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## **AN ALTITUDINAL AND STABLE CARBON ISOTOPE SURVEY OF C<sub>3</sub> and C<sub>4</sub> GRAMINOIDS ON MOUNT KENYA**

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### **ABSTRACT**

An altitudinal survey of grasses and sedges was conducted on the Sirimon and Chogoria tracks on Mount Kenya to supplement previous surveys restricted to the Timau track. Thirty seven grasses and twenty three sedges were recorded and stable carbon isotope analysis was used to identify the photosynthetic pathway (C<sub>3</sub> or C<sub>4</sub>) used by these species. The occurrence of a group of C<sub>4</sub> graminoids was confirmed close above the tree line, and the literature suggests this may also hold for the Aberdares Range and other East African mountain massifs. Lower altitude graminoids are C<sub>3</sub> forest species, and this distribution upsets the assumption that C<sub>4</sub> gives way to C<sub>3</sub> with increasing altitude. The significance of this is discussed in relation to the interpretation of palaeoenvironments through carbon stable isotope proxies.

### **INTRODUCTION**

Mount Kenya has been the focus of research dedicated to reconstructing Late Quaternary vegetation change in the tropics (Coetzee, 1967; Street-Perrott, 1994; Street-Perrott *et al.*, 1997; Ficken *et al.*, 1998; Huang *et al.*, 1999a, b; Wooller *et al.*, 2000), which relies on a comprehensive understanding of the present altitudinal distribution of plants. Although a number of botanical surveys have been conducted (Bussmann, 1993; Ongaro, 1997) information on the precise distribution of grasses and sedges is lacking. Poaceae and

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Cyperaceae are particularly interesting families in that they are split between using the C<sub>3</sub> and C<sub>4</sub> photosynthetic pathways, each of which would have been favoured at different times during Late Quaternary climate change (Ehleringer *et al.*, 1991; 1997; Street-Perrott *et al.*, 1997). Grasses, like other plants, fix carbon dioxide from the atmosphere by photosynthesis but there are three primary photosynthetic pathways: CAM, C<sub>3</sub> and C<sub>4</sub>. Only the latter two are relevant to this investigation since the CAM pathway (used by succulents) does not occur in the grass (Hattersley, 1992) or sedge (Hesla *et al.*, 1981) families. The C<sub>3</sub> pathway is used by almost all trees, most shrubs and herbs, and cool climate grasses (Cerling & Quade, 1993; MacFadden & Cerling, 1994). On a global basis, the majority of C<sub>4</sub> taxa are grasses (Downton, 1975; Teeri and Stowe, 1976; Hattersley, 1983;) and sedges (Teeri *et al.*, 1980). Almost 60% of the ~10,000 grass species that exist today use the C<sub>3</sub> photosynthetic pathway, while approximately 40% use the C<sub>4</sub> pathway (Brown, 1977; Hattersley, 1992; Henderson *et al.*, 1995).

### Environmental variables controlling C<sub>3</sub> and C<sub>4</sub> grass distribution

Previous studies concerned with the altitudinal distribution of C<sub>3</sub> and C<sub>4</sub> grasses have shown a diminishing abundance of C<sub>4</sub> grasses and a concomitant increase in C<sub>3</sub> grasses with altitude (Tieszen *et al.*, 1979; Rundel, 1980; Long, 1983 and references therein; Young & Young, 1983). The distribution of C<sub>3</sub> and C<sub>4</sub> grasses is determined by a number of factors. Past environments have differed in concentrations of atmospheric CO<sub>2</sub>, which must have influenced the relative success of C<sub>3</sub> and C<sub>4</sub> plants, since the C<sub>4</sub> pathway has the more efficient method of capturing CO<sub>2</sub> (Ehleringer *et al.*, 1997). In modern vegetation, where large variations in ambient CO<sub>2</sub> do not occur, it is the temporally varying combination of temperature, rainfall, fire and light that determine competitive interactions between C<sub>3</sub> and C<sub>4</sub> grasses (Gillison, 1983; Hattersley, 1992; Lee-Thorp & Beaumont, 1995; Epstein *et al.*, 1997; Fredlund & Tieszen, 1997).

### Stable carbon isotopes

C<sub>3</sub> and C<sub>4</sub> plants can be distinguished from each other by analysis of the ratio of carbon stable isotopes preserved in their organic (e.g. leaves and roots) and inorganic (e.g. phytoliths) components (Kelly *et al.*, 1991). There are three isotopes of carbon; <sup>12</sup>C, <sup>13</sup>C and <sup>14</sup>C, only two of which—<sup>12</sup>C and <sup>13</sup>C—are stable, while <sup>14</sup>C is unstable and decays over time. The <sup>12</sup>C isotope forms 98.9% of the atmospheric inventory of carbon while <sup>13</sup>C occupies 1.1% (O'Leary *et al.*, 1992). Differential capture of the stable isotopes occurs during carbon dioxide assimilation in photosynthesis and is due to the more rapid diffusion of CO<sub>2</sub> formed with the lighter isotope <sup>12</sup>C and partial exclusion of <sup>13</sup>C (O'Leary *et al.*, 1992; Gillon *et al.*, 1998). One of the physiological characters of C<sub>3</sub> plants is that they discriminate between the stable carbon isotopes (<sup>12</sup>C and <sup>13</sup>C) during carbon assimilation to a greater extent than C<sub>4</sub> plants (Peisker and Henderson, 1992). Conventionally the carbon isotope composition of a specimen is expressed as δ<sup>13</sup>C in parts per thousand (‰) with respect to the Pee Dee Belemnite (PDB) standard (Craig, 1957) using the formula:

$$\delta^{13}\text{C} \text{ ‰} = \frac{[\frac{^{13}\text{C}}{^{12}\text{C}} \text{ sample} - \frac{^{13}\text{C}}{^{12}\text{C}} \text{ standard}]}{\frac{^{13}\text{C}}{^{12}\text{C}} \text{ standard}} \times 1000$$

