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Giant senecios and alpine vegetation of Mount Kenya

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Summary

1. Quantitative patterns of alpine plant community structure throughout the upper Teleki Valley on Mount Kenya are described. Data on the frequency of all (61) vascular plant species found in 45 transects were analysed using canonical correspondence analysis (CCA) and an agglomerative cluster analysis. Data on the density and size of giant senecios at these transects were also analysed.
2. *Senecio keniodendron* (high) and *S. keniensis* (low) separate along an altitudinal gradient, with a distinct hybrid zone in areas of sympatry. *Senecio keniodendron* occurs in stands of even-sized trees, which may be even-aged.
3. Vegetation analyses revealed a continuum of plant community composition. Mid- and lower-altitude ridges were floristically more similar to wet valley bottoms than to dry slopes, a finding with conservation and management implications.
4. Eleven environmental factors were measured at each transect and included in the canonical correspondence analysis. Included among these measurements was the average tree height of even-sized stands of *Senecio keniodendron*. The first three axes identified by CCA were associated with percentage vegetation cover (soil moisture), altitude, and mean *S. keniodendron* stand height, respectively.
5. An analysis of mid-altitude slope transects revealed that the mean height of *S. keniodendron* trees was the dominant environmental determinant of community composition in these sites. There appears to be considerable variation in plant community composition associated with a natural cycle of establishment, growth and senescence of even-sized *S. keniodendron* stands.

Key-words: community structure, stand dynamics, tropical vegetation

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Introduction

The alpine zone of Mount Kenya is the site of some of the most intensive ecological research in East Africa (Rehker 1989; Young 1990). These studies are important for several reasons.

1. Mount Kenya has been designated an international Biosphere Reserve.
2. The ecology of Mount Kenya has profound effects on large surrounding agricultural and tourism areas, largely through hydrological influences (Winiger 1986, 1990).
3. The impacts of intensive tourism in the alpine zone have led to local habitat destruction that is in critical need of amelioration. In particular, the level valley bottoms become muddy easily, encouraging trail proliferation that has led to wide swathes of vegetation loss (Mahaney 1979). In addition, large numbers of *Senecio keniodendron* trees are

being lost to alpine visitors for fuelwood (Mabberly 1986).

An analytical understanding of Mount Kenya's alpine plant communities and the factors that are correlated with differences in community composition are therefore desirable. Although there have been several descriptions of the plant communities of Mount Kenya, all have been subjective delineations of 'types' based on informal observations or detailed relevés (Fries & Fries 1948; Hedberg 1951, 1964; Coe 1967; Rehder *et al.* 1981; Nievergelt *et al.* 1987; Rehder, Beck & Kokwaro 1988, 1989). Common to all of these descriptions is a fundamental distinction between higher-altitude communities dominated by *S. keniodendron* and lower-altitude communities dominated by *S. keniensis* (formerly *S. brassica*).

Many tree and shrub populations occur as even-sized or even-aged stands in nature (Mueller-Dombois 1985, 1986; Jimenez, Lugo & Cintron 1985; Young & Lindsay 1988; Itow & Mueller-Dombois 1988). When these species are community dominants, the

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age of the stand can affect community composition (Agnew 1985; Young & Augspurger 1991). Changes in plant community composition associated with patterns of recruitment, growth and senescence of natural even-sized stands represent a form of cyclical succession whose effects on community composition have only rarely been studied (Agnew 1985).

Senecio keniodendron (nomenclature follows Jeffrey 1986; Agnew 1974; Polhill 1957–89) is a sparsely branched giant rosette plant that grows up to 6 m in height. It is endemic to alpine Mount Kenya, where it is the dominant woody species, often forming dense stands with nearly closed canopies (Smith & Young 1982). Many of these stands are strikingly even-sized and presumably approximately even-aged. Two factors may enforce even-sized stand structure. First, flowering is gregarious and occurs at intervals of 5 to >20 years (Smith & Young 1982; Mabberly 1986). Secondly, experimental evidence indicates that *S. keniodendron* adults suppress juveniles (Smith & Young, in press). After older stands die, because of elephant herbivory (Mulkey, Smith & Young 1986), fire (Smith & Young, in press) or stand senescence, large numbers of juveniles are quickly recruited (Smith & Young, in press). We have observed that *S. keniodendron* stands with taller trees appear to support a very different understorey plant community than do shorter stands. Most characteristic of taller stands is a dense cover of the shrubs *Alchemilla argyrophylla* and *A. johnstonii*.

