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The importance of occasional droughts for afroalpine landscape ecology

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Abstract: The paper presents climatic and plant ecological data for unusually severe dry-season conditions on Mt. Elgon (Uganda/Kenya) and the Bale Mountains (Ethiopia). There is clear evidence that plants are exposed to desiccation stress during high-altitude droughts, which occur on average every 7–10 y in the study sites. Although high vapour-pressure deficits and consequently high potential evapotranspiration led to conspicuous wilting of several plant species, no lethal damage was observed and plant communities maintained increased flowering activity under drought conditions. Moreover, highest outposts of ericaceous vegetation were regularly found on thin soil covering rocky outcrops, where water stress apparently is high. Probably more important than direct water stress are the extensive fires occurring under drought conditions, which cause large-scale replacement of woody vegetation by grasslands. Additional consequences of drought include adverse conditions for seedling establishment.

Key Words: afroalpine grassland, alpine climatology, drought, fire, tropical mountains

INTRODUCTION

But it cannot be too strongly emphasized that the abnormal is of great, and often more than transitory, importance. (Moreau 1938)

The eastern part of Africa is particularly notorious for its variable climate; inter-annual variability is often higher than average figures (Nieuwolt 1978, Rohde & Virji 1976, Wood 1979). Although the often disastrous consequences of droughts for the lowlands have been well described, little information is available on high-altitude environments in tropical Africa. There is virtually no permanent climatic weather station above 3500 m and short-term measurements made during expeditions are also rare. This lack of data is easily explained by adverse working conditions and the low probability of experiencing unusually dry conditions during a short-term field expedition.

Tropical alpine climatology has focused primarily on the impact of low temperatures rather than moisture stress (Grubb 1977, Körner 1999, Troll 1959). Tropical-alpine environments usually have low seasonal but high diurnal temperature changes and are considered aseasonal. Nonetheless, seasonal changes in precipitation totals are found in most tropical mountain ranges, and occasional droughts occur in all but the most per-humid sites (Hedberg 1964, Kitayama 1996, Luteyn 1999, Wesche *et al*. 2000). Even in average years most mountains in eastern Africa experience one or two dry seasons, one of which extends over several months (Griffiths 1972*a*, *b*).

Several authors point to water as a potential limiting factor for plant growth in tropical mountains. There is clear evidence that moisture stress occurs in some tropical-alpine environments (Beck 1994, Kitayama & Mueller-Dombois 1994, Leuschner 1996, 2000; Leuschner & Schulte 1991, Meinzer *et al*. 1994, Pérez 1987), while authors working on extratropical mountains consider desiccation a rare phenomenon (Halloy 1989, Körner 1999). The present paper will not attempt to review the eco-physiological literature on the topic, but will concentrate on the striking impact of drought conditions on entire communities.

STUDY SITES

I had the opportunity to work in two afroalpine areas (Figure 1). Mount Elgon is an extinct volcano of tertiary origin straddling the border of Uganda and Kenya. It reaches an altitude of 4321 m with extensive areas above the present timberline at 3300 m. One year's fieldwork was carried out on the western slopes of Mt. Elgon from November 1996 to November 1997 and a further 4-week visit was possible in 1999. The main field-study sites (around Dirigana Camp) were at altitudes of 3600–3900 m, i.e. in the transition zone of ericaceous vegetation and afroalpine grasslands.

