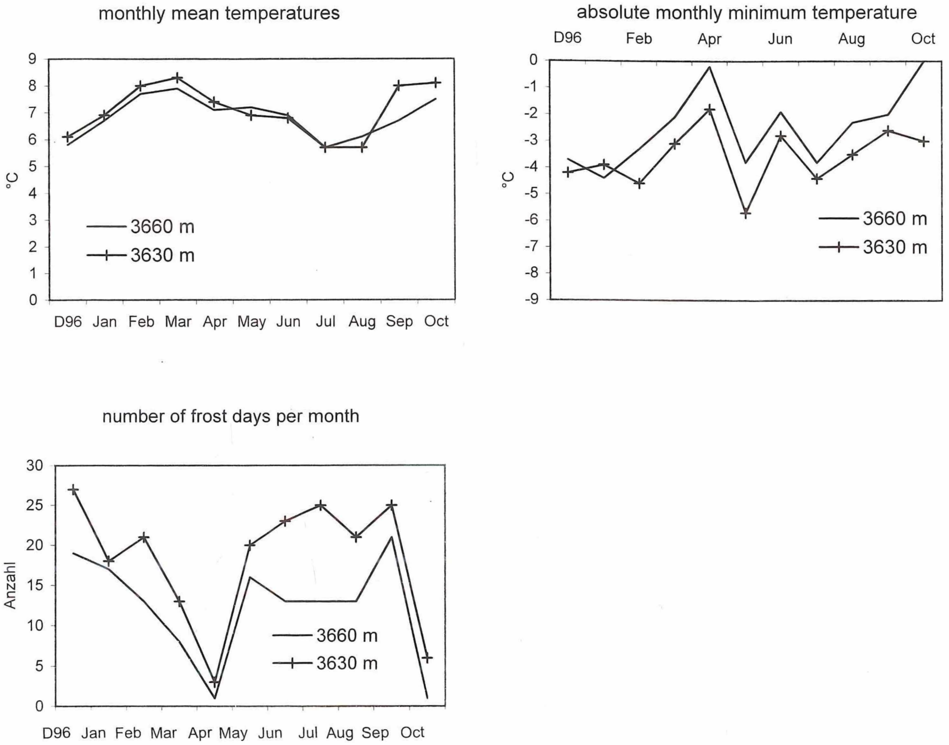

Fig. 2: Thermal conditions at an afroalpine valley (3630 m) and the adjacent slopes (3660 m). The logger was placed in a weather screen 20 cm above ground.

pronounced for the absolute monthly minimum temperature and the number of frost days per month. Both parameters indicate that cold air accumulates at the valley bottom so that *Erica* forests there suffer colder rather than warmer conditions compared to the surrounding grasslands. Therefore, there is no support for a thermal background to the presence of *Erica* forests in afroalpine valleys. In summary, data from both the Kenyan and the Ugandan sides suggests that the forest distribution is controlled by factors other than the thermal difference.

The evidence for fire as an important factor in most study sites is overwhelming. Fires in the ericaceous vegetation and upper montane forest were repeatedly observed on Mt. Elgon. Following 7 dry weeks in 1997 an estimated 60% of the afroalpine and ericaceous belt of Mt. Elgon burnt (fig. 3a); a similarly intensive fires occurred after 5 dry weeks in 1999. Southern Ethiopia was hit by a drought in 2000 resulting in large-scale fires at various sites in the country. We observed severe fires in the upper montane forest at the northern declivity of the Bale Mts. (fig. 3b). Traces of former fires are easily found everywhere in the Aberdare range, where dead trunks indicate the former presence of closed *Erica excelsa* forests at several sites (fig. 3c). The exception is again Ruwenzori. Charred trunks are found rarely and only near the upper limit of *Erica* forest, and forests generally appear to be intact.

Observations in the Bale Mts. and Mt. Elgon revealed that ericaceous vegetation burns fiercely and relatively hotly as a consequence of the large surface areas of the small leaves. Fires are similarly hot as in dense *Alchemilla* scrub; whereas, those in afroalpine grassland are less severe. They create a patchy fire pattern with usually some leaves remaining. Fires in ericaceous vegetation, in contrast, consume all leaves and spare only the largest branches (fig. 3c). Surprisingly, *Erica excelsa* and *E. trimera* were not killed by the fires, but started resprouting within a few weeks after the fire. Monitoring on Mt. Elgon revealed that *E. excelsa* developed new shoots of some 30-40 cm length within two years after a fire. *Erica trimera* bushes on Mt. Elgon developed shoots of a mean length of 21 cm within two years. Plants survived but the original vegetation structure was not nearly recovered within the two years of monitoring.