Agnew (1985) has suggested that on the Aberdare Mountains there exists a cyclical succession between communities dominated by *A. argyrophylla* on the one hand and *Festuca pilgeri* on the other. Rehder, Beck & Kokwaro (1988) found variation in community composition in '*S. keniodendron* woodland' understorey, dominated by either *Festuca pilgeri* or *A. argyrophylla*. They attributed this variation to a similar cyclical succession, driven either by fire (at

lower altitudes) or by synchronous senescence of *Alchemilla* stands (at higher altitudes). The potential role of *S. keniodendron* stands in these dynamics was not explored.

As part of a long-term study on Mount Kenya's alpine ecology, a quantitative survey of plant distributions was carried out in the upper Teleki Valley. The multivariate analysis presented here provides the opportunity to examine the effects of *Senecio keniodendron* stand height and other environmental variables on community composition, and to discuss their implications for park management and our basic understanding of tropical alpine ecology. It also provides a rare look at a plant species whose dynamics has strong influences on community composition.

Methods

The field work was carried out in 1979–80 in the upper Teleki Valley on the western side of Mount Kenya at altitudes of 3870–4900 m a.s.l. A total of 45 transects was run, representing a stratified sample of the plant communities in the upper alpine zone of Mount Kenya, at altitudes from 3870 to 4540 m a.s.l. At each of six 1-km intervals along the valley, a series of seven transects was run: south ridge, south slope, south valley bottom, streamside, north valley bottom, north slope, and north ridge (Fig. 1). Ridge transects ran along the crest of the ridge. Slope transects ran transversely across the slope at a location midway between the valley bottom and the ridge. Valley-bottom transects ran parallel to the stream and 30 m from it. Streamside transects ran along the stream itself, with individual quadrats placed against the stream edge out into the terrestrial vegetation. In addition, transects were run through the rocky alluvial pan at the head of the valley (41 in Fig. 1), and in high-valley and stream sites at 4340 m (37 and 38 in Fig. 1).

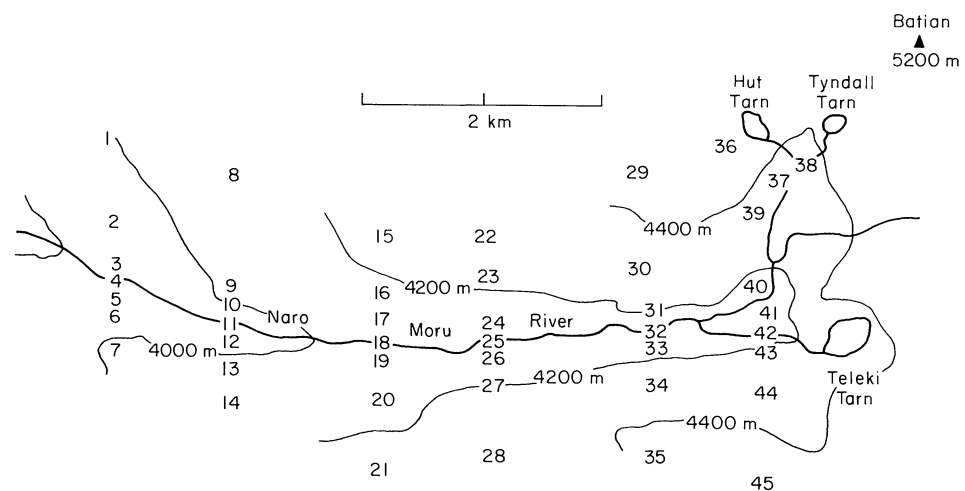


Fig. 1. The locations of the 45 transects in the upper Teleki Valley on Mount Kenya.