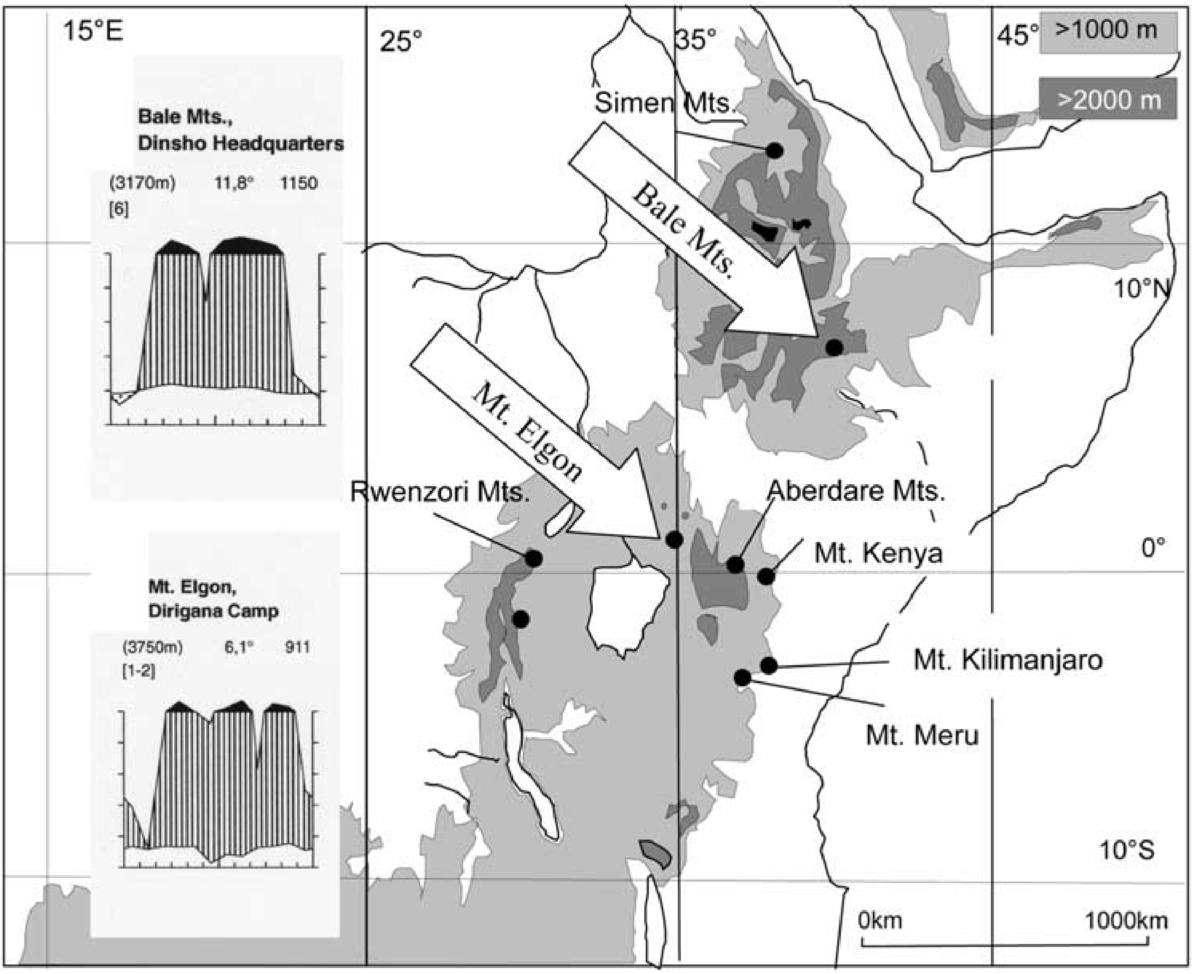

Figure 1. Location of the study sites and the major equatorial mountain ranges of Africa. The diagrams (following a design by Walter & Lieth 1960–1967) give the climatic conditions for the two study sites in Ethiopia (6°45′N, 39°45′E, Miehe & Miehe 1994) and Uganda (1°09′N, 34°30′E). Numbers in the first two lines indicate elevation, annual mean temperature, annual mean precipitation totals, and number of years for which data were available (on Mt. Elgon 1 year for temperature, 2 years of precipitation records). X-axis runs from January to December. Interval is 1:10 °C for the temperature data (lower line); 1:20 mm for the monthly precipitation totals. Monthly totals higher than 100 mm were drawn at an interval of 1:200 and indicated in black. Relatively moist periods are hatched.

Fieldwork in the Bale Mountains in south-eastern Ethiopia lasted from 10 to 25 March 2000 at the end of a dry season. The Bale Mountains are a volcanic plateau with the largest afroalpine area in Africa. The expedition stayed on the south-western part of the Sanetti plateau at about 3880 m asl, where only afro-alpine grassland and *Helichrysum* scrub are found (Menassie & Masresha 1996).

Both sites have a typical subhumid climate with a bimodal precipitation pattern (Figure 1). Dry conditions occur on average mainly between December and January, but due to the high variability dry conditions may be encountered at any time of the year. Annual precipitation at the upper slopes varies between 950 and 1500 mm in both mountain ranges (Miehe & Miehe 1994, Wesche in press).

On Mt. Elgon no rain fell between 27 January and 26 March 1997. After an average year in 1998, in 1999 another drought occurred from December to February. So figures for February 1997 were compared directly with the Bale readings. Fieldwork there coincided with a severe dry season, because the small rains in December and January were lacking in 2000 and the dry season continued until the end of March. Thus fieldwork in the Bale Mountains took place under drought conditions; there had been no rains in February and March (weather station Dinsho Headquarters, Bale Mountains NP, *pers. comm.*).

Human impact is tremendous at both sites. Cultivation on Mt. Elgon extends up to 2800 m, but honey hunters and poachers travel the entire afroalpine belt. Cultivation in the Bale Mountains reaches almost 3000 m, while pastoralists rear livestock on a semi-permanent base up to the summit region at 3900 m.

METHODS

Climatic measurements were carried out with LI 1000 dataloggers (Li-cor, Lincoln, Nebraska) connected to sensors for air temperature and relative humidity (LI 1400-14), global radiation (LI 200A pyranometer) and soil temperature (LI 1000-15). Soil temperatures were recorded with Hotdog DT1 dataloggers (Elpro, Schorndorf, Germany). The sensors were calibrated by the manufacturers in 1997 and recalibrated in 1999. All sensors for temperature and relative humidity were additionally tested in a shady well-aerated room and compared with readings from an Assmann psychrometer (Lambrecht, Göttingen), deviation among different sensors and systems was less than 0.3 K and 4% relative humidity absolute.

Air temperature and relative humidity sensors were placed in white ventilated screens at +20 and +200 cm above grassy ground. All dataloggers stored hourly readings: on Mt. Elgon for a full year, in the Bale Mountains from 11 to 16 March. Daily means were based on 24-h readings. Measurements on Mt. Elgon were supplemented by a wind gauge in the summit region and wind estimates on the Beaufort scale calibrated with a handheld anemometer. In the Bale Mountains instantaneous measurements of air temperature, surface temperature and wind speed were taken with a hand anemometer and a hand-held IR thermometer.

Precipitation was recorded with standard Hellmann rain gauges (100 cm^2). For Mt. Elgon, monthly totals of precipitation were measured for a period of 28 mo. In the Bale Mountains the National Park Headquarters operate a rain gauge at 3200 m at the northern slopes of the range. Potential evaporation (PET) was measured with Piche evaporimeters (Lambrecht, Göttingen) on Mt. Elgon, which were placed 20 cm above ground at well-ventilated sites. In the Bale Mountains a balance evaporimeter with a standard pan (200 cm^2) was used. Because Piche measurements are notorious for yielding unreliable data, I calculated potential evaporation by means of the Penman approach for Mt. Elgon (as provided by Barry 1992). This method was repeatedly shown to model evaporation of standard pans quite well (Nullet & Juvik 1994, Taffu 1994). Estimates are improved if data are summarized for full months and are generally more reliable for the crucial dry-season conditions (Chiew & McMahan 1992).

