

VEGETATION SUCCESSION IN RELATION TO GLACIAL FLUCTUATION IN THE HIGH MOUNTAINS OF AFRICA

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ABSTRACT Dramatic changes are taking place in the glacier-covered high mountains of Africa. The glacier-covered area on Kilimanjaro is now only half as large as it was in the 1970s. The Tyndall Glacier on Mt. Kenya, which retreated at approx. 3 m yr^{-1} from 1958 to 1997, retreated at ca. 10 m yr^{-1} from 1997 to 2002. Pioneer species such as *Senecio keniophytum*, *Arabis alpina*, mosses, lichen, and *Agrostis trachyphylla* have advanced over areas formerly covered by the glacier. The rate at which this vegetation migrated up the former bed of the glacier ($2.1\text{--}4.6 \text{ m yr}^{-1}$ from 1958 to 1997) is similar to the rate of glacial retreat (2.9 m yr^{-1}). In the interval from 1997 to 2002, pioneer species advanced at a rapid rate of $6.4\text{--}12.2 \text{ m yr}^{-1}$ when the glacier retreated at 9.8 m yr^{-1} . Rapid glacial retreat has been accompanied by rapid colonization by plants. Pioneer species improve soil conditions and make habitat suitable for other plants. If warming continues, alpine plant cover may extend all the way to mountain summits, and then eventually diminish as trees colonize the areas formerly occupied by the alpine plants. Larger woody plants such as *Senecio keniodendron* and *Lobelia telekii*, which showed no obvious advances before 1997, have advanced quickly since 1997.

Key Words: Vegetation; Deglaciation, Global warming; Environmental change; Alpine zone; Africa.

INTRODUCTION

Vegetation at glacier fronts is commonly affected by glacial fluctuations (Coe, 1967; Spence, 1989; Mizuno, 1998). Coe (1967) described vegetation zonation, plant colonization, and the distribution of individual plant species on the slopes below the Tyndall and Lewis Glaciers. Spence (1989) analyzed the advance of plant communities in response to the retreat of the Tyndall and Lewis Glaciers for the period 1958 to 1984. Mizuno (1998) addressed plant communities' responses to more recent glacial retreat by conducting field research in 1992, 1994, 1996, and 1997. These studies illustrated the link between ice-retreat and plant colonization near the Tyndall Glacier and Lewis Glacier. In addition, till age and substrate stability are critical controls on vegetation patterns around the glacier (Mizuno, 1998).

Numerous studies have been carried out on the glaciers of Mt. Kenya (Gregory, 1894, 1900; Mackinder, 1900; Troll & Wien, 1949; Charnley, 1959; Coe, 1964; Kruss & Hastenrath, 1983; Hastenrath, 1983, 1984). Many of these studies dealt with glacial fluctuations and deposits (Baker, 1967; Mahaney, 1979, 1982, 1984, 1989, 1990). Recently, mountain glaciers in Africa have been retreating at an accelerated rate (Hastenrath, 1997; Thompson *et al.*, 2002). This study focuses

on glacial fluctuations over the period 1997 to 2002; it clarifies the response of plant communities to recent glacier retreat, and discusses the effects of glacial retreat on ecosystems. The habitats of large woody plants such as *Senecio keniodendron* and *Lobelia telekii*, which are characteristic plants of tropical high mountains, are examined.

STUDY AREAS AND METHODS

I. Study Area

Mt. Kenya is an isolated, extinct, denuded volcano that lies on the equator ($0^{\circ}6'S$, $37^{\circ}18'E$), approx. 150 km NNE of Nairobi. The summit, Batian, is 5,199 m above sea level (Fig. 1). The mountain was built up by intermittent volcanic eruptions between 3.1 and 2.6 million years ago (Bhatt 1991), and the volcanic plug was dated to 2.64 million years ago (Everden & Curtis, 1965; Mahaney, 1990). Rocks of the volcanic massif consist of basalt, phonolite, kenytes, agglomerates, trachyte, and syenite (Baker, 1967; Baker *et al.*, 1972; Bhatt, 1991; Mahaney, 1990).

The Tyndall Glacier is the second largest glacier on Mt. Kenya, after the Lewis Glacier. Fluctuations of these glaciers have been recorded in detail (Gregory, 1894, 1896, 1900, 1921; Mackinder, 1900, 1901; McGregor Ross, 1911; Dutton, 1929; Light, 1941; Howard, 1955; Hastenrath, 1984; Mahaney, 1990). Mahaney (1984, 1990) subdivided Neoglacial deposits into two advances (Tyndall advance and Lewis advance) on the basis of several relative dating (RD) criteria, including topographic position, weathering characteristics, and degree of soil profile expression.