Each transect was 30 m long. Ten 1-m × 1-m quadrats were placed at alternating sides along each transect at 3-m intervals. In each quadrat, the presence of each vascular plant species was recorded, providing a frequency of each species for each transect ranging from 0 to 10. In addition, the area 10 m either side of the transect was surveyed for plant species not found in the quadrats. This 20-m × 30-m area was also surveyed for all individuals of *Senecio kenioidendron*, recording the height of each to within 0.5 m, and all rosettes of *S. keniensis* were counted. Species were identified using keys for reproductive (Hedberg 1957; Agnew 1974) and vegetative (Young & Peacock 1985) material, and our identifications were confirmed at the herbarium of the National Museums of Kenya.

The dominant alpine plant on Mount Kenya, *Festuca pilgeri*, presented some special problems. First, it was found in two very different forms — a sterile form with leaves twisted in broad spirals that often occurred in distinct stands, and an often fertile form with linear leaves that was far more common (Rehder, Beck & Kokwaro 1988). Detailed study of vegetative characters (Young & Peacock 1985) indicates that the sterile form is indeed *F. pilgeri*. Secondly, at lower altitudes, small fertile culms of *Carex monostachya* often occurred in large non-flowering tussocks of *F. pilgeri*. This has led in the past to misidentification of *F. pilgeri* as *C. monostachya* (E. Beck, personal communication).

Three species pairs were difficult to distinguish in the field: *Poa schimperii* and *P. leptoclada*, *Cerastium octandrum* and *C. afromontanum*, and *Erica (Phillipia) trimera* and *E. arborea*. For *Poa* and *Cerastium*, species were recorded when flowering, but distinguished only to genus otherwise. The traditional

generic distinctions between *Phillipia* and *Erica* are not appropriate for much African material (Oliver 1989; Beentje 1990). Therefore, we relied on species differences identified specifically in Mount Kenya material (see Young & Peacock 1985).

At each transect site, altitude was determined using a field altimeter and checked against published maps. For each quadrat in each transect, we recorded (i) slope, measured with a clinometer, (ii) aspect, measured with a compass, and (iii) percentage cover of vegetation, bare ground, rock, water, and detritus. Aspect was further broken down into a north–south component (due north = 1, due south = 0) and an east–west component (due east = 1, due west = 0). Table 1 shows a summary of environmental characters measured at each transect. In addition, soil samples were taken at 18 sites late in the dry season (February 1980). These were weighed at the Department of Botany of the University of Nairobi, dried to constant weight at 95 °C, and weighed again.

Multivariate analyses were carried out on the frequency data using CANOCO (ter Braak 1987). Canonical correspondence analysis (CCA) was carried out on the plant frequency and environmental data from the 45 transects. The variables *Senecio kenioidendron* density and mean height and *S. keniensis* density were included as three additional potentially influential factors. Species present in the 20-m × 30-m area around each transect but not occurring in any quadrats were arbitrarily assigned a frequency of 0.5. For this analysis, frequency data for *S. kenioidendron* and *S. keniensis* were eliminated from the data set to ensure independence of dependent and independent variables.

To elucidate more clearly the relationship between

Table 1. Environmental factors for the 45 transects from Mount Kenya used in canonical correspondence analysis. The three *Senecio* variables were only used in analyses excluding *Senecio* frequency data. There were 10 estimates of slope, aspect and percentage cover for each transect. The variables with an asterisk were used for the slope analysis (limited to transects 4000–4300 m a.s.l. and sloping 18–31°), in order to keep the number of environmental variables less than the number of transects in the sample

Variable	Mean	Range of (mean) values for transects
Altitude* (m a.s.l.)	4157	3870–4540
Mean slope angle* (degrees)	13.4	1.6–30.5
Mean north–south aspect*†	0.50	0–1
Mean east–west aspect‡	0.40	0–0.75
<i>Senecio kenioidendron</i> density* (per 100 m ²)	2.76	0–13.0
Mean <i>S. kenioidendron</i> height* (m)	1.48	0–4.75
<i>S. keniensis</i> density (per 100 m ²)	12.3	0–104
Mean percentage cover		
vegetation*	73.1	0.8–98.8
bare ground	13.3	0.3–80.1
rock and water	6.5	0–59.9
detritus	7.0	0–21.1

† 0 = due south, 1 = due north.