### Aim

Surveys of C<sub>3</sub> and C<sub>4</sub> grasses on Mount Kenya have been restricted to the northern flank (Timau track) where grasses are dominant over most of the altitudinal range (Tieszen *et al.*,

1979; Young & Young, 1983). However, the simple model of a cross-over of dominance from C<sub>4</sub> to C<sub>3</sub> grasses with an increase in altitude is complicated by the presence of C<sub>3</sub> dominated vegetation (montane rainforest) at intermediate altitudes in much of the tropics (Hedberg, 1955; Schmitt, 1991) and there is some evidence for high-altitude sites with C<sub>4</sub> grasses (e.g. RamaDas & Vats, 1993). We surveyed the altitudinal distribution of C<sub>3</sub> and C<sub>4</sub> graminoids (grasses and sedges) on the Chogoria and Sirimon tracks, which pass through montane rainforest on Mount Kenya. Rather than enquiring into the physiological mechanisms determining graminoid distribution, we wished to establish and describe their altitudinal distribution, although some causal mechanisms are discussed.

### Study site

Mount Kenya is located on the Equator in Kenya (figure 1). The climate is dominated by the seasonal passage of the inter-tropical convergence zone (ITCZ), with large diurnal temperature oscillations and small monthly variations during the course of the year. Rainfall maxima in March–June (heavy long rains) and October–November (short rains) (Coe, 1967) correspond with the double passage of the ITCZ, which lags behind the zenith position of the sun (Ogallo, 1991). Dry seasons (July–September and December–February) occur between the periods of high rainfall (Archibold, 1995) and have at least one month of less than 60 mm of rain and a mean monthly temperature minimum of 18°C. Regular fires in low altitude dry vegetation types at the end of the main dry seasons reinforce this annual climatic rhythm (Vesey-Fitzgerald, 1973; Smith, 1987; Archibold, 1995). Mount Kenya, like other tropical mountains (Hedberg, 1955), currently has essentially discrete zones of vegetation distributed over an altitudinal gradient (Fries & Fries, 1948). We recognised the basic vegetation zones outlined by Fries and Fries (1948), Hedberg (1955), and Coe (1967) (figure 2). A gap in the forest on the northern flank of Mount Kenya corresponds with relatively low rainfall values on the mountain and Bussmann (1993) suggested that this originated as a result of human disturbance.

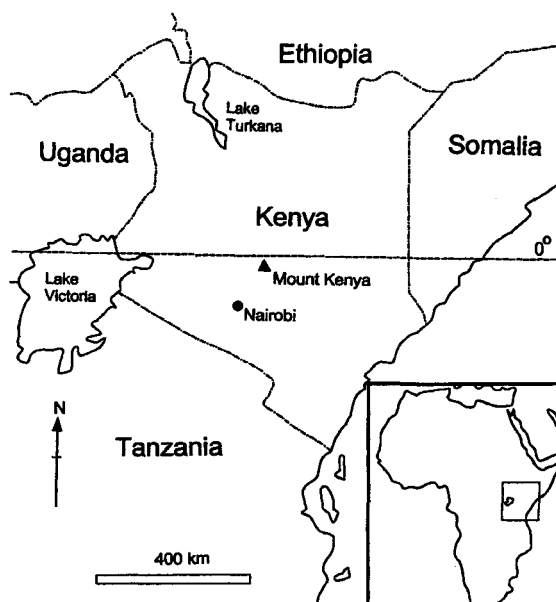


Figure 1. The location of Mount Kenya, Kenya, East Africa.

