

Local distribution of C₃ and C₄ grasses in sites of overlap on Mount Kenya

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Summary. A zone of C₃–C₄ grass overlap has been identified on the northern slopes of Mount Kenya at elevations of 2,800–3,200 m. At higher elevations, C₃ grasses predominate; below, C₄ grasses predominate. At each of three elevational sites of overlap, a series of transects was surveyed for C₄ and C₃ grass composition. All transects were located in structurally similar vegetation (high elevation grassland) within 150 m of each other. Transects were run in a variety of topographic situations. Within each transect, several environmental parameters were measured. Both unweighted (species presence/absence) and weighted (by frequency) measures of %C₄ composition were significantly correlated with dry season soil moisture. Drier transects contain significantly more C₄ species, in greater frequency, than wetter transects. Other correlations of C₄ composition (e.g. factors which tend to parallel soil moisture) were also found. This local trend parallels the larger scale tendency of C₃ grasses to replace C₄ grasses with increasing elevation. Finer scale habitat partitioning may account for C₃–C₄ overlap within transects.

Introduction

Large-scale distributional patterns of C₃ and C₄ metabolism have helped to elucidate the influence of these two physiological pathways on the ecology of the plants possessing them. Multivariate analyses of the abundance of C₃ and C₄ grasses and herbs of North America have indicated that high moisture availability and low temperatures are strong correlates of relative C₃ abundance (Teeri and Stowe 1976; Stowe and Teeri 1978). Large-scale elevational transects in Wyoming (Boutton et al. 1980), Kenya (Tieszen et al. 1979), and Costa Rica (Chazdon 1978) show, with increasing elevation, a transition from C₄ to C₃ as the predominant photosynthetic pathway. Both drought stress and temperature tend to decrease with increasing elevation in these studies. These studies illustrate the physiological and ecological differences between C₃ and C₄ plants. The C₄ photosynthetic pathway has higher temperature and light optima and is more water efficient than the C₃ photosynthetic pathway (Black 1973).

Recently, a region of C₃–C₄ overlap on the northern

slopes of Mount Kenya was described showing a transition from predominantly C₄ grasses at 2,500 m to predominantly C₃ grasses at 3,300 m (Tieszen and Imbamba, personal communication). There are two possible explanations for the coexistence of C₃ and C₄ species in areas of overlap. First, coexisting species of C₃ and C₄ grasses may be physiologically similar to each other. If there is sufficient overlap in the edaphic requirements of some C₃ and C₄ species, they may be expected to co-occur. On the other hand, C₃ and C₄ species may separate locally on differences between microsites, either spatially or temporally. As long as there is sufficient diversity of microsites at a given locale, both C₃ and C₄ species could coexist.

Temporal separations of C₃ and C₄ plants in communities have been measured and found to be significant in Wyoming (Boutton et al. 1980), Colorado (Kemp and Williams 1980), and South Dakota (Ode et al. 1980). These studies found C₃ species to be dominant, in either biomass or frequency, in the spring. In mid to late summer, C₄ species were dominant. Ode et al. (1980) found a bimodal distribution of C₃ species biomass over the growing season with peaks in spring and fall. This shift in species dominance may be accounted for by differential moisture and temperature responses by the two modes of photosynthesis. Even where temporal separation between C₃ and C₄ plants exists, it is not complete. There exist areas which, at certain times, consist of both C₃ and C₄ plant species. The purpose of this study was to determine if there are small-scale environmental correlates of C₃–C₄ grass abundance in such an area of overlap.

Study area and methods

This study was carried out in August 1980 on the Timau Track on the northern slopes of Mount Kenya in the Republic of Kenya at approximately 0°0′ latitude and 37°20′E longitude. Grassland is continuous between 2,800 m and 4,000 m on this slope of the mountain. Land below 2,800 m is heavily cultivated. Grass species lists were made at 2,860, 3,000, 3,200, 3,370, 3,535, and 3,800 m. Three sites of C₃–C₄ overlap were selected for detailed study at elevations 2,860, 3,000, and 3,200 m (Fig. 1). All sites were accessible to native grazing species (e.g. zebra, buffalo, eland, and duiker) and have also been grazed by domesticated sheep.