‡ 0 = due west, 1 = due east.

S. keniodendron stand height and vegetation composition, a separate CCA ('slope analysis') was carried out on all 10 transects 4000–4300 m a.s.l. with slopes between 18° and 31° (thus limiting variation in slope and altitude). These sites had the greatest densities of adult *S. keniodendron* plants.

In addition, cluster analysis was carried out on all the species frequency data from the 45 transects. Euclidian chord distances were calculated among transects, and an agglomerative cluster analysis was carried out using unweighted average linkage (Pielou 1984).

A map showing the location of the transects was overlaid on a vegetation map of alpine Mount Kenya (Rehder, Beck & Kolwaro 1989), and the putative 'community type' of each transect recorded. The results of ordination and cluster analyses carried out on the 45 transects were then compared to the vegetation classifications of Rehder, Beck & Kolwaro (1988).

Results

Senecio keniodendron occurs in stands of relatively even-sized trees on Mount Kenya (Fig. 2). Shorter individuals are absent from taller stands, and only reappear as stands begin to senesce. There is little evidence of self-thinning in the stands in the tran-

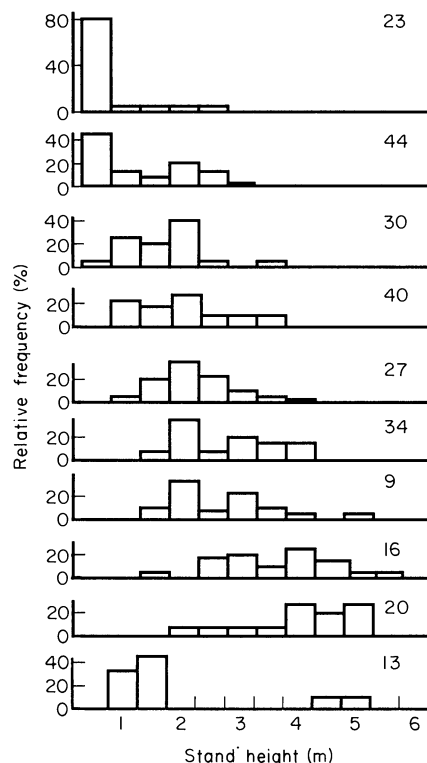


Fig. 2. *Senecio keniodendron* height histograms for the mid-altitude slope transects on Mount Kenya used in the 'slope analysis', showing the even-sized stand structure of this species. Numbers refer to transects in Fig. 1.

sects; there is only a weak negative correlation between mean *S. keniodendron* height and density in mid-altitude slope transects ($r = -0.27$, $P > 0.30$).

Excluding the three transects with virtually no vegetation (<5% cover), the presence of *S. keniodendron* plants was significantly negatively associated with the presence of *S. keniensis* plants among transects ($\chi^2 = 6.54$, $P < 0.02$), confirming their visually striking spatial separation (Hedberg 1964; Coe 1967; Beck *et al.* 1981). *Senecio keniodendron* increased in abundance with altitude, and *S. keniensis* was most common below 4000 m and was rare above 4200 m a.s.l. (Fig. 3). Interspecific hybrids were found in nine of the 14 sites (64%) where both species were present, producing a striking hybrid zone.