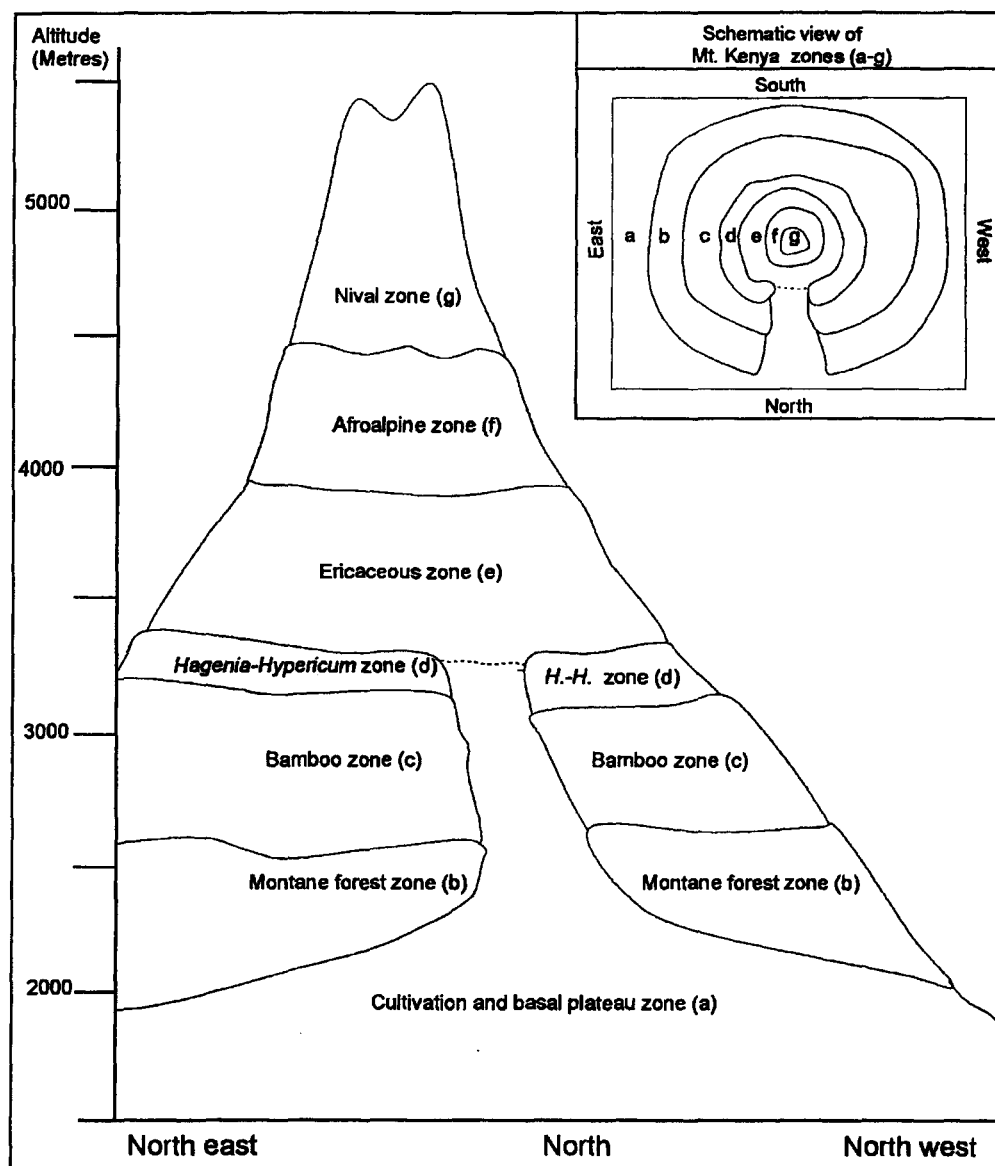


Figure 2. The general pattern in the distribution of plants on Mount Kenya. Adapted from Coe (1967). A gap in the forest zones exists on the north flank, which is dominated by grasses. (a) Basal plateau zone: dominated by grasses; (b) Montane forest zone: dominated by trees and shrubs<sup>2,3</sup>; (c) Bamboo zone: dominated by *Arundinaria alpina* (Bamboo); (d) Hagenia-Hypericum (H.-H.) zone: dominated by woody trees and shrubs<sup>2</sup> with grasses present<sup>1,2,3</sup>; (e) Ericaceous zone: dominated by woody shrubs and grasses<sup>1,3</sup>; (f) Alpine zone: dominated by tussock grasses<sup>4,5,6</sup>; (g) Nival zone: isolated grasses present in very sheltered areas<sup>1</sup>. 1, Coe (1967); 2, Bussmann (1993); 3, Fries and Fries (1948); 4, Young and Young (1983); 5, Tieszen et al. (1979); 6, Livingstone and Clayton (1980)

## METHODS

### Field survey

A vegetation survey of graminoids (grasses and sedges) along two altitudinal transects on Mount Kenya was carried out in 1997 (January to February). The survey design was based on that used by Young and Young (1983) to sample the local distribution of C<sub>3</sub> and C<sub>4</sub> grasses on Mount Kenya, in that vehicle tracks up the mountain were used as the basis for altitudinal transects, although all samples were at least 50 m distance from roads or major tracks to avoid areas obviously disturbed. The Chogoria track (Carr's Road) from the town of Chogoria (eastern flank), and the Sirimon track (north-western flank) were accessed from approximately 1300 metres above sea level (m.a.s.l.). The lowest altitude limit of the transect series was the edge of cultivation and disturbance (~1960 m.a.s.l.). A stratified sampling regime was used at two levels. A primary level was subjectively based on observation of the primary vegetation zones following previous vegetation surveys of Mount Kenya (Fries and Fries, 1948; Coe, 1967), including the lower montane forest, upper montane forest, bamboo, '*Hagenia-Hypericum*', ericaceous, lower alpine and upper alpine zones. A second level of stratification involved selecting, in most cases, three sites representing the topographic variation within each of the vegetation zones. Three quadrats were randomly placed at each of the sites. Quadrats 5 x 5 m were used in vegetation zones with a sparse ground layer (lower montane forest zone, upper montane forest zone and bamboo zone), whilst 2 x 2 m quadrats were used in vegetation with a dense ground layer (*Hagenia-Hypericum* zone, ericaceous zone, lower alpine zone and upper alpine zone). The position of each quadrat was randomised using a random walk method, where a random number from 1 to 360 determined the direction of travel from a starting point within the habitat and a number from 1 to 50 determined the number of single paces taken from the starting point.