At each elevation, six 30 m line transects were established running cross-slope. The different transects at each elevation were chosen to sample a variety of local topogra-

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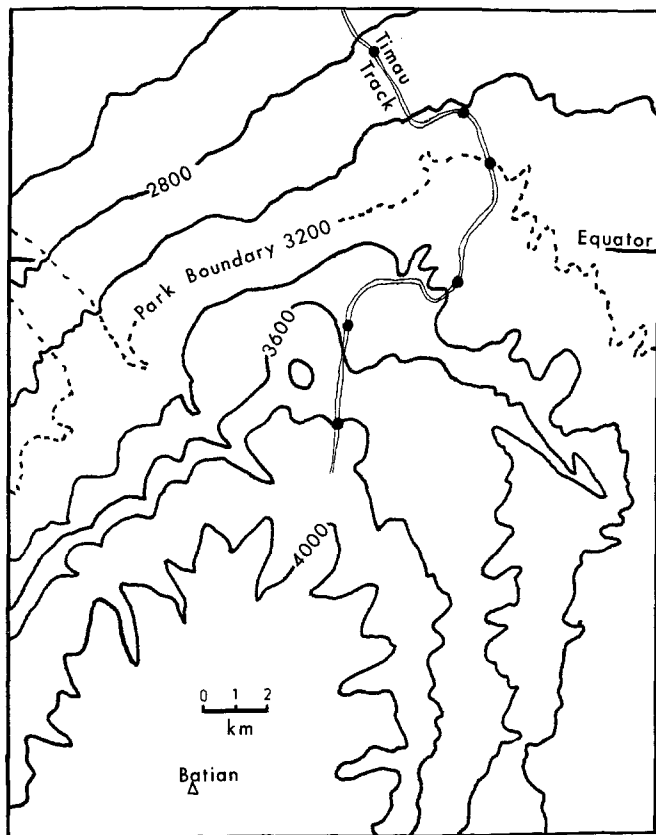


Fig. 1. Map of the northern slopes of Mount Kenya showing (●) the six elevations of grass collection. The three lowest elevations were selected as sites of C_3 - C_4 overlap

phy, from valley bottoms to ridge tops. Individual transects ranged from 10 to 30 m apart and all transects at a particular elevation were within 150 m of each other. All transects ran through vegetation of similar structure: high elevation grassland.

One soil sample was collected at the midpoint of each transect, at a depth of 10 to 15 cm. Approximately 100–200 g of soil was sealed in an airtight plastic bag and later weighed, dried at 95°C for 24 h, and weighed again to determine soil moisture. All samples were collected within a 2 day period (August 20–21, 1980) toward the end of a relatively dry period of several months.

Ten 0.5 m × 0.5 m quadrats were randomly located along each transect. In each quadrat, the presence of each grass species, the slope and aspect, an estimate of the proportion of daylight hours when the youngest leaf of each grass species was shaded, and the percent ground cover by vegetation, detritus, rock, and bare ground were recorded. The identification of grass species was determined following Clayton (1970, 1974) and confirmed by vouchers deposited at the National Herbarium of Kenya in Nairobi (H. Young #1–49, 70–78). Classification as C_3 or C_4 was based on tribal affiliations as listed by Downton (1975) and Raghavendra (1978).

Two measures of relative C_4 grass composition were calculated for each site of C_3 - C_4 overlap. 1) For each transect, the number of C_4 grass species present in at least one quadrat was divided by the total number of grass species present. This gave an unweighted estimate of % C_4 composition. 2) For each transect, each species was

Table 1. Presence of each species at each of six elevations on the northern slope of Mount Kenya. Not all species present at a given elevation were found in transects at that elevation