A total of 61 vascular plant species was recorded in the transects. Canonical correspondence analysis of 11 environmental variables and the 45 transects in the upper Teleki Valley ('full analysis') showed that percentage vegetation cover, altitude and *S. keniodendron* stand height were the dominant correlates of community composition (Table 2, Fig. 4). The first canonical axis was most strongly associated with percentage vegetation cover and its

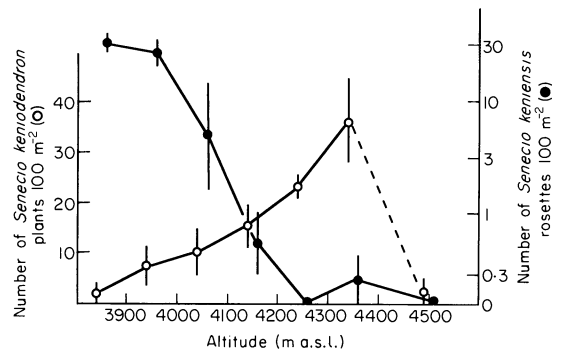


Fig. 3. Mean (\pm SE) densities of *Senecio keniodendron* and *S. keniensis* along an altitudinal gradient on Mount Kenya.

Table 2. Weighted correlations of environmental parameters with the first three axes of the canonical correspondence analysis of 45 alpine vegetation transects on Mount Kenya

Variable	Axis 1	Axis 2	Axis 3
Percentage vegetation cover	-0.751	-0.302	-0.296
Altitude	0.557	0.642	-0.043
Mean <i>S. keniodendron</i> height	0.256	-0.243	-0.531
<i>S. keniodendron</i> density	0.227	0.209	-0.288
<i>S. keniensis</i> density	-0.428	-0.206	0.095
Slope angle	0.429	-0.509	-0.360
East-west aspect	0.028	-0.273	-0.168
North-south aspect	0.115	0.144	-0.225
Percentage detritus cover	0.068	-0.274	-0.199
Cumulative percentage variation in community composition explained	30.0	49.6	61.6

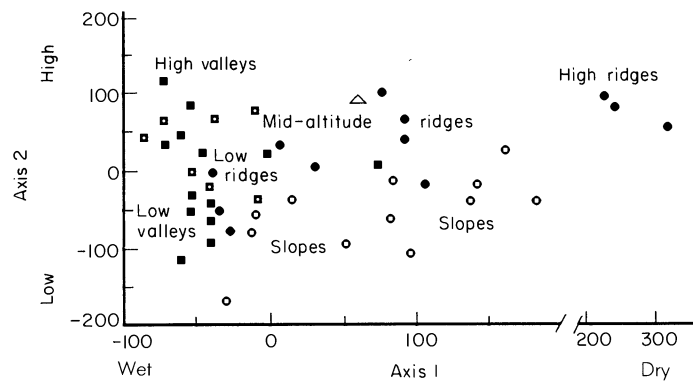


Fig. 4. Results of canonical correspondence analysis of species frequency data from 45 transects from the upper Teleki Valley on Mount Kenya: (●) ridges; (○) slopes; (■) valley bottoms; (□) streamsidcs; (△) alluvial pan.

inverse, percentage bare ground. Soil analyses showed that percentage vegetation cover was strongly positively correlated with dry-season soil moisture, based on samples taken over a broad range of habitat types ($r = 0.86$, $n = 18$, $P < 0.01$). The concentration and availability of most mineral nutrients also increases along this gradient of increasing soil moisture (Young 1984a). Long-term demographic data on giant senecios indicate that soil moisture is a limiting factor (Smith & Young, in press). The first canonical axis represented a shift from species common in wet sites (*Lobelia keniensis*, *Senecio keniensis*, *Luzula abyssinica*, *Haplosciadium abyssinicum*) to species common in dry sites (*Lobelia telekii*, *Senecio keniophyllum*, *Arabis alpina*, *Cerastium afroontanum*).

The second canonical axis was most strongly associated with altitude. Characteristic low-altitude species included *Lobelia keniensis*, *Deschampsia flexuosa*, *Helichrysum* spp. and *Erica* (*Phillipia*) *trimera*. Characteristic high-altitude species include *Crassula* spp., *Senecio keniophyllum*, *Carduus chaemophyllus*, *Carex runssoriense*, *Pentaschistis minor* and *Sagina afroalpina*.