Recovery rates are much faster for other afroalpine vegetation types. I burnt two afroalpine grassland sites experimentally on Mt. Elgon in 1997 and monitored recovery of the vegetation for the first 2 years after fire. Figure 4 gives examples from one of these experimentally burnt plots; only four subplots are shown to avoid overcrowding of the graph. All plots are floristically similar, as indicated by the shortness of the multivariate gradient (<130 units or 1.3 multivariate standard deviations). Start and endpoint of the arrows lay close together, and are therefore apparently similar. A cyclic recovery was observed so that 25 months after burning, plots had the same species set and species cover again. Vectors indicate that in the intervening months mainly the cover of shrubs was reduced, while vegetation cover as such changed only weakly, because grasses started to resprout as soon as two weeks after the fire. Overall species richness was not affected and does therefore not correlate with any of the ordination axes. In this respect, afroalpine grasslands differ strongly from ericaceous vegetation, because the latter had not recovered within the two years of study.

5. Discussion

An analysis of the status of *Erica* forests in eastern Africa requires an understanding of possible limiting climatic and edaphic site conditions; and in a second step, if those are not sufficient to explain the current vegetation pattern, of other factors, like the influence of fire. Table 1 reflects the wide attention these forests received by plant ecologists in the last years

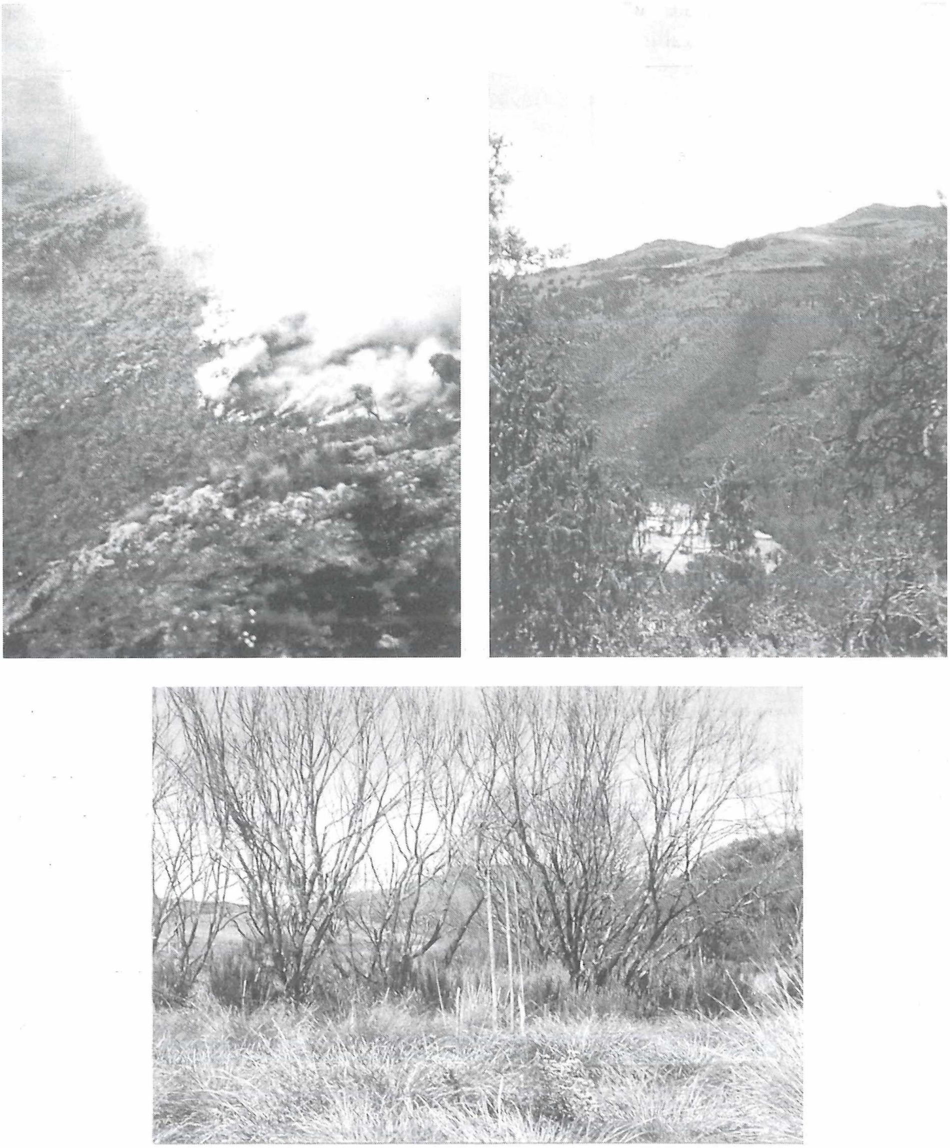

Fig. 3: Impact of fire in the upper montane and lower afroalpine belt.