Plant ecological work in the Bale Mountains had to be skipped since most species were completely wilted. The extended working period on Mt. Elgon allowed me to monitor plant phenological stages in some detail. Three sites of 1 ha each were chosen in afroalpine grassland around the base camp. Care was taken to cover representative situations with respect to terrain (valley bottom, valley shoulder and top of the ridge). Plots ranged in altitude between 3630 m and 3750 m asl. Phenological stages were monitored at 10 randomly chosen subplots within the 1-ha sites, recording interval was 1 mo. Phenological stages were recorded on a simple scale indicating if species were fruiting, flowering or growing sterile and whether they were wilted. Shrubs taller than 50 cm were sufficiently rare on the subplots to monitor survival individually.

The impact of fire was readily observed at both study sites. On Mt. Elgon the extent of fire in 1997 was mapped from the ground in the central caldera. For 1999 aerial imagery (1:25 000) of 1999's fire was available for the eastern slopes of the mountain only. Fires in the Bale Mountains were also extensive, but aerial imagery was not available and the sheer size of the range (afroalpine belt alone > 1500 km^2) rendered ground surveys impossible.

RESULTS

Drought season climatic conditions

Because climatic data for afroalpine regions are generally rare, I will first present data for the basic meteorological variables. Data for a whole year on Mt. Elgon demonstrate the seasonality of the climate (Table 1a). Mean daily global radiation shows a seasonal pattern with high figures in February and September. This correlates with high daily maximum temperatures and high mean vapour pressure deficits (VPD) at noon. Whereas this measure of humidity shows a clear seasonality, mean monthly temperatures and mean daily temperature minimum figures remain relatively constant and frost might occur almost every month. Therefore thermal seasonality is weak. The same pattern is found in the Bale Mountains (Table 1b). Thermal seasonality is weak, but mean relative humidity shows clear seasonal changes.

At both study sites lack of rain was correlated with clear skies and values of global radiation were high (Figure 2). Hourly means reached almost 1000 Wm^{-2} on Mt. Elgon and 1200 Wm^{-2} in the Bale Mountains. Skies were perfectly clear in the morning until noon, but in the afternoon thin cloud layers developed. These are mainly formed during convective uplift occurring from late noon onwards when a valley wind system usually established itself. Thus, afternoons gained less radiation and consequently, both distributions are skewed with higher standard deviations in the afternoon.

High radiation resulted in the well-known high diurnal climatic variation, which was particularly extreme near the soil surface (Figure 3). Hourly mean temperatures near the ground (+20 cm) rose up to 13 °C in both areas, but fell below zero at night. This caused a strong diurnal rhythm of changing relative humidity and, thus, vapour pressure deficits (VPD). Mean VPD attained around 1.5 kPa around noon and dropped to well below 0.5 kPa at

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Table 1a. Seasonality of climatic conditions on Mt. Elgon; figures for 3750 m asl and +20 cm above ground. The table presents monthly mean temperatures, monthly means of daily maximum and minimum temperatures, of vapour pressure deficits at 12h00 local time and mean daily sums of global radiation (recording period Nov 1996 – Oct 1997).

	N96	D96	J	F	M	A	M	J	J	A	S	O
Mean maximum temperature (°C)	17.6	16.3	17.5	20.2	19.7	15.5	17.7	11.2	13.2	12.4	20.4	17.4
Mean minimum temperature (°C)	0.6	−1.9	−1.4	−2.0	−0.6	1.7	−1.2	−0.1	−0.8	−0.8	−1.3	1.3
Mean VPD at noon (kPa)	0.45	0.40	0.55	1.16	0.95	0.38	0.69	0.25	0.25	0.22	1.08	0.83
Daily radiation (J cm^{-2} d^{-2})	1487	1094	1302	2145	1465	1328	1863	1111	1036	1091	2074	1567

Table 1b. Seasonality of climatic conditions in the Bale Mountains north of Sanetti plateau. Figures for Dinsho station, 3170 m, data from Hillman (1986).

	N96	D96	J	F	M	A	M	J	J	A	S	O
Mean maximum temperature (°C)	15.9	16.7	17.6	18.9	19.8	18.7	17.4	17	16.5	16.8	16.7	14.7
Mean minimum temperature (°C)	2.5	2.1	0.6	1.2	2.5	5.3	5.2	4.9	4.9	5.3	4.9	4.6
Mean monthly relative humidity (%)	62.9	59.1	45.1	39.5	50.1	71.1	86.2	91.6	86.3	85.5	96.4	70.3

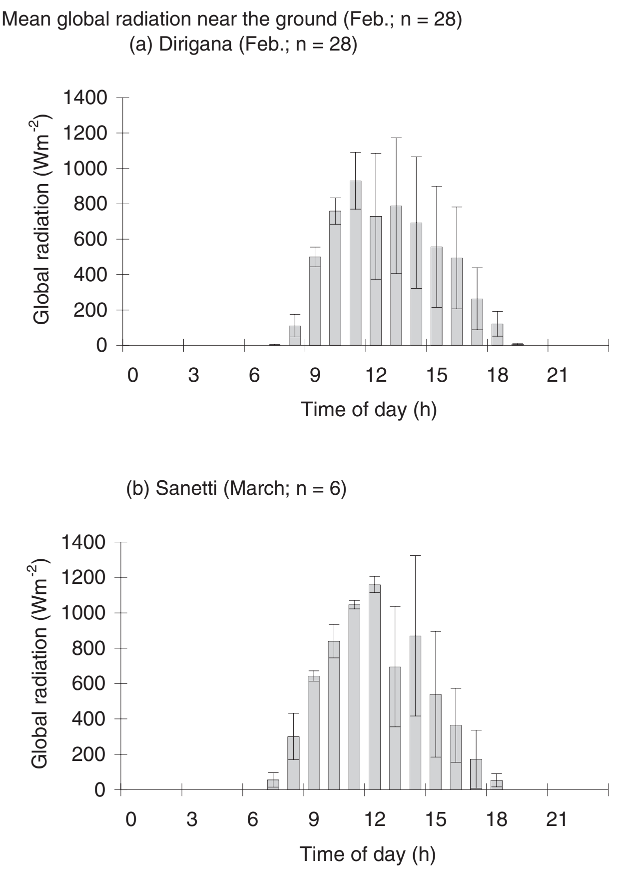

Figure 2. Hourly means of global radiation for the two study sites: (a) Dirigana Camp Mt. Elgon 3750 m asl, February 1997; (b) Sanetti Camp Bale Mountains 3880 m asl, March 2000. Vertical lines indicate standard deviation for the period considered (Dirigana n = 28; Sanetti n = 6).

night near the surface, while VPD was always below 1 kPa at +200 cm above ground. This is paralleled by a much smaller temperature range at the +200 cm height. The absolute humidity showed a less distinct diurnal variation and ranged mainly between 0.3 and 0.8 kPa at both sites (Figure 3c). A weak diurnal pattern with relatively high absolute humidity in the afternoon hinted at the convective influx of moister air from the lower slopes.