The third canonical axis was most strongly associated with mean height of *S. keniodendron* stands. There are several possible interpretations of this axis. First, the height of a given *S. keniodendron* stand may directly influence community composition. Secondly, an unidentified environmental factor may be correlated with both stand height and community composition. For example, an innate cycle associated with *Alchemilla* (cf. Agnew 1985; Rehder, Beck & Kokwaro 1988) may influence *S. keniodendron* stand structure. Thirdly, 'mean *S. keniodendron* height' may represent an underlying combination of the variables slope and altitude, with which it was positively correlated.

We carried out the second CCA ('slope analysis') on all slope transects, where *S. keniodendron* is most common, to elucidate covariation in stand height and plant community composition. The first

canonical axis of this 'slope' analysis explained 35% of the variance in community composition, and was strongly associated with both percentage vegetation cover ($r = 0.85$) and mean *S. keniodendron* height ($r = 0.77$).

The 'percentage vegetation cover' and 'mean *S. keniodendron* height' variables were nearly coincident ($r = 0.93$) in this slope analysis, but were nearly orthogonal ($r = 0.14$) in the full analysis. This allowed us to test which of the first two axes that were associated with these two variables in the full analysis was most similar to the dominant axis in the slope analysis. We compared the species ranks along the first axis of the slope analysis to their ranks along both the first axis (percentage vegetation cover) and third axis (mean stand height) of the full analysis. The 25 most abundant species were ranked by their locations along these three axes, and Spearman rank correlations carried out.

Species rankings of the first canonical axis of the slope analysis were significantly correlated with those of the third canonical axis of the full analysis ('mean *S. keniodendron* height', $r_s = 0.61$, $P < 0.01$). These axes represented a shift from *Pentaschistis minor* to *Poa leptoclada* (grasses) and from *Helichrysum brownei* and *H. cymosum* to *Alchemilla johnstonii* and *A. argyrophylla* (shrubs) among stands of increasing height (Fig. 5). This identifies *Alchemilla* species as important sources of variation in understorey community composition in *S. keniodendron* woodlands, as suggested by Agnew (1985) and Rehder, Beck & Kokwaro (1988), but does not identify *Festuca pilgeri* as the other key species. This may be because *F. pilgeri* only began to dominate in *S. keniodendron* stands with a mean height of >1 m. Taking this lag into account, *F. pilgeri* frequency decreased significantly with stand height ($r = -0.70$, $P < 0.05$).

Species rankings along the first canonical axis of the slope analysis were not correlated with those of the first canonical axis of the full analysis ('percentage vegetation cover', $r_s = 0.08$, $P > 0.50$). There-

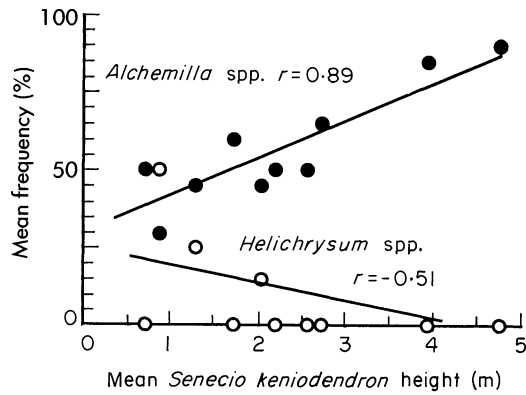


Fig. 5. The mean frequencies of (○) *Helichrysum* spp. (*H. brownei* and *H. cymosum*) and (●) *Alchemilla* spp. (*A. johnstonii* and *A. argyrophylla*) in transects dominated by *Senecio keniodendron* stands of different mean heights (ages) at mid-altitude slope sites on Mount Kenya.

fore, percentage vegetation cover was associated with two very different environmental gradients in these two analyses. Across many habitat types (such as in the full analysis), soil moisture was significantly correlated with percentage vegetation cover (see above). In contrast, among *S. keniodendron* woodland sites, soil moisture is not associated with variation in understorey community composition (Beck *et al.* 1981). *Alchemilla* species (characteristic of

taller *Senecio* stands) form a much denser cover than *Helichrysum* species or *F. pilgeri* (characteristic of shorter stands).