	Elevation (m)					
	2,860	3,000	3,200	3,370	3,535	3,800
C_3 species						
<i>Agrostis kilimandscharica</i> (AK)				X		X
<i>A. producta</i> (AP)	X	X	X	X		
<i>A. quinqueseta</i> (AQ)	X	X	X			
<i>A. volkensii</i> (AV)			X	X	X	X
<i>Anthoxanthum nivale</i> (AN)				X	X	X
<i>Brachypodium flexum</i> (BF)	X	X	X			
<i>Bromus leptocladus</i> (BL)			X	X		
<i>Dactylis glomerata</i> (DG)	X					
<i>Festuca abyssinica</i> (FA)	X	X	X	X	X	X
<i>F. pilgeri</i> (FP)		X	X	X	X	X
<i>Helictotrichon lachnanthum</i> (HL)	X		X			
<i>H. umbrosum</i> (HU)	X	X	X	X		X
<i>Hordeum vulgare</i> (HV)	X					
<i>Koeleria capensis</i> (KC)			X	X	X	X
<i>Pentaschistis borussica</i> (PB)		X	X	X	X	X
<i>Poa leptoclada</i> (PL)	X	X	X			X
<i>P. schimperiana</i> (PS)	X					
Total C_3 species	10	8	12	11	7	10
C_4 species						
<i>Andropogon amethystinus</i> (AA)	X		X			
<i>A. chrysostachyus</i> (AC)	X					
<i>A. longipes</i> * (AL)	X	X	X	X		
<i>Cymbopogon nardus</i> (CN)		X	X			
<i>Exothea abyssinica</i> (EA)	X	X	X			
<i>Eleusine jaegeri</i> (EJ)	X	X	X			
<i>Eragrostis kiwuensis</i> (EK)	X	X	X			
<i>E. schweinfurthii</i> (ES)	X	X	X			
<i>Pennisetum sphacelatum</i> (PS)	X	X			X	
<i>Sporobolus africanus</i> (SA)			X			
<i>S. olivaceus</i> (SO)		X				
<i>Setaria sphacelata</i> (SS)	X	X				
<i>Themeda triandra</i> (TT)	X	X				
Total C_4 species	10	9	7	2	0	0

* *A. longipes* occurs as high as 3600 m further south on Mt. Kenya (personal observation, TPY)

weighted by its frequency of appearance in the ten quadrats. These values were summed for all C_4 species and divided by the summed values for all grass species present to give a weighted estimate of % C_4 composition. In both cases, the sum of the % C_4 composition and the % C_3 composition was 100, for each transect.

For each overlap elevation site, a series of Spearman rank correlation analyses were carried out. This is a non-parametric analysis performed on untransformed data. For each set of six transects, both measures of % C_4 composition were compared to each other as well as to % dry season soil moisture, mean % shade, slope, and mean % cover by vegetation, detritus, and bare ground.

Results

For the six elevational species lists, % C_4 species composition decreased steadily with increasing elevation (Table 1).

Table 2a-c. C_4 and C_3 grass abundance and various environmental parameters for the six transects at each of the three overlap sites. All environmental parameters except soil moisture are the means of ten quadrats in each transect

2,860 meters	A	B	C	D	E	F	Total
a.							
# C_4 species	5	4	6	7	6	6	8
ΣC_4 frequencies	27	14	44	43	31	38	207
# C_3 species	3	5	2	2	5	0	6
ΣC_3 frequencies	10	12	11	8	22	0	77
% C_4 (unweighted)	62	44	75	78	55	100	57
% C_4 (weighted)	73	54	80	84	58	100	77
% soil moisture	20.2	21.8	20.9	14.8	24.6	11.9	
Mean % shade	9.3	15.2	0	0	15.9	0	
Mean slope ($^\circ$)	5.5	22.5	7.1	22.5	11.5	13.5	
Mean % cover by:							
Vegetation	94	70	90	94	100	79	
Bare ground	1	9	5	5	0	13	
Detritus	5	21	5	1	0	8	
3,000 meters	A	B	C	D	E	F	Total
b.							
# C_4 species	5	4	4	3	5	4	6
ΣC_4 frequencies	31	26	30	17	22	21	147
# C_3 species	5	4	2	6	3	2	6
ΣC_3 frequencies	15	14	11	15	7	9	71
% C_4 (unweighted)	50	50	67	33	62	67	33
% C_4 (weighted)	67	65	73	53	76	70	67
% Soil moisture	19.6	29.3	23.4	24.3	17.7	17.8	
Mean % shade	22.8	44.1	26.7	20.5	4.5	3.8	
Mean slope ($^\circ$)	12.2	11.5	13.0	7.5	19.5	9.0	
Mean % cover by:							
Vegetation	70	75	69	74	37	52	
Bare ground	17	14	19	11	51	32	
Detritus	13	11	12	15	12	16	
3,200 meters	A	B	C	D	E	F	Total
c.							
# C_4 species	3	3	2	5	4	2	6
ΣC_4 frequencies	8	17	12	15	17	14	83
# C_3 species	4	5	7	7	3	1	9
ΣC_3 frequencies	14	17	29	28	9	1	98
% C_4 (unweighted)	43	38	22	42	57	67	40
% C_4 (weighted)	36	50	29	35	65	93	46
% Soil moisture	28.9	30.1	31.4	28.4	28.1	13.8	
Mean % shade	27.2	26.7	8.9	18.4	22.6	15.8	
Mean slope ($^\circ$)	6.0	15.5	8.5	16.2	17.5	14.5	
Mean % cover by:							
Vegetation	45	62	99	81	58	43	
Bare ground	37	19	1	10	30	40	
Detritus	18	19	0	9	12	17	