The Lewis and Tyndall Moraines formed in front of the Tyndall Glacier (Fig. 1). The Lewis Till (the Lewis Moraine, ca. 100 yr BP) and Tyndall Till (the Tyndall Moraine, ca. 900 yr BP) are considered to be late Holocene in age,

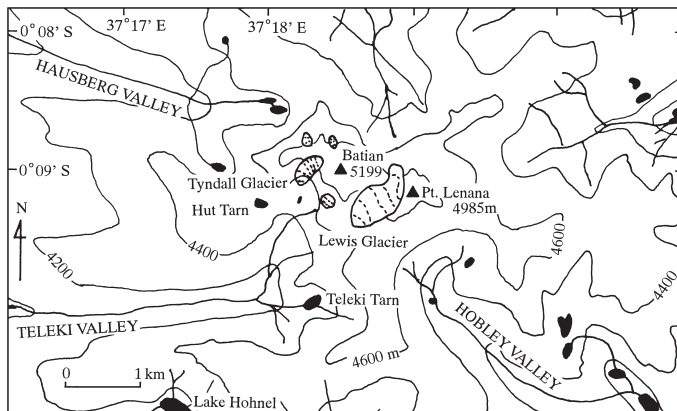


Fig. 1. Alpine zone of Mount Kenya.

based on soil development and weathering features (Spence & Mahaney, 1988; Mahaney, 1989, 1990; Mizuno, 1998). The Tyndall Moraine is divided into Tyndall Moraine I and Tyndall Moraine II on the basis of topographic position, weathering characteristics, and relative soil development (Mizuno, 1998, 2003a).

The elevations at which the annual minimum, mean, and maximum temperatures of the free atmosphere in East Africa are 0°C, are approx. 3,500 m, 4,750 m, and 6,000 m, respectively (Hastenrath, 1991). The precipitation is southeasterly maximum resulting from the classical monsoon, and secondary maximum on the western side (Mahaney, 1990). Annual precipitation is about 2,500 mm per year at 2,250 m on the southeast slopes of Mt. Kenya, grading to less than 1,000 mm per year at same altitude on the north slope (Hastenrath, 1991; Mahaney, 1984). Annual rainfall is highest between 2,500 and 3,000 m on the south, west, and east slopes, and decreases towards the peak (<900 mm at 4,500 m–4,800 m). Above 4,500 m, most of the precipitation falls in the form of snow and hail.

Vegetation on Mt. Kenya has been classified into the Alpine Belt (>3,600 m), the Ericaceous Belt (3,600 m to 3,400 m on the south slope, 2,900 m on the north slope), and the Montane Forest Belt (<3,400 m; Hastenrath, 1984). The vertical distribution of *Senecio keni dendron* and *Senecio brassica* is used to distinguish the upper and lower alpine zones, although there is considerable overlap in their distribution (Hedberg, 1951). In the lower alpine zone, tussock grasses, *Senecio brassica*, and *Lobelia keniensis* occupy the wetter areas, and *Alchemilletum* predominates in dry areas. In the upper alpine zone, *Senecio keni dendron* is present up to 4,500 m, together with *Carex monostachya*, *Agrostis* spp., *Cardus platyphyllus*, *Arabis alpina*, *Senecio keniophytum*, and *Lobelia telekii*.

II. Methods

The position of Tyndall Glacier's snout was established by measuring the distance from a sign at Tyndall Tarn. The leading edge of plant-cover was measured from the terminus of the glacier. Moraine positions were compiled on a topographic map (The Glaciers of Mount Kenya, 1:5,000, Hastenrath *et al.*, 1989) from field surveys and aerial photographs (1:50,000).

Plant communities and their environments were surveyed at nine sites (Plots 1 to 9, each 2 m×2 m and representing different terrain conditions). In each survey site, surface materials, land surface stability, lichen coverage on exposed rock, vegetation coverage, and species composition were investigated. The particle-sizes in the surface rubble layer were measured by the long-axis of rubble (30 to 100 measurements at each quadrat). Substrate stability was established using the deflection of a painted line. Lichen cover was used as a cross-check for identifying stability, and to estimate the elapsed time from glacier release. Lichen coverage is the percentage that lichen covers the exposed part of the debris. Soil profiles were surveyed at 12 sites (Plots a to l). A till age for each plot was estimated using its distance from the glacier front and established glacial retreat rates [2.9 m yr⁻¹ (1958–1992); 3.8 m yr⁻¹ (–1958); Charnley,

1959]).

Habitats of large woody plants such as *Senecio keniodendron* and *Lobelia telekii* were investigated around Plot 6. The relationship between the clast size of surficial material and the height of *Senecio keniodendron* and *Lobelia telekii* was studied at two sites (15 m×15 m): Plot A (4,390 m, on Tyndall Moraine I) and Plot B (4,390 m, on a debris flow and outwash slope).

RESULTS

I. Fluctuation of the Tyndall Glacier and Glacial Topography on Mt. Kenya

The Lewis and Tyndall Moraines formed in front of the Tyndall Glacier (Figs. 2 & 3). The Lewis Till (the Lewis Moraine, ca. 100 yr BP) and Tyndall Till (the Tyndall Moraine, ca. 900 yr BP) are considered to be late Holocene in age, based on soil development and weathering features (Spence & Mahaney, 1988; Mahaney, 1989; Mizuno 1998). The date of Tyndall Moraine corresponds to that of the leopard discovered from the snout of the Tyndall Glacier in 1997 (Fig. 4) (Mizuno, 2005; Mizuno & Nakamura, 1999). The Tyndall Moraine is divided into Tyndall Moraine I and Tyndall Moraine II on the basis of topographic position, weathering characteristics, and relative soil development. The climate fluctuated between warm and cold periods prior to 100 yr BP, and was accompanied by moraine deposition. In the last 100 yr, however, the Tyndall Glacier has retreated constantly and no new moraine material has been deposited. Figs. 5, 6, and 7 shows the extent of the Tyndall Glacier in 1992, 1997, and 2002, during the time it retreated rapidly. This very rapid rate of retreat from 1997 to 2002 (ca. 10 m yr⁻¹) contrasts with the average rate of ca. 3 m yr⁻¹ for the period from 1958 to 1997 (Fig.8). Comparing the photos of 1997 (Fig. 9) and 2002 (Fig. 10) illustrates the very rapid recent retreat.