Altitude, in meters above sea level (m.a.s.l.), determined using a Thommen Altitronic Traveler altimeter, and a site description were recorded for each site. Presence of graminoid species was recorded from each quadrat and a specimen of each was collected and dried within three days of field collection. Graminoid specimens were taken to a local town (Meru for the Chogoria transect and Naro Moro for the Sirimon transect), dried using an electric drier, and packaged for transportation to the University of Wales Swansea, UK. Descriptive notes were taken regarding the dominant trees and shrubs present in the vicinity of each site. Evidence of past fires (charred vegetation) and the presence of herbivore faeces were noted. The field survey was conducted during a single dry season and special efforts were made to locate dead or dying material representing annual grasses. Any standing dead grass or sedge material, representing specimens not previously encountered, were collected and stored in paper bags for transport to the UK for identification. All graminoid specimens were identified in the Herbarium, University of Wales Aberystwyth, UK, by the authors. Where any doubt existed as to the correct identification of a specimen it was taken for comparison with material at the Royal Botanic Garden, Kew, UK. Specimens are also to be deposited in the East African National Herbarium in the National Museums of Kenya.

### $\delta^{13}\text{C}$ analysis

A leaf from each species collected during the field survey was submitted to the NERC facility at East Kilbride, Scotland for analysis of carbon stable isotope ratios, to determine whether the graminoids encountered used the C<sub>3</sub> or C<sub>4</sub> photosynthetic pathway. C<sub>3</sub> and C<sub>4</sub> classifications were based on a  $\delta^{13}\text{C}$  range of -22 to -33‰ being indicative of C<sub>3</sub>

photosynthesis and a  $\delta^{13}\text{C}$  range of -9 to -16‰ being indicative of  $\text{C}_4$  photosynthesis (Deines, 1980).

## RESULTS

### Graminoid specimens and $\delta^{13}\text{C}$ data

Table 1 shows the total list of grass species recorded during the field survey of graminoids on the Chogoria and Sirimon tracks on Mount Kenya. Species of graminoids listed in table 1 are common to the upland vegetation of Kenya (Agnew, in preparation). All five of the grass subfamilies are represented in table 1. Table 2 shows the total list of sedges recorded during the field survey. The sedge *Rynchospora augdensis* Turrill is a first Kenyan record and was found on the raised bog at Lake Rumuiku. Tables 1 and 2 also show the  $\delta^{13}\text{C}$  values derived from graminoid specimens taken during the field survey. Two  $\delta^{13}\text{C}$  values are shown for some specimens where sufficient specimens were available for more than one analysis.  $\delta^{13}\text{C}$  values for the graminoid species and subsequent classifications as either  $\text{C}_3$  or  $\text{C}_4$  are consistent with other data available on the photosynthetic pathway used by the species (Watson and Dallwitz, 1994), with the exception of *Andropogon schirensis*, which is classified as  $\text{C}_3$  in table 1 and is an Andropogonid, all of which are cited as  $\text{C}_4$  (Watson & Dallwitz, 1994). This result indicates that the taxonomic identification of the *Andropogon schirensis* specimens should be questioned, which is considered in the discussion section.

### The altitudinal distribution of grasses on the Chogoria and Sirimon tracks on Mount Kenya

The following are brief descriptions of vegetation zones (strata) along each altitudinal transect, giving the general features of the sampling sites at which the nine quadrats were recorded. Zone names are in bold and we emphasise the field criteria used in their demarcation. Six zones were identified and used as strata in the sampling regime: upper montane forest zone, bamboo zone, *Hagenia-Hypericum* zone, ericaceous zone, lower alpine zone, and the upper alpine zone.

#### Chogoria altitudinal transect

Altitudinal limits of the graminoids observed during the field survey of the Chogoria track are shown in table 3 where species are ordered according to the centres of their respective altitudinal distributions. The vegetation survey started at ~1960 m.a.s.l. on the Chogoria track in moist montane rainforest, below which the landscape was agricultural.

Most of the forest surveyed on the Chogoria track was dominated by the genera *Cassipourea* sp., *Macaranga* sp., *Podocarpus* sp. and *Tabernaemontana* sp., while *Canthium* sp., *Celtis* sp., *Buddleja* sp., *Maesa* sp., *Psychotria* sp. and *Vitex* sp. were also evident. The boundary between the **upper montane forest** and the bamboo zone was distinct. The sites surveyed had topographical gradients that ranged between 10° and 20°. Vegetation of the **bamboo zone** was dominated by *Arundinaria alpina* (bamboo), which formed a dense canopy 5 to 15 m high with a cover of 30% to ≥95%. Large stems of the trees *Podocarpus latifolius*, *Hagenia abyssinica* and *Juniperus procera* and the shrub *Erica arborea* were interspersed between the dense stands of *Arundinaria alpina*. The boundary between the

Table 1. The total list of grass species identified from an altitudinal survey of graminoids on Mount Kenya and classified as using the C<sub>3</sub> or C<sub>4</sub> photosynthetic pathway according to  $\delta^{13}\text{C}$  values derived from the analysis of specimens retrieved during the survey.