3a: Downhill spread of a fire in the lower afroalpine belt of Mt. Elgon, 3700 m asl. (March 1997).

3b: Recently burnt slope at the northern declivity of the Bale Mts. Afromontane *Juniperus procera* forest survived at steep valley shoulders while it was burnt on the ridges and relatively shallow valleys (left), ca. 2900 m (March 2000).

3c: *Erica excelsa* stand in the Aberdare Mts. few years after a fire. Fire has killed the upper branches and plants resprouted from the base. Tussock grassland with *Cyperus kerstenii* has invaded the site, 3100 m (March 2001).

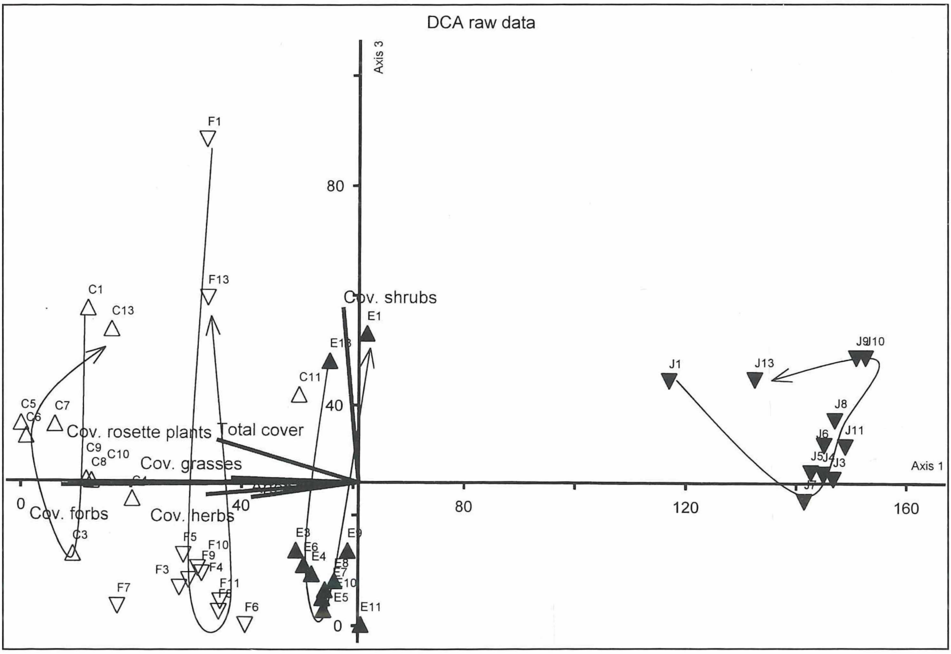

Fig. 4: Recovery of afroalpine grassland after experimental burning. 4 subplots "C,E,F,J" of an experimentally burnt area were monitored before the fire (e.g. "C1"), for ten month after the fire (e.g. "C2, C3") and again after 25 months (e.g. "C13"). Arrows connect same plots along the time axis, vectors indicate the correlation of main cover of various life form groups with ordination axes (DCA, raw data, Eigenvalue/post hoc correlation axis 1: 0.23/0.42; Axis 3 0.04/0.15).

and demonstrates the general similarity of afroalpine and afromontane vegetation in eastern Africa. This refers not only to the general floristic similarity, but also to the apparent lack of character species. The latter might hint at the transitional character of *Erica* forest, but more data are needed, especially from the Ruwenzori. The importance of disturbances is, however, apparent in Table 1, because most companions of the forest are species adapted to open afroalpine vegetation. Given that not only the general appearance, but even the floristic structure is surprisingly similar, we may deduce that results from one mountain range are transferable to the others.