Potential physiological desiccation stress was more extreme than indicated by the VPD figures, since insolated surfaces warmed up much faster by radiant heating than the screened sensors used here. This was demonstrated on the Sanetti plateau. At midday, soil surface temperatures reached 26–43 °C and rocks heated up to 35 °C, while just 1 m up air temperatures did not even reach 16 °C (Figure 4). At night the pattern was quickly reversed and frost occurred near the ground as early as 20h00. Temperature conditions are clearly more extreme near the ground, and as a related figure, diurnal changes in VPD are more extreme, too. Thus small plants are especially likely to suffer from drought stress.

Measured (Piche) and calculated potential evapotranspiration (Table 2) were correlated on Mt. Elgon (Pearson product moment correlation r = 0.88). Dry conditions were most pronounced from February to March. Measured Piche evaporation totalled 300 mm for the 60 dry days in 1997, and therefore the average daily Piche evaporation was 6.3 mm. The corresponding figure (mean pan evaporation) was 7.5 mm d^{-1} in the Bale Mountains during the drought in 2000.

These were not, however, average conditions. In both study sites locals complained about the severe and unusual drought, which caused difficulties for crop production and livestock grazing. Unfortunately, because no long-term climatic records exist from high altitude sta-

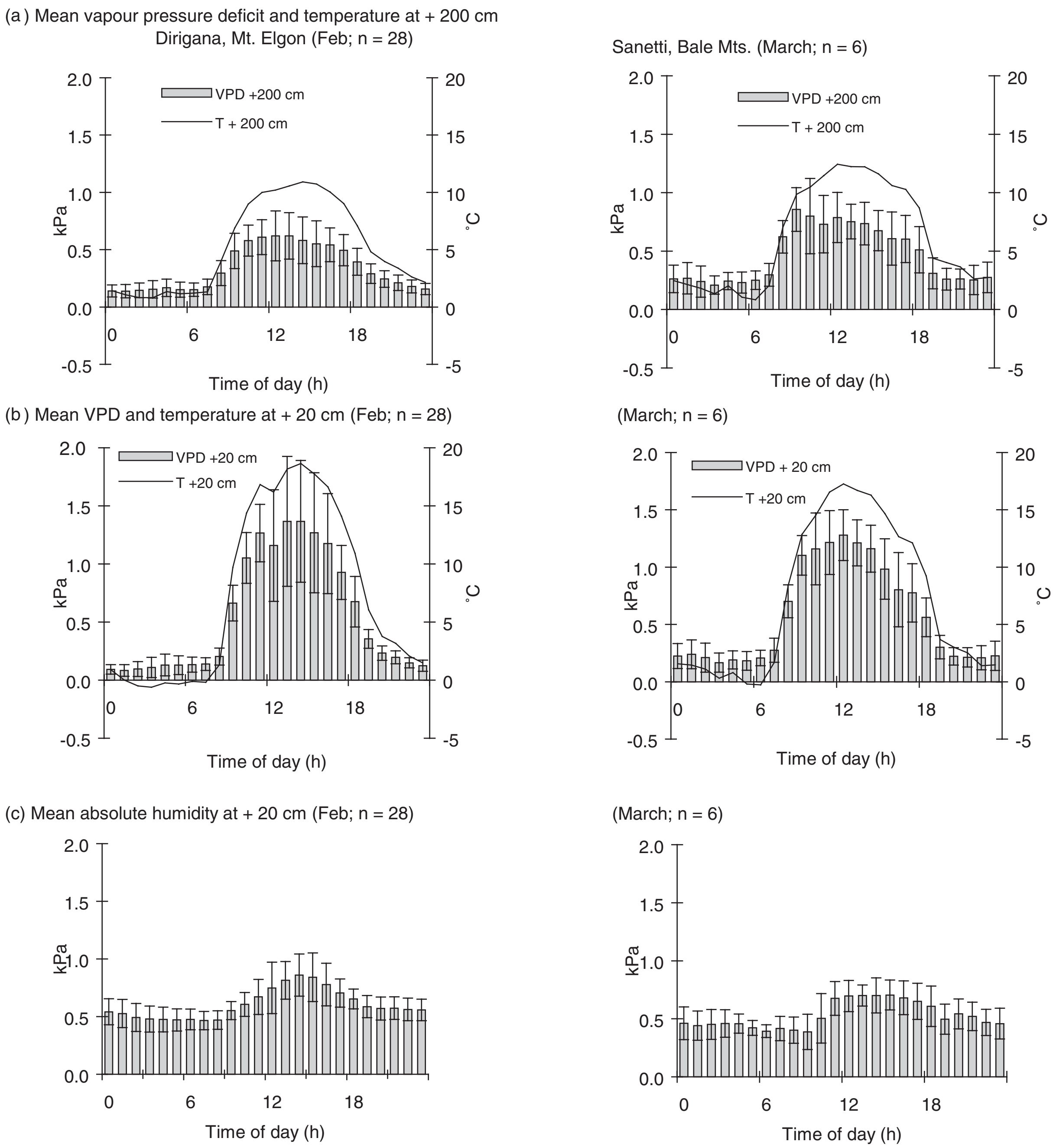

Figure 3. Comparison of hourly means of temperature and moisture values for Dirigana Camp, Mt. Elgon (3750 m, February 1997) and Sanetti plateau, Bale Mountains (3880 m asl, March 2000). Vertical lines indicate standard deviation for the given period. (a) Mean vapour pressure deficit and temperature at +200 cm above the surface. (b) Mean VPD and temperature at +20 cm above the surface. (c) Absolute humidity (real vapour pressure) at +20 cm above the surface.

tions in any of the African mountains, this inter-annual variability of rainfall could only be analysed for a lowland station in the vicinity of the study sites.