II. Plant Succession in Response to Deglaciation

Fig. 8 shows changes in the position of the glacier front and the leading edge of each advancing plant species (arrow inclination indicates speed of advancement). For example, in 2002, no plants were present within 12 m of the glacier front, and *Senecio keniohytum* and *Arabis alpina* were in areas >12 m away from the glacier front. Moss and lichen were present at distances of 27 m and more.

The first species to colonize new till was *Senecio keniohytum* (Fig. 12b), which advanced at an average rate of 2.7 m yr⁻¹ from 1958 to 1984, and 2.1 m yr⁻¹ from 1984 to 1992. These rates of advance are similar to the rate of glacial retreat (2.9 m yr⁻¹). Other pioneer species, such as *Arabis alpina*, moss, lichen, and *Agrostis trachyphylla*, advanced at rates between 2.1 m yr⁻¹ and 4.6 m yr⁻¹ in response to glacial retreat rates of 2.9 m yr⁻¹. *Senecio keniohytum* advanced at 8.8 m yr⁻¹ and *Arabis alpina* advanced at 12.2 m yr⁻¹, in response to the



Fig. 2. The summit of Mt. Kenya (5,199 m) and the Tyndall Glacier (left). The upper slope is the Lewis Moraine (white) and the lower slope is Tyndall Moraine I (black).



Fig. 4. Leopard remains discovered on the Tyndall Glacier, Mt. Kenya, in 1997.

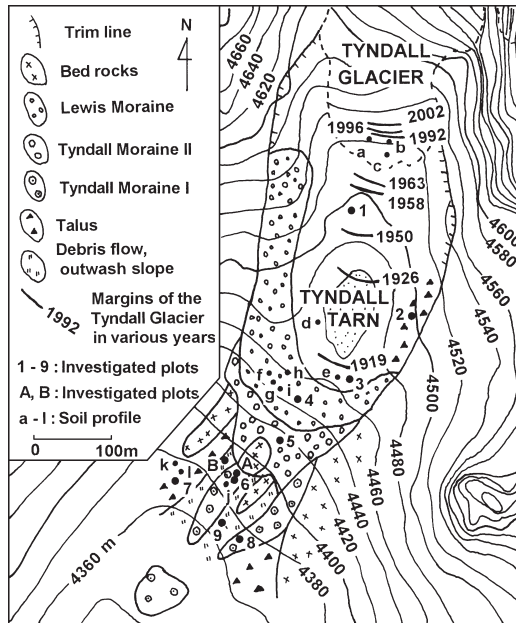


Fig. 3. Geomorphological map for the environs of the Tyndall Glacier, Mt. Kenya. Margins of the Tyndall Glacier for 1919, 1926 and 1963 are from Hastenrath (1983); for 1950 and 1958 from Charnley (1959). Lewis Moraine (Lewis Till) and Tyndall Moraine (Tyndall Till) are from Mahaney (1982, 1989) and Mahaney and Spence (1989).

glacial retreat of 9.8 m yr^{-1} for the interval from 1997 to 2002. *Arabis alpina* eventually got ahead of *Senecio keniophytum*: the leading edge of the area containing *Arabis alpina* was 11.56 m from the glacier front, whereas that of *Senecio keniophytum* was at 11.80 m. Mosses and lichen advanced at a rate of 10.2 m yr^{-1} , and *Agrostis trachyphylla* also advanced at the rapid rate of 6.4 m yr^{-1} . Large woody plants such as *Senecio keniodendron* and *Lobelia telekii*, which did not advance prior to 1997, advanced rapidly at 17.2 m yr^{-1} and



Fig. 5. Tyndall Glacier in 1992.



Fig. 6. Tyndall Glacier in 1997.



Fig. 7. Tyndall Glacier in 2002.