Species	$\delta^{13}\text{C}$	Species	$\delta^{13}\text{C}$
C <sub>3</sub> grasses		C <sub>3</sub> grasses	
<i>Acritochaete volkensii</i> Pilg.	-31.2	<i>Pentstschistis minor</i> (Ballard & Hubbard) Ballard	-25.4
<i>Agrostis kilimandscharica</i> Mez	-26.5	<i>Phalaris arundinacea</i> L.	-27.3, -26.4
<i>Agrostis quinqueseta</i> (Steud.) Hochst.	-25.9	<i>Poa annua</i> L.	-28.0
<i>Agrostis schimperana</i> Steud.	-24.8	<i>Poa leptoclada</i> A. Rich.	-30.5 -25.1
<i>Agrostis trachyphylla</i> Pilg.	-30.3	<i>Poa schimperiana</i> A. Rich.	-28.7
<i>Agrostis volkensii</i> Stapf	-28.0 -24.7	<i>Stipa dregeana</i> Steud.	-29.0, 30.5
<i>Andropogon schirensis</i> A. Rich.	-25.5	<i>Streblochaete longiarista</i> (A. Rich.) Pilg.	-30.8 -32.9
<i>Anthoxanthum nivale</i> K. Schum.	-24.1 -27.8	C <sub>4</sub> grasses	
<i>Arundinaria alpina</i> K. Schum.	-28.2 -27.7	<i>Andropogon lima</i> (Hack.) Stapf	-10.8
<i>Brachypodium flexum</i> Nees	-27.3, -27.0	<i>Andropogon amethystinus</i> Steud.	-12.7
<i>Bromus leptoclados</i> Nees	-23.7 -29.6	<i>Cymbopogon nardus</i> (L.) Rendle	-13.9 -12.6
<i>Calamagrostis hedbergii</i> Meld.	-28.5	<i>Digitaria abyssinica</i> (A. Rich.) Stapf	-11.3
<i>Ehrharta erecta</i> Lam. ( <i>E. abyssinica</i> Hochst.)	-29.9 -29.8	<i>Eleusine jaegeri</i> Pilg.	-12.0
<i>Festuca africana</i> (Hack.) Clayton ( <i>Pseudobromus silvaticus</i> K. Schum.)	-27.3	<i>Exotheca abyssinica</i> (A. Rich.) Anderss.	-12.0
<i>Festuca costata</i> Nees	-27.4	<i>Miscanthus violaceus</i> (K. Schum.) Pilg.	-11.2
<i>Festuca pilgeri</i> as in St. Yves	-25.9 -23.2	<i>subalbidum</i> Kunth	-12.2
<i>Isachne mauritiana</i> Kunth	-29.5	<i>Pennisetum clandestinum</i> Chiov.	-10.9
<i>Koeleria capensis</i> (Steud.) Nees	-24.2 -28.4	<i>Setaria megaphylla</i> (Steud.) T. Durand & Schinz	-11.3
<i>Opismenus compositus</i> (L.) P. Beauv.	-33.7 -33.0		
<i>Pentstschistis borussica</i> (K. Schum.) Pilg.	-29.6 -28.8		



Table 2. The total list of sedge species identified from an altitudinal survey of graminoids on Mount Kenya and classified as using the C<sub>3</sub> or C<sub>4</sub> photosynthetic pathway according to  $\delta^{13}\text{C}$  values derived from the analysis of specimens retrieved during the survey.

Species	$\delta^{13}\text{C}$	Species	$\delta^{13}\text{C}$
<b>C<sub>3</sub> sedges</b>		<b>C<sub>3</sub> sedges</b>	
<i>Carex chlorosaccus</i> C.B.Cl.	-28.2 -32.8	<i>Cyperus</i> sp.	-34.3
<i>Carex conferta</i> A.Rich.	-29.9	<i>Isolepis fluitans</i> A.Rich	-28.4
<i>Carex elongensis</i> Nelmes	-24.9	<i>Rhynchospora augdensis</i> Turrill	-27.0
<i>Carex johnstonii</i> Boeck.	-32.3	<b>C<sub>4</sub> sedges</b>	
<i>Carex monostachya</i> A.Rich.	-25.6	<i>Bulbostylis atrosanguinea</i>	-11.4
<i>Carex peregrina</i> Link	-30.6	(Boeck.) C.B.Cl.	-11.2
<i>Carex petitiana</i> A.Rich.	-26.4 -27.4	<i>Cyperus niger</i> Ruiz & Pav.	-10.0
<i>Cyperus ajax</i> C.B.Cl.	-30.8	<i>Cyperus atroviridis</i> C.B.Cl.	-11.1
<i>Cyperus denudatus</i> L.f.	-27.3	<i>Cyperus kerstenii</i> Boeck.	-11.3
<i>Cyperus dereilema</i> Steudel	-29.8	<i>Cyperus nigricans</i> Steud.	-10.6
<i>Cyperus fischerianus</i> A.Rich.	-31.4	<i>Cyperus sesquiflorus</i> (Torr.) Mattf.	
<i>Cyperus dichroostachyus</i>		& Kuk.	-11.4
A.Rich.	-30.5	<i>Cyperus tomaiophyllus</i> K.Schum.	-11.3