Tororo station is situated in the south-western foot of Mt. Elgon (1170 m), which has the wettest exposure. Annual precipitation totals over the last 50 y were highly variable (Figure 5a), but sums of dry-season precipitation (January and February) showed an even larger annual variation (Figure 5b). If we consider a precipitation of less than 50% of the long-term mean as indicative of drought conditions (Nieuwolt 1978), then unusually severe dry seasons occurred every 7–10 y. On Mt. Elgon 28 mo of rain records at an altitude of 3750 m were available to analyse the relationship between lowland and highland

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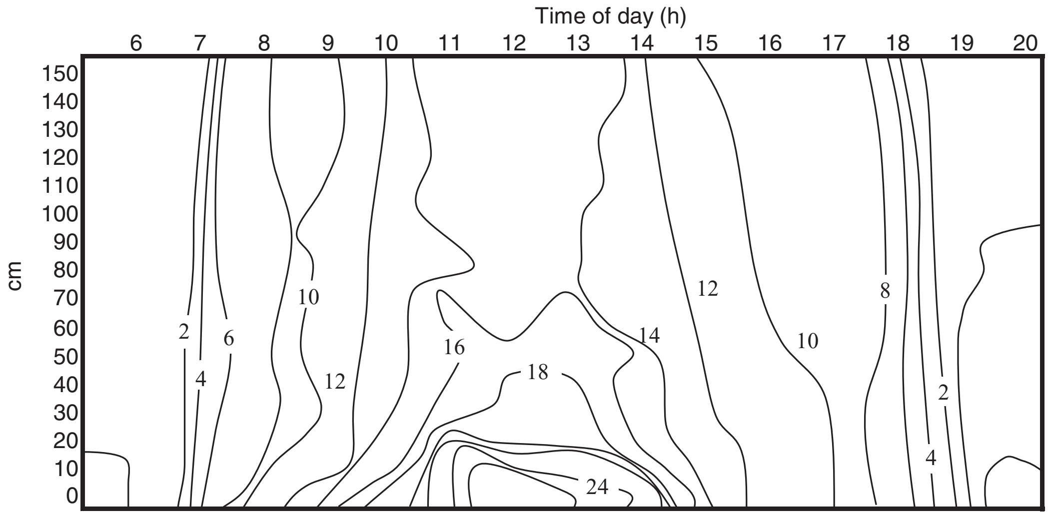

Figure 4. Vertical distribution of air temperatures at a typical dry-season day on the Sanetti plateau (3880 m; 12 March 2000). The lines are simplified thermoisopleths connecting similar temperature values measured at various heights above ground.

stations. A comparison indicated a similar seasonal pattern at both stations (data not shown).

Impact of drought on afroalpine vegetation

A striking consequence of drought was the wilting of leaves, which was particularly conspicuous in giant groundsels. On Mt. Elgon *Dendrosenecio elgonensis* (T. C. E. Fr.) E. B. Knox ssp. *elgonensis* showed badly wilted leaves and rosettes that appeared to be almost dead in March 1997. Continued observations revealed that damage was not permanent, however: with the onset of the rains in April plants recovered quickly and signs of damage disappeared. *Erica trimera* (Engl.) Beentje bushes showed similar signs of desiccation on Mt. Elgon and up to 50% of leaves died, but the plants always survived. The highest stands occurred at some 3950 m on rocky shallow soils with low water retention capacity. Although dried wood gave evidence of previous droughts, plants had freshly green leaves at most branches.

Similar phenomena were observed in the Bale Mountains, although the species concerned were partly different. Drought there was so severe in 2000 that it was difficult to find any green plant matter at all. The local giant rosette plant *Lobelia rhynchopetalum* Hemsl. showed similar drought effects to the giant groundsels on Mt. Elgon. Again the damage was not permanent (Masresha Fetene, *pers. comm.*).

While the temporary impacts of drought stress are visually striking, plant phenology appears to be little affected. The richness of plant species on Mt. Elgon did not change during the study period and was independent of monthly rain totals. Most species were perennials and not strongly influenced by drought, virtually no species disappeared from any of the subplots. None of the shrubs higher than 30 cm died during the drought. Seedlings were generally rare all year around; most species were perennials with apparently limited recruitment.

The fraction of species flowering was low at any given time of the year, but slightly more species flowered under dry conditions, notably in December and January. A weakly negative relationship between monthly rain totals and number of species flowering was found. Plants were apparently able to enhance reproductive activity even under drought conditions. Another consequence of drought conditions was more striking than phenological changes: extensive fires were observed in both study areas.

Afroalpine fires

After the vegetation on Mt. Elgon had sufficiently dried in 1997, severe fires destroyed the larger part of the afroal-

Table 2. Potential evapotranspiration for Mt. Elgon, Dirigana Camp (3750 m). Evapotranspiration was estimated with Piche evaporimeters, data are given for 20 cm height above ground. These estimates were compared to a theoretically derived value based on the Penman approach (E_T, Barry 1992) and to the actual precipitation (all figures in mm).