This was due mainly to the loss of C_4 species. The absolute number of C_3 species present was independent of elevation ($r = -0.01$, $N=6$, ns), whereas the absolute number of C_4 species was strongly negatively correlated with elevation ($r = -0.95$, $N=6$, $p < 0.01$). The overlap sites at 2,860, 3,000, and 3,200 m had 50%, 53%, and 37% C_4 grass species, respectively.

At these three elevational sites, both unweighted and weighted estimates of C_3 - C_4 abundance were calculated

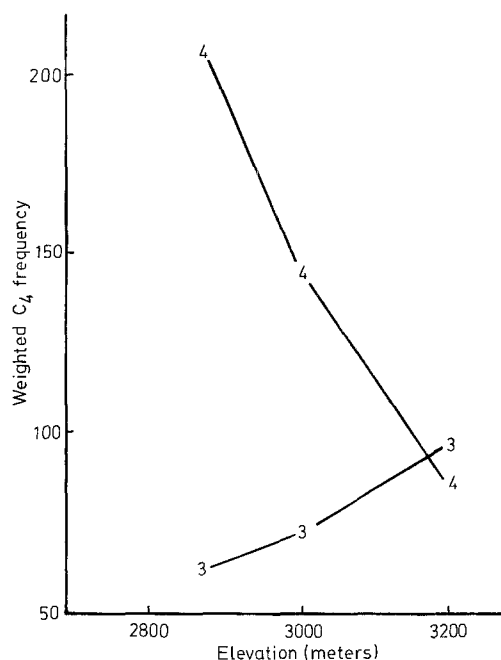


Fig. 2. Weighted C_3 and C_4 composition as a function of elevation at the three sites of overlap of C_3 and C_4 grasses on Mount Kenya

for each of the six transects as well as for the entire sites (Table 2). The C_3 flora consists of less frequent species than the C_4 flora in these sites. Weighted % C_4 composition was always greater than unweighted % C_4 composition, a trend also found in Hawaiian grasses (Rundel 1980). The weighted % C_4 composition decreases with elevation mainly because weighted C_4 abundance drops off dramatically (207 to 147 to 83) while weighted C_3 abundance increases only moderately (63 to 71 to 98), (Fig. 2). Mean dry season soil moisture increased with increasing elevation among these sites (Table 3).

The results of the Spearman rank correlation analyses are shown in Table 3. The two % C_4 composition measures are always significantly positively correlated. Within each site, the % dry season soil moisture is significantly negatively correlated with % C_4 composition, except for the unweighted measure at the 3,000 m site, (Fig. 3). Percent C_4 composition is significantly correlated with estimates of % shade only at the lowest (driest) site, where more shaded transects have lower % C_4 composition. The % cover by vegetation in each transect is significantly negatively correlated with both measures of % C_4 abundance at the highest site, where transects with more vegetation had lower % C_4 composition.

Discussion

In areas of overlap on the northern slopes of Mount Kenya, C_3 and C_4 grasses partition the environment on the basis of local habitat differences. C_4 grasses are more frequent in drier areas and C_3 grasses are more frequent in wetter areas. Tieszen et al. (1979) found a highly significant correlation between the relative abundance of C_4 grasses and estimates of available soil moisture along a transect in Kenya. These data were collected along an elevational transect and thus may reflect an interacting effect of decreasing temperature with increasing elevation and soil moisture.

Table 3. Results of Spearman rank correlation analyses between two measures of C_4 abundance and various environmental parameters at each of three sites. Percent soil moisture is negatively correlated with C_4 abundance (* $p < 0.05$, ** $p < 0.01$). Sample size of each analysis is six. Confidence intervals are one standard error