Canonical correspondence analysis shows a relatively gradual change in plant community composition among the 45 transects (Fig. 4; see also Smith & Young 1987). There was a topographic gradient of community composition from valley bottoms and low-altitude ridges to mid-altitude ridges to slopes to high ridges. The slopes and high ridges were characterized by the driest vegetation and the stream-sides and low ridges by the wettest vegetation.

Cluster analysis (Fig. 6) shows general agreement between the ordination analysis and the subjective 'types' of Rehder, Beck & Kokwaro (1988), although their community boundaries may not always be the most appropriate. There does appear to be a clear distinction between the two dominant valley-bottom plant communities in the upper Teleki Valley. Cluster analysis indicates that the valley and stream transects below 4100 m a.s.l. were very different from those above 4100 m (N and K, respectively, in Fig. 6). The boundary between these two vegetation types coincides with a small headwall along the valley floor that is associated with a dramatic drop in rainfall as one ascends the valley (Young 1984a). This may represent a steep environmental gradient that produces a relatively clear distinction in plant community composition.

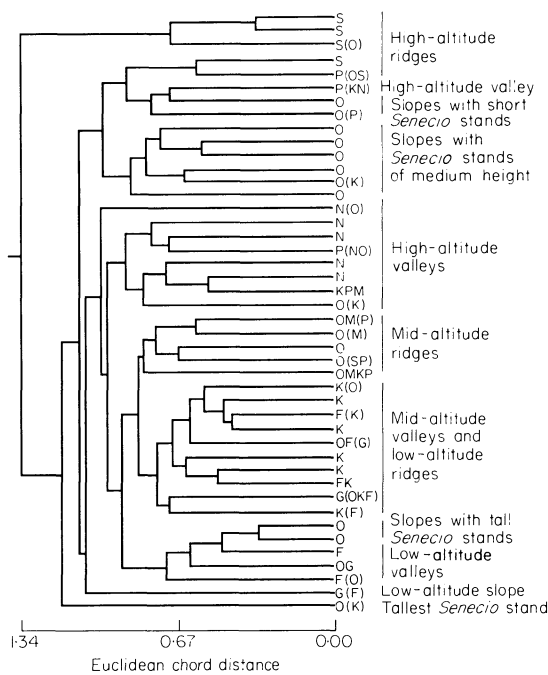


Fig. 6. Cluster analysis of 45 vegetation transects from the upper Teleki Valley on Mount Kenya. Small capital letters represent the 'community type' of the transect assigned by Rehder, Beck & Kokwaro (1989). Multiple letters indicate a transect on the boundary of two or more mapped plant communities, and parenthetical designations are mapped 'types' near the transect. Note the admixture of many of the community designations.

Discussion

Variation in alpine plant community composition on Mount Kenya is correlated with soil moisture, altitude, slope and *Senecio keniodendron* stand height. Soil moisture is strongly correlated with percentage vegetation cover (over a wide range of sites), and also declines with increasing altitude (Sarmiento 1986) and slope (Young & Young 1983; Young 1984a), and it is likely that the availability of soil moisture is the most important edaphic factor determining plant community composition high on Mount Kenya.

The lack of an effect of north-south aspect is not surprising in a tropical environment. On the other hand, because mornings are usually clear and afternoons are usually cloudy on Mount Kenya and direct irradiation can have profound effects on microclimate (Young 1984b; Young & Robe 1986), one might expect east-west aspect to have an effect on community composition (Salt 1954; Hedberg 1964). However, most of the slope transects were located on north- or south-facing slopes, so our analysis was not sensitive to differences in east-west aspect.