	N96	D96	J	F	M	A	M	J	J	A	S	O	Total
Piche Evap.	53.7	74.9	103.6	177.4	140.3	65.5	155.2	93.4	39.8	49.8	149.1	80.9	1183.6
Daily Mean	1.8	2.4	3.3	6.3	4.5	2.2	5.0	3.1	1.3	1.6	5.0	2.6	3.3
Penman Evap.	82.9	69.3	87.0	116.3	92.8	67.9	101.5	60.0	48.7	49.6	106.5	79.7	962.2
Precipitation	85.2	29.7	45.6	0.0	44.4	205.0	44.8	59.7	113.6	156.9	112.2	144.4	910.7

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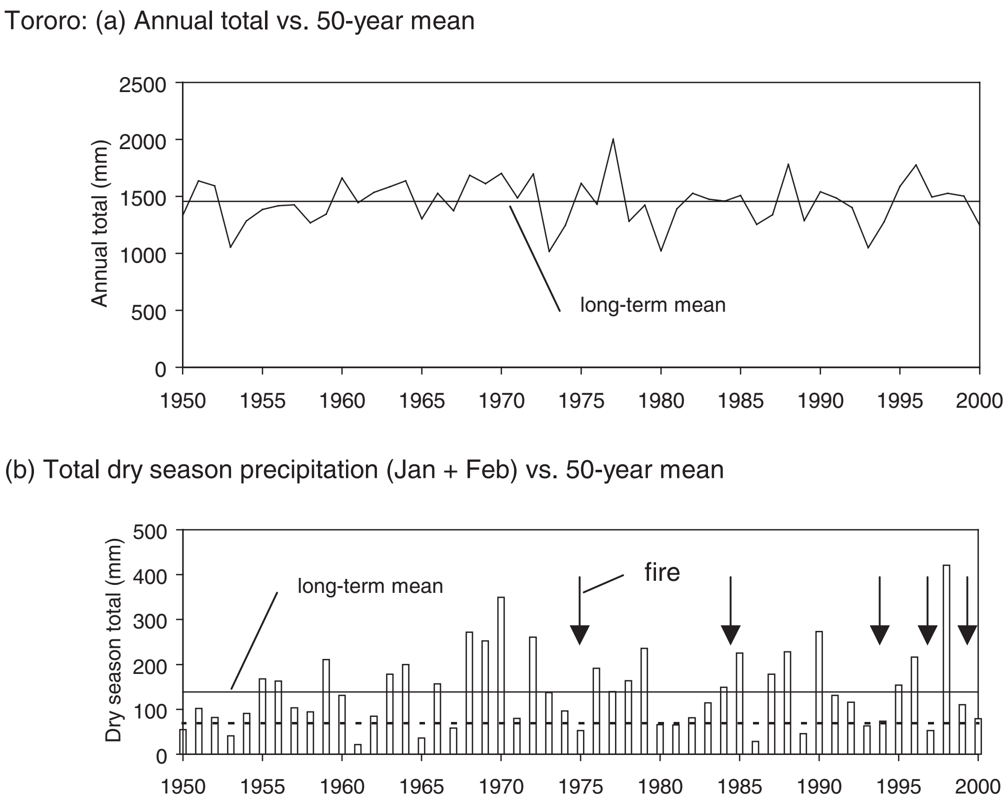

Figure 5. Inter-annual rainfall variability in the Mt. Elgon region. (a) Annual totals for the years 1950–2000 in relation to the long-term mean for the same period. (b) Rainfall for the main dry season (January and February only), the broken line gives the 50% threshold of the 50-year mean. Arrows indicate years for which published records of severe fires in the afroalpine belt of Mt. Elgon are available.

pine vegetation in February and March. Fires scorched afroalpine grasslands as well as *Carex runssoroensis* K. Schum. bogs and ericaceous vegetation; whereas, moist upper montane forest retained sufficient moisture to prevent burning (cf. Wilson & Agnew 1992). Because mostly grasslands and scrub were involved, fires were largely ground fires; in cases of higher ericaceous vegetation with *Stoebe kilimandscharica* O. Hoffm., *Erica trimera* and *E. excelsa* (Alm & Fries) Beentje crown fires were common. In these instances virtually all leaves were combusted. Ericaceous plants survived the fire and resprouted within weeks. Grassland fires were usually fast and relatively cool; whereas fires among ericaceous vegetation were intense due to the amount of fuel available. Still, the peaty soils were rarely affected and direct impact of fires was visible in soil pits up to 2 cm depth. Fires covered about 60% of the central caldera, and the percentage was roughly similar on the outer slopes with the drier eastern slopes being more seriously affected. All fires were human-made; poachers lit the vegetation wherever possible to improve hunting conditions (low grass, fresh green pasture for duikers). Thunderstorms were not observed on Mt. Elgon during the dry season.

Fires in the severe dry season of 1999 on Mt. Elgon were again disastrous. This time most of the afroalpine vegetation on the western slopes that was spared in 1997 was destroyed. Dry montane forests with *Juniperus procera* Endl., *Olea europaea* L. ssp. *africana* (Mill.) P. Green and *Podocarpus falcatus* Mirb. burned on the eastern slopes while on the moister slope complexes only bamboo forest (*Sinarundinaria alpina* (K. Schum.) Chao & Renv.) caught fire. Upper montane forest with *Hagenia abyssinica* (Bruce) J. F. Gmel. and *Erica excelsa* survived only in small depressions. This is clearly seen in an aerial picture, where dark grey bands of forest along small brooks are differentiated against light grey, freshly burned vegetation (Figure 6).

A very similar situation was encountered in Ethiopia. Here the drought in early 2000 resulted in extremely heavy fires that gained wide public attention. Fires were particularly severe in the south-east of the country and were easily observed in the Bale Mountains. In a striking parallel to Mt. Elgon, montane forests near the timberline often survived in small gullies creating a pattern similar to Figure 6.

DISCUSSION

It is obvious that afroalpine plants are exposed to potentially desiccating conditions during drought periods.