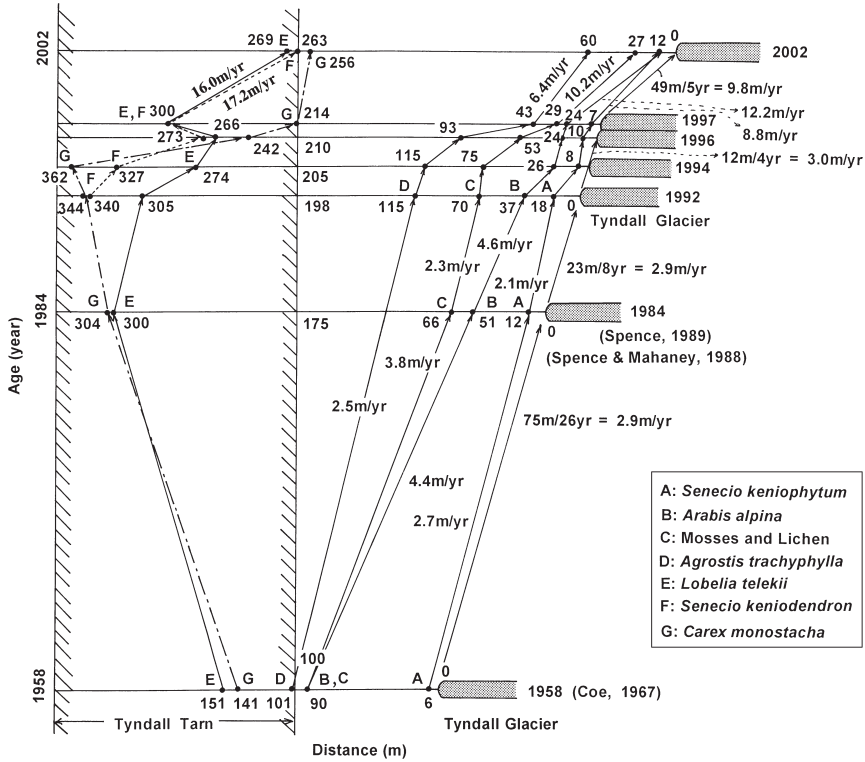


Fig. 8. Glacial fluctuations and succession of alpine plants. The horizontal axis: distance (m) from the margin of Tyndall Glacier to the front of each plant distribution. The vertical axis: date (the length of the vertical axis indicates years). The arrow: movement of the glacial margin or the front of each plant distribution (the inclination of the arrow indicates speed of movement).



Fig. 9. The front of the Tyndall Glacier in 1997.



Fig. 10. The front of the Tyndall Glacier in 2002, taken from the same location as Fig. 9.

16.0 m yr⁻¹ respectively, from 1997 to 2002.

Near the glacier, the earliest colonizing species, *Senecio keniophytum*, is sparse in the eastern area, which receives less solar radiation owing to the shade of the summit. This species prefers cracks in bedrock on convex slopes

such as ridges or banks, because the fine material within the cracks retains water, and the bedrock slope is stable.

III. Plant Succession and Soil Development

Plants change the environments they colonize when they advance into areas formerly covered by glacial ice. Fig. 11 shows the soil profile and till ages (yr) for the study plots, or the time since release from glacial ice. This age, or time, is estimated using the distance between the glacier front and each plot, and the glacial retreat rates [2.9 m yr^{-1} (1958–1992); 3.8 m yr^{-1} (1926–1958)]. For example, the time since release from the glacier ice at Plots a, b, and c (i.e., the till ages) are estimated at 5–13 yr. Soil near the glacier is sandy (loamy sand, sandy loam, and sand) with much fine gravel. Soils are immature, lacking humus content, and thus exhibits dark grayish yellow (2.5Y4/2), grayish olive (5Y4/2), and yellowish gray (2.5Y4/1) colors. In the area closest to the ice-front, only *Senecio keniophyllum* grows abundantly. At Plot e, where 79 years have elapsed since glacial release, soil is fine-grained (e.g., silty clay), and its color is brownish-black (7.5YR2/2, 10YR2/2) because of a significant humus content. Soils of this type can support growth of the large woody plant *Senecio keniodendron*.

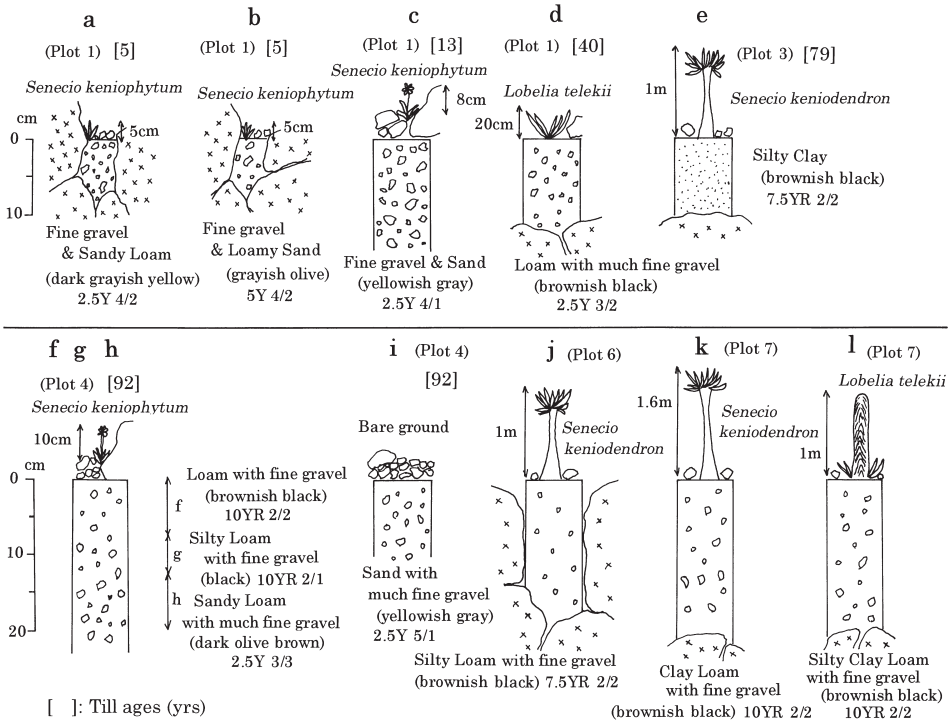


Fig. 11. Soil profiles of plots (Fig. 3). Till ages (yr) of the plots are estimated from glacial retreat rates [2.9 m/yr (1958–1992); 3.8 m/yr (–1958); Charnley, 1959].