Terminological problems

A word of caution is necessary on nomenclature. Various authors named similar vegetation types differently. There are two general overviews of afroalpine vegetation (HEDBERG 1951, KNAPP 1973), but both are not based on a sufficient number of vegetation samples. The summary table demonstrates that prospects for a phytosociological synopsis of afroalpine vegetation are promising. A synopsis of afromontane vegetation was already presented for Mt. Kenya (BUSSMANN & BECK 1995a), but has not received widespread appreciation so far. A new synopsis of all available phytosociological samples might help to clarify the syntaxonomy of the montane forests as well. Another terminological problem is related to the term "subalpine." Various authors designated various formation types from upper montane forest to scrub high above the timberline as "subalpine" or "subafroalpine." I doubt that the term subalpine is of great use because its meaning is so vague (LÖVE 1970). HEDBERG (1951, 1964) avoided the term largely and named the entire transition zone from broadleaved montane forest to truly afroalpine communities the "ericaceous belt." For the time being, I regard all forests below the timberline as montane, and those communities directly above as lower alpine, although I think they are largely replacement communities of montane vegetation.

The impact of fire

The status and nature of the ericaceous vegetation has been a matter of debate for decades, but by now evidence is overwhelming that patterns can not be explained by climatic or edaphic conditions alone (MIEHE & MIEHE 1994a, HEMP & BECK 2001, WESCHE 2002). This is clearly demonstrated by the measurements presented for Mt. Elgon, where lower afroalpine valleys with *Erica excelsa* are apparently colder than ridges devoid of this community and, moreover, the timberline on the entire eastern side is lower although temperatures are higher than on the western side.

Fires were described for virtually every mountain range in eastern Africa (review in WESCHE et al. 2000) and central Africa (HALL 1973). Unfortunately, studies on the regeneration of afromontane and afroalpine vegetation are few (BECK et al. 1986, EKKENS 1988, SCHMITT 1991, BUSSMANN & BECK 1995b, LANGE et al. 1997), and information about ericaceous vegetation is even more scattered. The data presented above suggest that eastern African *Erica* species survive even high intensity fires, but recovery of vegetation types takes several years. This agrees with observations on Mt. Kilimanjaro (HEMP & BECK 2001). Tussock grasslands in turn regenerate within one or two years (cf. WESCHE 2002); thus have the potential of replacing ericaceous communities under high-frequency fire regimes. Detailed fire records are unfortunately rare for afroalpine environments except for the Aberdare Mts. (SCHMITT 1991) but severe fires appear to be triggered by severe droughts (WESCHE in press) and might occur every 2-10 years. However, the available evidence is sufficient to state that afroalpine timberlines were depressed by recurrent fires for several hundred vertical metres and that the groves found above the present timberline are remnants of a former forest vegetation, which survived in fire-sheltered places. This is in line with observations on *Polylepis* forests in the Andes (KESSLER 1995, 2000, ELLENBERG 1996).

Although patterns at the upper limit of *Erica* forest are partly understood by now, the status of the lower limit of *Erica* forest is still unclear (HEMP & BECK 2001). *Erica excelsa* is a tree of clearly secondary vegetation in the montane forest belt below 2800 m on Mt. Kilimanjaro and on Mt. Elgon. Given that, unlike the broad-leaved montane forest species, it survives fire like *Rapanea melanophloeos*, HEMP & BECK hypothesized that upper montane *Erica excelsa* forest below the timberline are a replacement community of broad-leaved montane forest under recurrent fires. This agrees with observations on *Calluna* and *Erica* species in Europe, which are absent from late successional forest communities but are promoted by disturbance like fires (e.g. MALLIK & GIMINGHAM 1983, MESLÉARD & LEPART 1991, LÜTKEPOHL & STUBBE 1997). Ericaceous communities depend on regular disturbance and regenerate fast from persistent seedbanks or by resprouting (e.g. GONZÁLEZ-RABANAL & CASAL 1995, GRIME et al. 1996, VALBUENA et al. 2000). Therefore the idea of *Erica* forest as a "climax" vegetation on the East African Mountains appears to be surprising from a European perspective.