An interesting outcome of the canonical correspondence analysis is the demonstration that, at least at altitudes below 4200 m a.s.l., the vegetation on ridge tops was more similar to valley-bottom

vegetation than to slope vegetation (Fig. 4). This is apparently because the ridges are relatively level and so less well drained. Our recognition of this similarity was instrumental in the design of new trails by Mount Kenya National Park personnel. In order to avoid the wet muddy valley bottoms, an early decision was made to put a new trail on supposedly dry ridges in order to minimize human impact. We were able to show that the ridges at these altitudes were floristically similar to the valley bottoms and presumably equally unsuitable for trails. Our recommendation to place the trail on the drier slopes instead was implemented.

There was also a major community gradient associated with mean *S. keniodendron* stand height. Although it is not possible to age these trees directly, there are reasons to believe that the variation in mean *S. keniodendron* height is due to differences in stand age. Long-term demographic data from 480 *S. keniodendron* plants in the Teleki Valley indicate that individuals grow throughout life (Smith & Young, in press), and that growth rate does not decrease with plant height (personal observations). These data also suggest that individuals are probably many decades old at the time of senescence (Smith & Young, in press; see also Mabberly 1986).

We suggest that the great variation in the community composition of *Senecio keniodendron* stands at intermediate altitudes (Figs 4 and 6) is caused by a cyclical pattern of recruitment, growth and senescence of these even-sized stands. The tendency for the understorey of older *S. keniodendron* stands to be dominated by *Alchemilla* shrubs, when adjacent sites whose stands are short or absent are dominated by *Festuca*, can be seen in the photographs of Hedberg (1964, Photo 84) and Rehder, Beck & Kokwaro (1988, Photo 12). Our analysis indicates that after stands senesce and *S. keniodendron* juveniles are recruited into these sites, the understorey vegetation opens up and becomes dominated by *F. pilgeri* and *Helichrysum*. As these stands mature, *Alchemilla* gradually becomes more dominant (Fig. 5). *Helichrysum* was restricted to sites with low frequencies of *Alchemilla* (Fig. 7). The closed canopy of tall dense *S. keniodendron* stands seems to provide more-suitable habitat for *Alchemilla* species, which are also found in the understorey of the high-altitude forest, but not in open alpine habitats (Fries & Fries 1948; Rehder, Beck & Kokwaro 1988). The other possibility is that an inherent cycle in the understorey (Agnew 1985; Rehder, Beck & Kokwaro 1988) drives the dynamics of *S. keniodendron* stands. However, our observations of older stands indicate that the senescence of *S. keniodendron* stands precedes the disappearance of *Alchemilla* shrubs and the increase of *F. pilgeri* grasses. If *Alchemilla* species require a dense overstorey, then the senescence of old *S. keniodendron* stands could cause the disappearance of

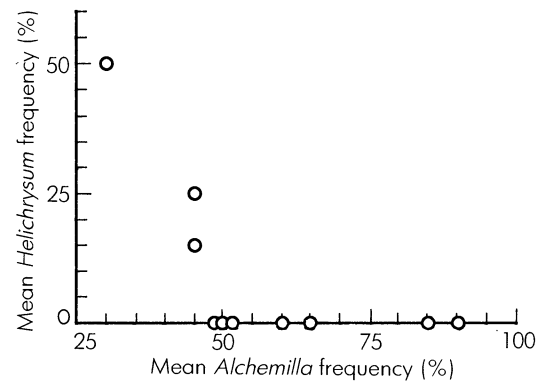


Fig. 7. Relationship between the mean frequencies of *Alchemilla* spp. and *Helichrysum* spp. at mid-altitude slope sites on Mount Kenya.

Alchemilla. In timberline sites on the Aberdare Mountains, a similar *Festuca*–*Alchemilla* cycle appears to occur without *S. keniodendron* (Agnew 1985), and may have different causes. However, at intermediate alpine altitudes on Mount Kenya, it appears that *S. keniodendron* is a key species, whose even-aged stand structure produces cyclical changes in plant community composition. The local destruction of slow-growing *Senecio keniodendron* stands through over-exploitation for firewood (Mabberly 1986) therefore represents long-term losses, and is likely to have profound effects on plant community composition.

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