Table 1. Environments and composition of alpine plant communities at each plot (Fig. 3) around the Tyndall Glacier.

	Plot	1	2	3	4	5	6	7	8	9
Till age (yrs)*	40			79	92					
Landform	Cirque bottom		Talus	Hollow	Lewis Moraine	Tyndall Moraine II	Tyndall Moraine I	Talus	Tyndall Moraine I	Debris flow & outwash slope
Grain-size distribution of surface rubble layer (cm) (): Average	1-500 (70)	Debris over fine-grained materials 1-500 (30)	Debris over fine-grained materials 1-300 (50)	1-300 (50)	Debris over fine-grained materials 1-500 (30)	50-500 (150)	20-300 (100)	1-300 (50)	50-500 (150)	1-200 (30)
Stability of land surface										
Stable ← → Unstable	A	B	C	A	C**	A	A	A	A	B
Distance from margin of the glacier	Short ←									Long →
Lichen coverage on exposed block (%)	0	0	30	30	30	90	95	70	90	40
Vegetation										
Vegetation coverage (%)	1	1	9	2	2	10	36	45	40	28
<i>Senecio keniophytum</i>	1	1	5	2	2	8	5	5	5	2
<i>Arabis alpina</i>	+		1			+				
Tussock Grass (<i>Agrostis trachyphylla</i> etc.)	+		+				18	15	14	20
<i>Carex monostachya</i>			+							
<i>Lobelia telekii</i>			1	+		1	3	10	1	1
<i>Senecio keniodendron</i>			1			1	10	20	20	5

* Till ages of the plots are estimated ages based on glacial retreat rates (2.9 m/yr: 1958-1992, 3.8 m/yr: 1958, Charnley, 1959).

** The maximum movement of land surface was 610 cm during two years from 1994 to 1996 and 3,200 cm during 8 years from 1994 to 2002.

Soils capable of supporting the growth of diverse plants develop in environments near the glacier front as a result of improvements made by the roots and humus of pioneer species. Dense growths of *Senecio keniodendron*, *Lobelia telekii* and tussock grass become possible in areas where ice retreat took place ca. 500 yr BP, judging by moraine location and retreat speed of the glacier. At other sites, such as Plot i, few plants were growing in the sandy, yellowish-gray (2.5Y5/1) soil, despite 92 elapsed years since glacial retreat, because of substrate instability (Table 1). The maximum movement of land surface in Lewis Moraine (Plot 4, Plot i) was 610 cm during two years from 1994 to 1996 and 3,200 cm during eight years from 1994 to 2002 (Table 1). The air temperature changed from 0.2°C (8:00 AM) to 5.4°C (3:00 PM) and the soil temperature of bare ground (5 cm in depth) changed from -0.4°C (8:00 AM) to 10.7°C (3:00 PM) at Plot 4 on 5 August, 1994 (Mizuno, 1998). Land surface is unstable due to daily active solifluction from the freeze-thaw. Vegetation coverage is low in Lewis Moraine, because of substrate instability and steep slope. In places with large daily air and soil temperature fluctuations, such as tropical high mountains, daily freeze-thaw cycles cause substrate instability, which strongly influences vegetation distribution.

IV. Habitat of the Large Woody Plants *Senecio keniodendron* and *Lobelia telekii*

Areas where glacial retreat took place a few hundred years ago are generally occupied by large woody plants such as *Senecio keniodendron* and *Lobelia telekii* (Table 1, Fig. 12a). The habitats of *Senecio keniodendron* and *Lobelia telekii* were investigated near Plot 6, where glacial retreat took place ca. 500 years ago. *Senecio keniodendron* and *Lobelia telekii* are particularly present on Tyndall Moraine I and on talus below 4,400 m (Table 1).

The clast size of surficial material and the height of *Senecio keniodendron* and *Lobelia telekii* plants were surveyed at Plot A (4,390 m altitude; Tyndall Moraine I) and Plot B (4,390 m; debris flow and outwash slope) (Fig.3). Large clast sizes are present at Plot A, where about 50% of clasts covering land surface have long-axis diameters of 40 to 70 cm, and over 20% have long-axis



Fig. 12a. Large woody plants of *Senecio keniodendron* (Left) and *Lobelia telekii* (Center).



Fig. 12b. Pioneer species of *Senecio keniohytum*.

diameters over 100 cm (Fig. 13a). Smaller clast sizes are prevalent on debris flow and outwash slopes, where debris with long-axis diameters of 10 to 40 cm occupy about 70% of land surface (Fig. 13b).

The population of *Lobelia telekii* is 49 on Tyndall Moraine I (Fig. 14a), and 115 on the debris flow and outwash slope (Fig. 14b). *Lobelia telekii* is generally only 10–20 cm high in August, at both locations, because it dies and regrows mostly every year.