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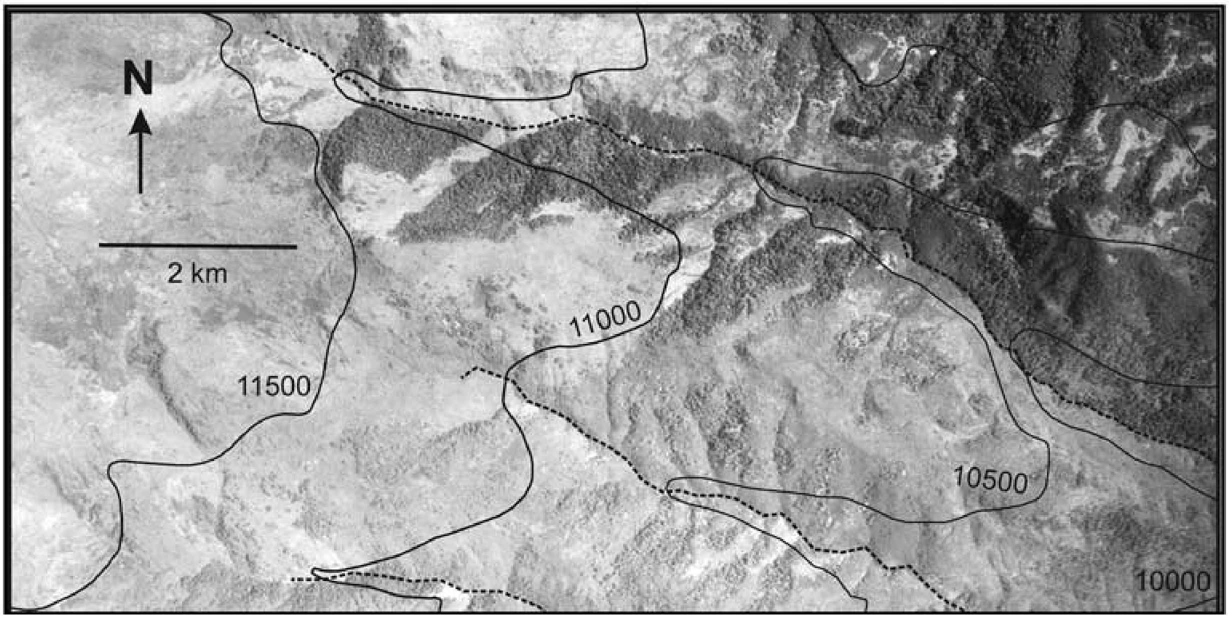

Figure 6. Aerial photograph (scale 1:25 000) of the upper eastern side of Mt. Elgon after the severe fires in 1999. Broad-leaved montane forest with *Hagenia abyssinica* survived in small valleys only. Contour lines were enlarged from 1:50 000 topographic maps of Mt. Elgon area (D.O.S. 1962), but are given only for every 500 feet (broken lines = river courses).

Values for VPD in tropical mountains commonly attain 1.0 to 2.0 kPa at noon (Kitayama 1992, Kitayama & Mueller-Dombois 1994, Leuschner & Schulte 1991, Masresha *et al*. 1998). Although values for VPD are usually higher in the lowlands due to the higher temperatures in the shade, insolated surfaces can heat up well above ambient temperature in highlands (Cabrera *et al*. 1998, Hedberg & Hedberg 1979, Leuschner & Schulte 1991, Walter & Breckle 1984, Young 1983). This effect is even more pronounced if leaves are situated near the soil surface, with its diurnal temperature extremes (Braun 1997, Diemer 1996, Kitayama 1992, Masresha *et al*. 1998, Pfitsch 1988). Consequently, leaves in mountain areas also experience high saturation deficits (Körner 1999). This corresponds to calculations based on general climatic models, which suggest that plant transpiration increases or decreases only weakly with elevation depending on the leaf characteristics assumed (Leuschner 2000, Smith & Geller 1979). In any case, modelled and measured transpiration rates are in the same order of magnitude for lowland and highland plants, i.e. 2–10 mm d^{-1} (Körner 1999).

The correlation between potential evaporation and elevation appears to be weakly negative on many tropical and subtropical mountains (Keig *et al*. 1979, Nullet & Juvik 1994). This is different, when a high altitude temperature inversion is present, so that clear skies can result in high potential evaporation figures. This is most often found in subtropical mountains but such inversions have also been reported from tropical East Africa (Winiger 1986). A similar situation is found on some outer oceanic islands, where potential evaporation increases with altitude (Kitayama & Mueller-Dombois 1994).

In the tropical Andes modelled annual evaporation exceeds 1100 mm above 4000 m asl (Henning & Henning 1981). These data are comparable to figures from Mt. Elgon, where measured and modelled PET ranged between 950 and 1150 mm y^{-1}, compared with some 900 mm of precipitation. Mean annual pan evaporation for lowland stations around Mt. Elgon is higher; 1600 mm at Eldoret (2080 m), while Tororo records 2100 mm (Griffiths 1972*a*). Mean annual precipitation is above 1500 mm at both sites. Thus, deficits in the water budget are equally probable on top of Mt. Elgon as in the surrounding lowlands.

Data for the Ethiopian plateau suggest a Piche evaporation of 1800–2000 mm and modelled PET ranges between 1700 mm for the lower and 1050 mm for the upper montane regions (Gamachu 1990, Griffiths 1972*b*). Mean annual precipitation on the plateau is 1300–2000 mm. Given that precipitation generally peaks in the montane belt and decreases in the uppermost belts (Barry 1992, Lauer 1975, Leuschner & Schulte 1991), deficits in the water balance on tropical mountains are to be expected on both theoretical and empirical grounds (Leuschner 2000).

However, PET figures usually overestimate actual evaporation. Piche and pan evaporimeters are fed with a continuous water supply; whereas, evaporation in soil or plants ceases or decreases with time, if water becomes limited. The Penman approach models the evaporation of a water surface, again a quite inadequate model for actual

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evaporation of a given ecosystem. Unfortunately, in most cases no data for actual evapotranspiration are available to evaluate the value of measured or modelled PET figures in tropical mountains. The figures discussed above suggest higher water losses than gains, which is obviously an exaggeration. Most tropical mountains feed permanent rivers; thus they are clearly water-surplus sites. Deficits are at most temporary and indeed river discharge in the afroalpine zone of Mt. Elgon stopped only for some few weeks in the middle of the dry season, and is normally continuous.