Bamboo zone and the *Hagenia-Hypericum* zone was sharp and distinct. The sites surveyed had slopes between 20° and 45°. Elephants were seen grazing in this vegetation and animal trails were evident throughout the zone. Buffalo tracks and animal dung were also evident throughout the vegetation surveyed. The *Hagenia-Hypericum* zone occurred in a narrow altitudinal range (~2900 to 3000 m.a.s.l.). Patches were dominated by *Hagenia abyssinica* and *Hypericum leucoptychodes*, separated by grasses and *Erica arborea* scrub. *Clusia* sp., large *Juniperus procera* stems and some *Arundinaria alpina* were also present. The boundary between the *Hagenia-Hypericum* vegetation and the ericaceous zone was sharp. The sparse canopy (15% to 30% cover) at the sites surveyed varied between 45 and 60 m in height. The sites had topographical gradients from 10° and 45°. Buffalo dung and trampled vegetation were evident at all of the sites surveyed and buffaloes and elephants were seen. The **Ericaceous zone** was dominated by *Erica arborea*, which formed a sparse and low canopy 1 to 5 m high. *Protea* and other woody genera (often ericoid) were present in the sites surveyed. Evidence of past fires, including the observation of singed tussocks and charred woody plants, was recorded at four of the five sites surveyed. The boundary between the ericaceous vegetation and the lower alpine zone was not distinct and was marked by the upper limit of ericaceous species. The sites surveyed had gradients from 5° to 35° and animal droppings were present at all. The **lower alpine vegetation** was dominated by tussock grasses, *Senecio brassica* and *Lobelia* spp.. The boundary between the lower alpine zone and the upper alpine zone was not distinct and was marked by the absence of *Senecio keniodendron* in the lower alpine vegetation. There was no evidence of past fires at any of the sites surveyed, although a large area of burnt tussock grassland was observed on the Chogoria track between the sites surveyed. Topographical gradients ranged from 5° to 20°. Tussock grasses dominated the vegetation of the **upper alpine vegetation**. The presence of *Senecio brassica* extended from the lower alpine into the upper alpine vegetation and *Lobelia* spp. were also present. Plant cover was sparse beyond ~4190 m.a.s.l., although the grass species *Agrostis trachyphylla* was recorded and collected from sheltered niches between boulders at 4500 m.a.s.l. Animal droppings were present in some of the sites surveyed. Topographical gradients ranged between level and 45° and the sparse cover of vegetation and

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the bare rock of the nival zone marked the upper altitudinal boundary of the upper alpine vegetation.

#### *Sirimon altitudinal transect*

Altitudinal limits of the graminoids observed during the field survey of the Sirimon track are shown in table 4, where species are ordered according to their centres of altitudinal distributions. The vegetation survey started at ~2780 m.a.s.l. on the Sirimon track in montane forest, where agriculture stopped.

The **upper montane forest zone** was dominated by *Podocarpus latifolius*, forming a dense canopy (50% to 85% cover) 35 to 50 m high. *Juniperus procera* was also present and *Arundinaria alpina* occurred in the understorey at the upper altitudinal limit of the zone. The sites surveyed had slopes that ranged between 20° and 35°. Trampled vegetation and the dung from elephants and buffalo demonstrated the presence of herbivores. The understorey was generally open and seedling trees and graminoids dominated the ground cover. The boundary between the upper montane forest zone and the bamboo zone was sharp. The **bamboo zone** was dominated by *A. alpina* (bamboo), which formed a dense canopy ( $\geq 95\%$ ) ~10 m high, with scattered large stems of *Juniperus procera* and *P. latifolius*. The sites surveyed had topographical gradients that ranged from 20° to 30° and animal trails, elephant dung and buffalo dung were evident. The boundary between the bamboo zone and the *Hagenia-Hypericum* zone was distinct. The ***Hagenia-Hypericum* zone** occupied a narrow altitudinal range and was dominated by large *Hagenia abyssinica* stems, which provided a canopy cover of 50% to 75%, 7 to 45 m high. Large stems of *J. procera* were also present. *A. alpina* and other woody species were present in the understorey and animal paths were evident throughout. The sites surveyed had slopes from 20° to 35° and the boundary between the *Hagenia-Hypericum* zone and ericaceous zone was distinct. The **ericaceous zone** was dominated by *Erica arborea*, which formed a sparse canopy ~3 m high. Animal droppings and evidence of past fires were present at some of the sites surveyed and topographical gradients ranged from 10° to 15°. The boundary between the ericaceous zone and the lower alpine zone was marked by the absence of ericaceous species in the lower alpine zone. The **lower alpine zone** was dominated by tussock grasses with *Senecio brassica*, *Lobelia* spp. and woody shrubs (not *Erica arborea*). The boundary between the lower alpine zone and the upper alpine zone was marked by the absence of *Senecio keniodendron* in the lower alpine zone. The quadrats had slopes from 5° to 35° and animal droppings were present in some of the sites surveyed. Tussock grasses dominated the vegetation, which was characterised by the presence of *Senecio keniodendron* in the upper alpine zone. The presence of *Senecio brassica* extended from the lower alpine zone into the **upper alpine zone** and *Lobelia* spp. were also present in the upper alpine zone. Plant cover was sparse beyond ~4190 m.a.s.l. Animal droppings were present in some of the sites surveyed and topographical gradients ranged from 5° to 30°. The sparse cover of vegetation and the bare rock of the nival zone marked the upper limit of the zone.

#### *Field results summary*

Our grass distribution data from the two altitudinal transects on Mount Kenya indicate that the forest floor grasses (<2500 m.a.s.l.), beneath tree canopy cover of >50% are generally from the Panicoid and Arundinoid subfamilies. The bamboo zone (~2500 to 2800 m.a.s.l.) is dominated by the Bambusoid grass *Arundinaria alpina*, which achieves nearly 100% cover. A large proportion (20% to 95%) of the vegetation cover above the treeline (>3000 m.a.s.l.) is composed of grasses. Patches of tall grasses from the Panicoid subfamily, and

Table 4. The altitudinal distribution of C3 and C4 grass and sedge species on the Sirimon track, Mount Kenya.