Although the population density of *Senecio keniodendron* is similar at the two sites, plant heights are different. On Tyndall Moraine I, 81% of *Senecio keniodendron* plants are over 50 cm high and 62% are over 100 cm (Fig. 15a). On the debris flow and outwash slope, however, *Senecio keniodendron* plants over 50 cm high form only 22% of the total (Fig. 15b). Although 6 specimens over 50 cm high were present, reflecting long lifespans, the other 21 specimens

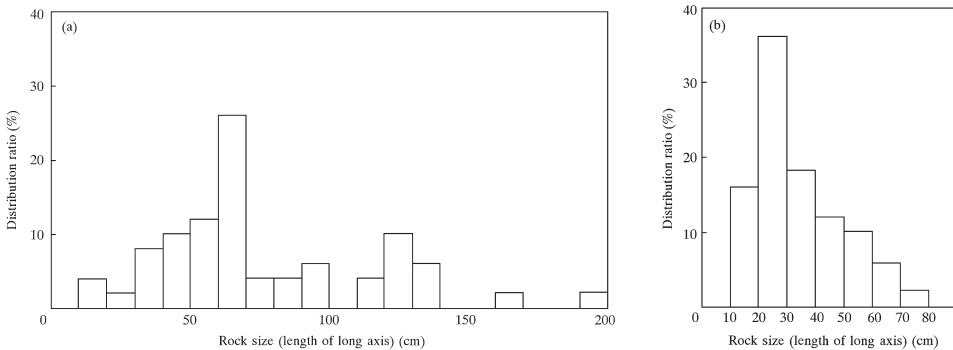


Fig. 13. Debris distribution on (a) Tyndall Moraine I (Plot A) and (b) the debris flow and outwash slope (Plot B).

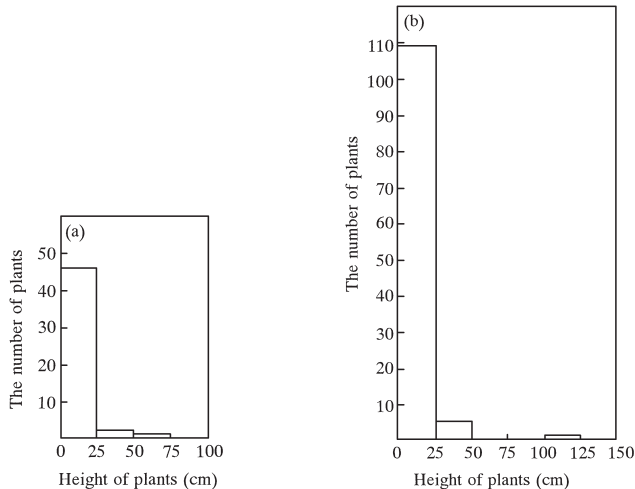


Fig. 14. Height of *Lobelia telekii* on (a) Tyndall Moraine I and (b) the debris flow and outwash slope (August 2002).

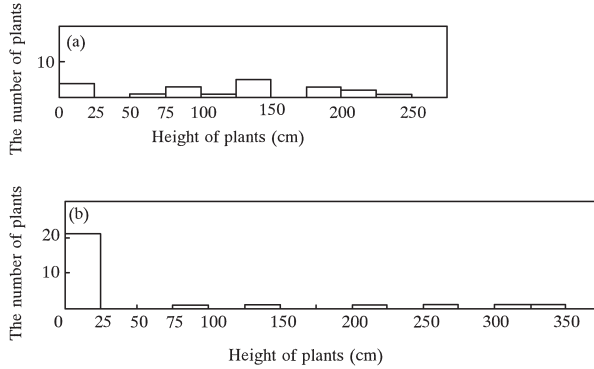


Fig. 15. Height of *Senecio keniodendron* on (a) Tyndall Moraine I and (b) the debris flow and outwash slope (August 2002).

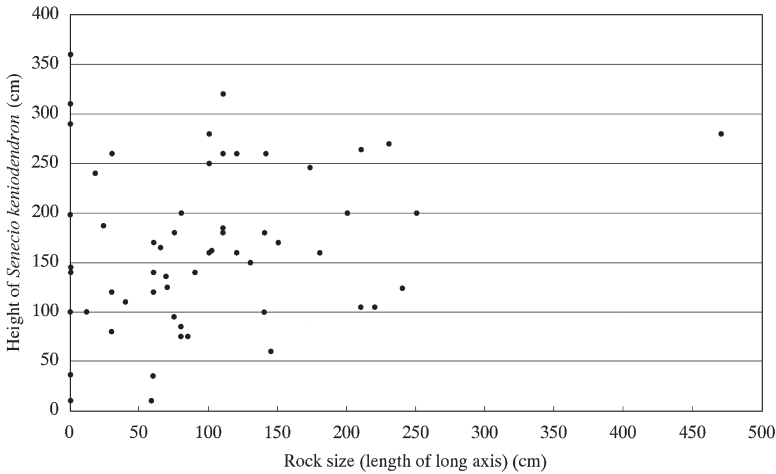


Fig. 16. Relationship between *Senecio keniodendron* height and size of clast long axes in surrounding debris (August 2002). Clast sizes were measured for the biggest debris in ones standing close to *Senecio keniodendron*.