Still, evidence is scarce that upper afromontane *Erica* forests are largely secondary. In the uppermost stands between 3200 and 3800 m *Erica* is the climax forest community, because no other forest communities could grow there. Stands near the present timberline are formed by *Erica* and *Hagenia*, which is definitely favoured by disturbance (LANGE et al. 1997). Stand structure and composition often indicates disturbance by fires and the lack of character species might hint in the same direction. However, personal observations in the Aberdare Mts.

and on Mt. Elgon indicate that *Erica excelsa* forest without any traces of former fires (and without *Hagenia abyssinica*) occur in steep rocky valleys. Moreover, the most extensive *Erica* forests of the region are found in the Ruwenzori Mts., where fires certainly are least frequent of all the ranges mentioned here. These forests are definitely not a fire-induced replacement community of broad-leaved montane forests. Still, *Erica* species might be favoured by other disturbances than fire. Stands at steep sites as in the Aberdare Mts. or in the deeply dissected Ruwenzori are presumably influenced by rock avalanches or other types of rock debris and boulder movement. Nevertheless, these forests are built by mature *Erica* trees and not by early successional pioneer scrub.

The way ahead

This discussion highlights the need to acquire more detailed information on the regeneration of eastern African *Erica* species. *E. arborea* regenerates from the lignotuber after fire, but colonises burnt areas relatively fast. It is common in heavily disturbed afroalpine ericaceous scrub. Seeds are abundantly produced and germinate slowly after some weeks without any stratification (unpublished data). In the Mediterranean region, *E. arborea* regenerates preferably by resprouting, with reseeding being rather rare (CANADELL & LÓPEZ-SORAI 1998, FERNÁNDEZ-PALACIOS & ARÉVALO 1998) and occurring only in open vegetation (MESLÉARD & LEPART 1991, ARÉVALO & FERNÁNDEZ-PALACIOS 1998). This is also found in other Mediterranean *Erica* species (LLORET & LÓPEZ-SORIA 1993, VILA & TERRADADAS 1995, LLORET 1998, CRUZ & MORENO 2001), while *Calluna vulgaris* easily regenerates by reseeding (GONZÁLEZ-RABANAL & CASAL 1995, VALBUENA et al. 2000). This general pattern contrasts with *Erica* species from South Africa, where reseeding is the dominant mode of regeneration (OJEDA 1998, BELL & OJEDA 1999). Since the East African *Erica* species formerly known as *Philippia* (e.g. "*P. trimera, P. excelsa*") show strong taxonomical relationships to south African heathers (OLIVER 1987, 1989) reseeding can be expected to be common. Seedlings from E. *excelsa* and *E. trimera* are found in the field, but they are relatively rare in the shade of the *Erica* forest and not common in open vegetation either.

Several authors proposed regeneration schemes for *Erica* forests (SCHMITT 1991, MIEHE & MIEHE 1994b, HEMP & BECK 2001, WESCHE 2002) that nicely demonstrate how closed forest degenerates into open woodland and eventually ericaceous scrub under repeated burning. Regeneration by means of reseeding is usually only hypothesised, however, and observational and experimental evidence is sparse. Stands often appear to be even-aged (HEMP & BECK 2001, WESCHE 2002), but tree-ring analyses in *E. arborea* and Mediterranean *Erica* species proofed to be difficult (PAUSAS 1999, WESCHE et al. 2000). So I doubt that analyses of age structure will yield valuable information. I believe that the next logical step in the analysis of the vegetation patterns found at afroalpine timberlines is a detailed study on the seed and seedling biology of the dominant tree heather species.

Acknowledgements

The work would not have been possible without the help of several governmental and academic institutions in the host countries, of which KWS (Kenya), UWA & Makarere University (Uganda) and the Addis Ababa University (Ethiopia) should be mentioned. Financial support was kindly granted by DFG, DAAD and Studienstiftung des Deutschen Volkes. Masresha Fetene, V. Clausnitzer and S. & G. Miehe helped at various stages of fieldwork and data analysis.

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Zeitschrift/Journal: Berichte der Reinhold-Tüxen-Gesellschaft

Jahr/Year: 2002

Band/Volume: 14

Autor(en)/Author(s): Wesche Karsten

Artikel/Article: Structure and dynamics of Erica forest at tropical-African treelines 145-159