Altitude l m.a.s.l.	C4 taxa			C3 taxa		
	<i>Cyperus sesquiflorus</i>	<i>Cyperus niger</i>	<i>Andropogon amethystinus</i>	<i>Bulbostylis atrosanguinea</i>	<i>Carex peregrina</i>	<i>Stipa dregaeana</i>
						<i>Ehrharta erecta</i>
						<i>Streblochaete longiarista</i>
						<i>Cyperus derelima</i>
						<i>Arundinaria alpina</i>
						<i>Carex petitiara</i>
						<i>Festuca africana</i>
						<i>Cyperus sp</i>
						<i>Pentaschistis minor</i>
						<i>Brachypodium flexum</i>
						<i>Bromus leptoclados</i>
						<i>Poa annua</i>
						<i>Poa schimperiana</i>
						<i>Isolopis fluitans</i>
						<i>Poa leptoclada</i>
						<i>Carex conferta</i>
						<i>Pentaschistis borussica</i>
						<i>Carex monostachya</i>
						<i>Calamagrostis hedbergii</i>
						<i>Agrostis trachyphyla</i>
						<i>Festuca pilgeri</i>
						<i>Anthoxanthum nivale</i>
						<i>Koeleria capensis</i>

NB: X = located in at least one quadrat in a set of three; - - - - = Treeline

sedges, amongst tussock Pooid grasses, occur above the bamboo and treeline vegetation up to ~3600 m.a.s.l. Dense Pooid tussock grasses ( $\leq 95\%$  ground cover) dominate the vegetation above ~3600 m.a.s.l. Animal droppings were recorded over a wide altitudinal range, whereas fire in the vegetation was observed to be restricted to the area above treeline (~3000 m.a.s.l.).

## DISCUSSION

### Field sampling and data

Previous investigations of grasses on Mount Kenya have focused on the grassland dominated drier northern flank of Mount Kenya (Tieszen *et al.*, 1979; Livingstone & Clayton, 1980; Young & Young, 1983). Our sampling regime differed markedly from previous studies in that a stratified random design was used rather than a systematic one. Whereas the north flank is dominated by relatively continuous grassland, other flanks have forested vegetation zones, where a stratified sampling design was deemed appropriate.

Some studies have noted that the relative abundance of  $C_3$  and  $C_4$  grasses changes seasonally, particularly in areas that have distinct growing seasons. Thus Tieszen *et al.* (1997) found that  $C_3$  grasses were dominant during the spring growing season in the American Great Plains, while  $C_4$  grasses were dominant during the summer season. Our field survey took place in January to February 1997, the first annual dry season, and provided a 'snap shot' of the vegetation. If a warm wet season, which occurs later in the year, favours  $C_4$  grasses (Hattersley, 1992) then their recorded cover during the survey could be an underestimation. Survey access would be considerably more difficult during the wet seasons. As a single 'snap shot', the fieldwork may also have missed some of the annual grasses and sedges, which are limited in number in Upland Kenya (Agnew, in preparation). Every attempt was made to retrieve any standing dead examples of grasses or sedges for identification, which may have represented the only remaining evidence of annual graminoids. Despite these problems the fieldwork has, at the very least, served the purpose of identifying the dominant graminoid species over a wide altitudinal range in natural vegetation on the northern and eastern flanks of Mount Kenya.

$\delta^{13}C$  analysis provided an effective method for identifying the photosynthetic pathways used by the graminoids recorded. Only one grass, *Andropogon schirensis*, produced  $\delta^{13}C$  values that indicated a  $C_3$  diagnosis, in disagreement with the classification of the grass as a  $C_4$  species on the basis of taxonomic affiliation. Rather than being indicative of an intermediate species (Hattersley, 1984) or a species that may be able to 'switch' pathways (Ehleringer *et al.*, 1991) it is believed that the  $\delta^{13}C$  data may imply that the identification of the specimen should be questioned. These specimens were vegetative and subsequent examination of the cuticles from *Andropogon schirensis* by the authors did not show Panicoid-type (dumbbell-shaped) phytoliths, which are indicative of the Andropogonids (Watson and Dallwitz, 1992). Since the distribution of  $C_3$  and  $C_4$  grasses presented in tables 3 and 4 is based on  $C_3$  and  $C_4$  diagnoses from  $\delta^{13}C$  data, the questionable taxonomic identification of the *Andropogon schirensis* specimens does not influence the interpretation of the data presented in these tables. However, if indeed the specimens do represent an Andropogonid that is able to switch between the  $C_3$  and  $C_4$  photosynthetic pathways, its photosynthetic biochemistry should be examined in each hydrological season.