were less than 20 cm high. These latter were new plants that sprouted less than a year before; few of these specimens would survive into ensuing years. As the debris flow and outwash slope site is located in an area of concave topography, plant growth at this site is commonly affected by debris flows or outwash. In contrast, on Tyndall Moraine I the convex topography is not affected by debris flows and outwash, and the substrate is stable, so that *Senecio keniodendron* plants can grow for longer and attain larger sizes. It is interesting to note, however, that the three specimens of *Senecio keniodendron* over 200 cm high at the stable site on Tyndall Moraine I are less than 250 cm high; on the unstable debris flow and outwash slope, however, two of the four specimens over 200 cm high, are actually over 300 cm high. *Senecio keniodendron* height reliably indicates plant age regardless of environment because this plant does not



Fig. 17. *Senecio keniodendron* growing close to large debris clasts.

die and regrow every year. Tyndall Moraine I, characterized by large debris, is a good environment for the growth of *Senecio keniodendron*.

To elucidate this point further, 60 specimens of *Senecio keniodendron* were selected randomly, and the relationship between their heights and the long-axis diameter of the largest debris clasts in the plants' immediate vicinity were measured (Fig. 16). Although the relationship did not emerge as clear-cut, 9 specimens (69%) among the 19 individuals of *Senecio keniodendron* over 250 cm high were associated with debris clasts over 100 cm in diameter. Out of 50 plants over 100 cm high, 34 specimens (72%) were associated with debris over 50 cm in diameter (Fig. 17).

DISCUSSION

I. Deglaciation in the High Mountains of East Africa

The Tyndall Glacier of Mt. Kenya retreated at a rate of ca. 3 m yr^{-1} from 1958 to 1997, but at a higher rate of ca. 10 m yr^{-1} from 1997 to 2002. Recently, acceleration in glacial retreat is prevalent among East African mountains. Fig. 18 shows glaciers on Kilimanjaro in the 1970s (Hastenrath, 1984, 1997) and in 2002 (Mizuno, 2003b). Glacier distribution in the 1970s is based on air photographs taken on 18 March 1972 (Geosurvey Ltd., Peter Gollmer, Nairobi), a photograph taken during a hot-air balloon flight over the Kibo crater on 10 March 1974 (Alan Root, Nairobi), and field observations by Hastenrath in 1971, 1973, and 1974. Glacier distribution in 2002 is based on photographs taken from a light aircraft on 17 August 2002 (Mizuno, 2003b). Glacier extent in 2002 is about half of what it was in the 1970s. This is a dramatic change after only 30 years. The retreat of glaciers on Mount Kenya is well documented for the periods 1899–1963 and 1963–1987 (Hastenrath & Kruss, 1992; Mahaney, 1990). Ice recession between 1899 and 1963 was strongly dependent on solar radiation geometry on any given glacier. In contrast, ice thinning between 1963 and 1987 amounted to about 15 m for all glaciers, regardless of location. This suggests that climatic factors other than solar radiation became more important. The long-term precipitation records for the Kenyan highlands do not support

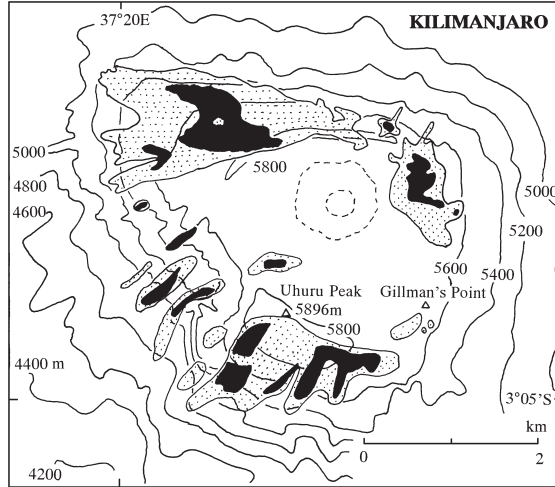


Fig. 18. Glacial cover of Kilimanjaro in the 1970s (stippled; Hastenrath, 1984) and in 2002 (black).

precipitation deficits of such a massive magnitude. Solar radiation/cloud changes, as well as dust/albedo effects, are ruled out by the spatial uniformity of the observed ice thinning. This leaves, as possibly pertinent, the following three heat-budget terms: downward-directed sensible heat transfer from air to ice, which is primarily controlled by the air temperature; upward-directed latent-heat transfer, which is mainly dependent on specific humidity; and net long-wave radiation, which varies mainly with changes in dry-atmospheric composition (“greenhouse effect”), the impact of changing atmospheric moisture being of subordinate importance at the altitude of Mount Kenya (Hastenrath and Kruss, 1992).

II. Vegetation Succession in Response to Deglaciation

All plant species near the glacier advanced as the glacier retreated. The first colonists of new till were *Senecio keniophytum*, *Arabis alpina*, moss, lichen, and *Agrostis trachyphylla*. Their advance rate of 2.1–4.6 m yr⁻¹ from 1958 to 1997 was similar to the speed of glacial retreat (2.9 m yr⁻¹). When glacial retreat accelerated to 9.8 m yr⁻¹, from 1997 to 2002, pioneer species advanced at a faster rate: 12.2 m yr⁻¹ for *Arabis alpina*, 10.2 m yr⁻¹ for moss and lichen, 8.8 m yr⁻¹ for *Senecio keniophytum*, and 6.4 m yr⁻¹ for *Agrostis trachyphylla*. *Senecio keniodendron* and *Lobelia telekii* showed no obvious advances before 1997, but advanced rapidly at rates of 16.0 m yr⁻¹ and 17.2 m yr⁻¹ after 1997.