Therefore, the debate on possible hygric limitations of high-altitude plants centres not on the occurrence but on the significance of dry conditions. Various authors reported data that suggest severe and potentially limiting water stress at the upper limit of plant growth (Beck 1994, Leuschner 2000, Meinzer *et al.* 1994, Pfitsch 1988), but direct evidence is rare. Plants at high elevations show similar morphological traits to those from arid environments, e.g. small and furrowed leaves of sclerophyllous shrubs like *Erica trimera*. Such scleromorphic features tend to become more common with increasing elevation in afroalpine environments (Hedberg 1964). The apparently moisture-controlled presence of C4 grasses on Mt. Kenya is another example for the significance of a moisture-conserving trait in afroalpine environments (Young & Young 1983). The most prominent example in eastern Africa is the summit region of Mt. Kilimanjaro, which experiences an annual precipitation well below 100 mm, such that the vegetation gives a desert-like impression. Scleromorphic species are equally common in alpine regions elsewhere (Smith & Young 1987, Tranquillini 1964, Wardle 1974), although occasionally species might show hygromorphic properties as well (Halloy 1989). Hence, it has been repeatedly hypothesized that desiccation stress is significant for high-altitude plants.

If this were the case, however, effects in the field should have been more straightforward. Observations on Mt. Elgon and in the Bale Mountains do not support the idea of water-related limits to adult plant growth. Plant communities on Mt. Elgon showed increased flowering activity during dry-season conditions, although increased reproductive effort can also be interpreted as a response to potentially life-threatening conditions (Beck *et al.* 1986). The fact that the highest remote stands of ericaceous vegetation were regularly found on the driest slopes (Miehe & Miehe 1994) contradicts the idea of water limitations. The same refers to Mt. Elgon's *Erica trimera* outposts on rocky outcrops with a thin soil cover and a low water-retention capacity. If water availability were the limiting factor, plants should reach higher elevations on well-developed soils, which provide water during dry-season conditions. This was the case neither on Mt. Elgon nor on the Bale Mountains, and none of the *Erica* bushes on Mt. Elgon died on rocky outcrops. Because 1997 on Mt. Elgon and 2000 in the Bale Mountains were definitely extreme years, death should have occurred if water stress were the crucial factor.

These findings support the conclusion that alpine plants have adopted ways to cope with dry conditions at high altitudes, such that the experienced physiological stress is much lower than would be expected from climatic data alone (Halloy 1989, Körner 1999). This includes protective mechanisms on the level of the photosynthetic apparatus as have been demonstrated for *Lobelia rhynchopetalum* (Masresha *et al.* 1997). The relative unimportance of water relations for adult plants is indirectly confirmed by a recent analysis (Körner 1998) that reported a clear (and already well-known) coincidence of the upper treeline positions and mean temperatures all over the globe. Given that mountains display a wide variety of moisture conditions, such large-scale similarities should not be found if water relations were decisive for plant growth.

Consequently, I propose that precipitation has a more indirect influence in two ways, both related to the much-emphasized inter-annual variation. Fire is among the most striking consequences of dry conditions almost everywhere (e.g. Goldammer 1990). Droughts trigger severe fires in high-altitude environments as well, although unfortunately fire records are approximate for afroalpine environments, partly because the satellite imagery most widely used for global fire monitoring (NOAA-AVHRR) has only recently become available at a higher resolution (1×1 km) for Africa. Nonetheless, fires in high elevations have been reported for the majority of mountain ranges in East Africa, South-East Asia and South America (Corlett 1987, Horn 1997, Luteyn 1999, Wesche *et al.* 2000, Williamson *et al.* 1986).

There is no doubt that such fires have a tremendous impact on the physiognomy of the vegetation and cause a replacement of community types. Examples for a fire-induced change from woody to grassland vegetation in tropical-'alpine' environments are *Polylepis* woodlands in South America (Ellenberg 1979, Kessler 1995, 2000), ericaceous vegetation in East Africa (Miehe 2000, Miehe & Miehe 1994, Wesche *et al.* 2000), and Ericaceae-*Rapanea* forest in New Guinea (Corlett 1987). Most frequently, high-elevation stands of upper montane trees on rocky sites are remnants of a formerly more widespread woody vegetation, which survived on sites that are edaphically unfavourable but offer fire protection (Wesche in press).

While some information is available on fire and inter-annual rainfall variability, we know virtually nothing about their significance for plant establishment. Because microclimatic conditions in tropical-alpine environments are relatively extreme near the ground, the seedling phase might be the crucial stage in plant life. On Mt. Elgon the uppermost closed stands of *Erica trimera* are found on rocky outcrops, where the vegetation is too scattered to support a fire. Shrubs suffer from conspicuous drought stress, and regeneration has not occurred in recent years. Relatively moist years, as occurred in the late 1960s (Rohde & Virji 1976, cf. Figure 5) might have facilitated the establishment of trees on sites that are otherwise too extreme for regeneration. Although these trees appear to be of one size class, no definite conclusion can be drawn because dendrochronological dating is generally impossible (Kaeppeli 1998).

Thus, the current state of knowledge does not support the idea that water stress of the adult plant is the limiting factor in afroalpine environments and tropical mountains in general. Nevertheless, I follow Moreau (1938) and regard extreme precipitation in terms of abnormally wet and dry years as extremely important for the physiognomy of a given landscape. Extremely dry years trigger severe fires, while moist phases offer suitable conditions for tree seedling establishment. However, what is clearly needed is long-term precipitation data for tropical mountains and, perhaps even more importantly, research on population ecology. Such research should concentrate on the regeneration after fire and the modes of establishment of keystone species.

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