### Past and present C<sub>3</sub> and C<sub>4</sub> graminoids on Mount Kenya

Whereas previous surveys of graminoid distribution on Mount Kenya (Tieszen *et al.*, 1979; Young & Young, 1983) have focused on the northern flank, which is dominated by grasses, tables 3 and 4 present survey data from two altitudinal transects that passed through montane forest. It is surprising, therefore, that a simple crossover between the abundance of C<sub>4</sub> and C<sub>3</sub> grasses, as demonstrated by Tieszen *et al.*, (1979), was not found. However, tropical montane forest rarely has C<sub>4</sub> grasses in the understorey (Rundel, 1980), while they may be present as emergent grasses in more open vegetation at lake sites (Fries & Fries, 1948; Vesey-Fitzgerald, 1973) (e.g. *Miscanthus violaceus* at Lake Rumuiku, Mount Kenya). Rather than a simple decline of the C<sub>4</sub> grass abundance with altitude, as has been previously demonstrated (Tieszen *et al.* 1979; Young & Young, 1983), our surveys from the Chogoria and Sirimon transects revealed a concentration of C<sub>4</sub> graminoids (principally tall Panicoid grasses) just above treeline (tables 3 and 4), which is compatible with findings from the Aberdare mountains in Kenya (Schmitt, 1991). The abundant C<sub>4</sub> grass *Andropogon amethystinus* at high altitude (~3300 m.a.s.l.) associated with low temperatures was also noted by Tieszen *et al.* (1979) and Long (1983).

Although all five common grass subfamilies were observed during the field survey, Chloridoideae were not found within the survey quadrats, while Panicoid and Pooideae grasses dominated the field survey list. Tieszen *et al.* (1979) described the spatial distribution of C<sub>3</sub> and C<sub>4</sub> grasses along an altitudinal and moisture gradient in Kenya, showing increasing C<sub>3</sub> grasses with altitude and illustrating three general patterns in the distribution of the grass tribes. The C<sub>4</sub> tribes Chloridoideae, Eragrosteae, Sporoboleae and Aristideae (C<sub>4</sub> and predominantly NAD-ME) were abundant at low altitudes and low indices of available soil moisture. The Paniceae and Andropogoneae (C<sub>4</sub> and predominately NADP-ME) were common at intermediate altitudes and soil moisture. The C<sub>3</sub> tribes Aveneae, Festuceae and Agrostideae were found only at high altitudes with relatively high soil moisture. Soil moisture indices were defined by Woodhead (1970) and are based upon annual precipitation, soil water storage and estimates of potential evaporation. The C<sub>4</sub> plants above treeline identified during our fieldwork grow under high available moisture, indeed where Livingstone and Clayton (1980) suggest that the highest rainfall occurs.

This apparent paradox may be explained in two ways: C<sub>4</sub> grasses above treeline could represent the upper limit of their distribution with the intermediate zones of potential C<sub>4</sub> grassland displaced by montane forest, or the particular environmental factors operating just above the treeline may favour the C<sub>4</sub> strategy. It is difficult to argue for the former possibility, for the forest environment differs greatly from that of the grassland, except by invoking palaeoenvironmental changes of considerable magnitude. However, rainfall seasonality coupled with fire under low *p*CO<sub>2</sub> partial pressures, are environments that can favor C<sub>4</sub> grasses (Hattersley, 1992; Fredlund & Tieszen, 1997). We observed burnt vegetation in the area just above treeline where the abundance of C<sub>4</sub> graminoids is highest, agreeing with observations made by Bussmann (1993), who showed evidence of fires in treeline vegetation on Mount Kenya, and Beck *et al.* (1986) who recorded repeated vegetation fires above treeline on Mount Kilimanjaro, Tanzania. The C<sub>4</sub> presence above treeline may also reflect the decrease in atmospheric *p*CO<sub>2</sub> with altitude, which agrees with other independent investigations of C<sub>4</sub> Panicoid grasses at unusually high altitudes (RamaDas & Vats, 1993; Rundel *et al.*, 1980).

The presence of C<sub>4</sub> grasses just above treeline has implications for the reconstruction of past vegetation. If vegetation moved down-slope in response to glacial conditions (as assumed by Coetzee, 1964, 1967) this could account for the C<sub>4</sub>-type  $\delta^{13}\text{C}$  signal demonstrated in lakes

such as Sacred Lake on Mount Kenya, implying greater input from a C<sub>4</sub> source, (Street-Perrott *et al.*, 1997), which is currently below treeline. But our data suggest alternative hypotheses to account for  $\delta^{13}\text{C}$  enrichment in glacial-age sediments from Sacred Lake and Lake Rutundu: either i) up-slope movement of C<sub>4</sub> grasses from low altitude sites occurred, bringing them into sites like Sacred Lake (2350 m.a.s.l.) and Lake Rutundu (3080 m.a.s.l.), or ii) down-slope movement of C<sub>4</sub> species from sites above treeline occurred, again bringing C<sub>4</sub> grasses into the lake sites. Although grass cuticle remains support the former hypothesis (Wooller *et al.*, 2000), these competing hypotheses strengthen the need to establish greater taxonomic resolution regarding the C<sub>4</sub> signal derived from proxies of past vegetation at sites such as Sacred Lake and Lake Rutundu.

## CONCLUSION

Photosynthetic identities (C<sub>3</sub> or C<sub>4</sub>) of modern graminoid specimens collected during a field survey on the Chogoria and Sirimon tracks on Mount Kenya were established using  $\delta^{13}\text{C}$  analysis of their leaves, which generally agreed with classification based on taxonomic affiliation. A concentration of Panicoid C<sub>4</sub> grasses, along with a C<sub>4</sub> sedge, was evident immediately above treeline, a novel observation in relation to the previously established crossover from C<sub>4</sub> to C<sub>3</sub> grasses on the northern flank of Mount Kenya, where montane forest does not exist.

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