Elevation (m)	Mean soil moisture	% C_4 composition measure	Correlation with weighted C_4 frequency	% soil moisture	Slope	% shade	% Cover by:		
							Bare ground	Vegetation	Detritus
2,860	19.0 ± 2.6	Unweighted	(+)**	(-)*	ns	(-)*	ns	ns	ns
		Weighted		(-)**	ns	(-)*	ns	ns	ns
3,000	22.0 ± 1.9	Unweighted	(+)*	ns	ns	ns	(+)*	ns	ns
		Weighted		(-)*	(+)*	ns	(+)**	(-)*	ns
3,200	26.8 ± 2.6	Unweighted	(+)*	(-)**	ns	ns	ns	(-)*	ns
		Weighted		(-)*	ns	ns	ns	(-)*	ns

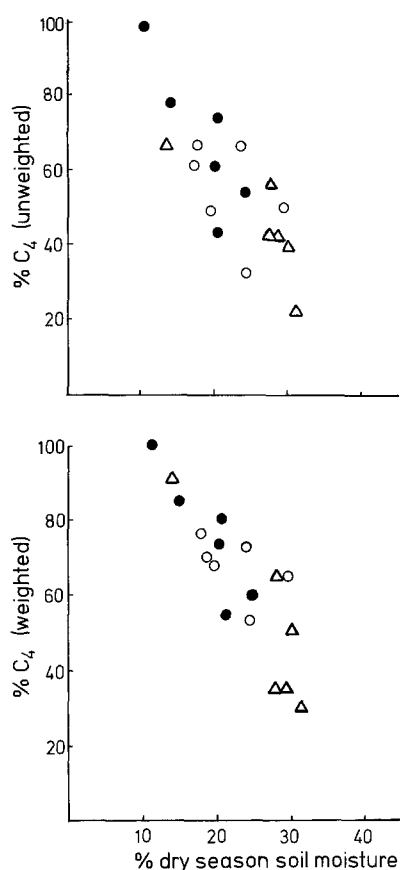


Fig. 3. Weighted (lower) and unweighted (upper) estimates of percent C_4 composition versus percent dry season soil moisture. Triangles represent transects at 3,200 m elevation, open circles 3,000 m, and closed circles 2,860 m

The present study has shown that at a given elevation, the relative abundance of C_4 grasses and soil moisture are significantly correlated. Since all transects at a given elevation were within 150 m of one another, temperature differences are not likely to be great. Care must be taken in this interpretation however, since higher on the mountain cold air drainage can result in temperature differences of several degrees centigrade between valley bottom and slopes (personal observation). In this study the moist transects with more C_3 grasses tend to be in valley bottoms, and the drier

transects with more C_4 grasses tend to be on the slopes or ridgetops.

Percent cover by vegetation has been shown to be significantly positively correlated with dry season soil moisture at elevations of 3,700 to 4,300 m on the western side of Mount Kenya (Young 1982). No such correlation was found to be significant on the northern slope in this study, although there were a few significant correlations between % C_4 composition and percent cover by vegetation or bare ground. These correlations (Table 3) do indicate that transects with more vegetative cover or less bare ground had relatively lower C_4 composition.

Plants with the C_4 photosynthetic pathway are able to maintain high rates of photosynthesis even under conditions of low water availability because of their relatively high affinity for CO_2 (Black 1971). They can continue to photosynthesize even when the stomates are partially closed (Das and Santakumari 1977; Long and Woolhouse 1978). With lower stomatal conductance, C_4 species have higher water use efficiency than C_3 plants under the same conditions of light and temperature. Ehleringer (1978) used computer simulations to show that the quantum yield of C_4 species decreased as temperatures decreased below 32° C and the quantum yield of C_3 plants exceed that of C_4 plants below this temperature. C_4 grasses may be competitively superior in hot, dry areas but experience a disadvantage in cool moist areas and are thus outcompeted by C_3 grasses.

There is considerable coexistence of C_3 and C_4 grasses within most transects. It is likely that further studies will reveal habitat partitioning on even a finer scale than that found here. Since Mount Kenya experiences pronounced wet and dry seasons, this partitioning could be temporal as well as spatial. Fine scale habitat partitioning is not likely to be based on temperature.

While descriptive studies of C_3/C_4 distributions have proliferated, experimental approaches have been largely ignored. An exception is the study of Öztürk et al. (1981) which analyzes the effects of water level and light intensity on the size and weight of C_3 and C_4 plants grown in pure and mixed culture. This provides a background for a study still needed, in particular, competition experiments growing C_3 and C_4 grasses together under an array of light, temperature, and soil moisture regimes. Such experiments will clarify the competitive basis of C_3/C_4 interactions, and help to determine the relative importance of thus far intercorrelated environmental parameters.

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