Rapid glacier retreat generally leads to a succession of vegetation, and causes subtle but serious ecologic changes. Pioneer species improve soil conditions and make the habitat suitable for other plants.

Spence (1989) points out that pioneer succession in front of the Tyndall and Lewis Glaciers proceeds with the appearance first of *Senecio keniophytum*, followed by *Arabis alpina*, and the *Senecio* has fruits with morphological

features aiding in wind dispersal and the *Arabis* as well as grasses lack such features. Those species, such as *Senecio kenioptum* and *Arabis alpine*, that can live at nival elevations on the mountain (>4,500 m), appear to be most successful in establishing (Spense, 1989).

Frost soil activity is intense on the till, and as well cold adiabatic winds sweep off the ice surface (Coe, 1967). In particular, when the particle-size of surficial material is small, high water content in the soil causes periglacial processes such as frost-creep and solifluction (Benedict, 1970; Washburn, 1973; Iwata, 1983). These processes, in turn, destabilize the land surface and restrict plant growth (Mizuno, 1998, 2002; Mizuno & Nakamura 1999).

One hundred years after glacial retreat, large woody plants such as *Senecio keniodendron* and *Lobelia telekii* can grow in formerly glacier-covered areas. In such places, the growth of large woody plants is not directly controlled by glacial retreat, but depends on the clast size of the debris covering the land surface and the difference of effect of debris flow and outwash (Table 1). For example, *Senecio keniodendron* can grow in areas of large debris clasts, probably because such substrates are stable. Other benefits of this environment include absorption of heat from sunlight by the debris in the daytime, concentration of water runoff from rock surfaces, and sheltering from wind and snow. Moraines with large clasts are therefore commonly characterized by *Senecio keniodendron*.

CONCLUSION

Atmospheric warming is causing global diminution of glacier cover. Mt. Kenya had 18 glaciers in the early 20th century, some of which have gradually

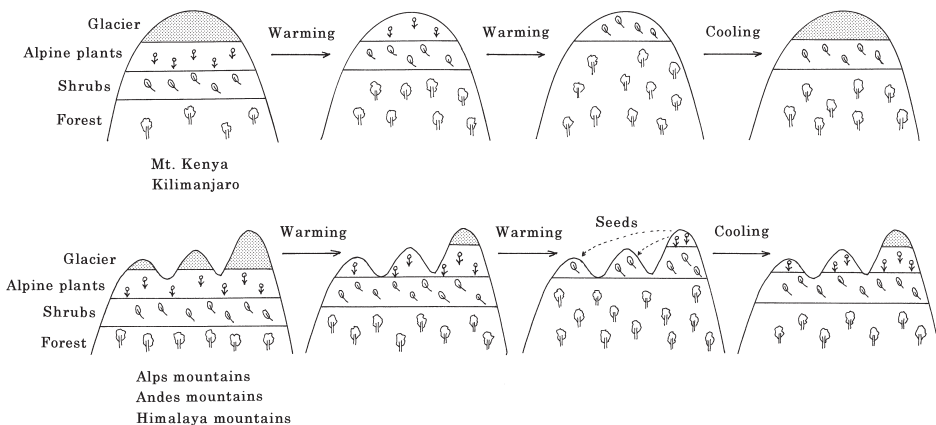


Fig. 19. Theoretical changes in vegetation zones as a result of climate change for an isolated mountain (upper) and for a mountain in a mountain range (lower). If, after an interval of warming, cooler conditions returned to an isolated mountain that caused the eradication of alpine plants, such plants would be unlikely to return. In a mountain belt, however, seed dispersal from one mountain to another would allow recolonization.

disappeared; at present, only 11 glaciers persist (Hastenrath, 1984). When glaciers covering mountain summits melt, plant-cover can expand up the mountains. If warming continues, alpine plant cover may extend all the way to mountain summits, and then eventually diminish as trees colonize the areas formerly occupied by the alpine plants. The Tyndall Glacier has retreated by approx. 300 m in horizontal distance over the 80 years since 1919. In extensive mountain ranges such as the Alps or the Andes, if alpine plants were to be eradicated from a given mountain, they could be replaced by the dispersal of seeds from another mountain. On isolated mountains such as Mt. Kenya or Kilimanjaro, if alpine plants disappear because of warming, it would be difficult for them to regenerate if the climate then cooled (Fig. 19). Ecosystems on high mountains are very sensitive, and apparently even small environmental changes can cause obvious changes in vegetation. Understanding the relationship between alpine vegetation and its environment is critical to tracking global environmental change.

ACKNOWLEDGEMENTS I thank Mr. Shinichiro Ishikawa (in 1996), Mr. Tatsuhiko Ouchi (in 1997), and Mr. Yuichiro Fujioka and Mr. Masaaki Ito (in 2002) for their field assistance. I would also like to thank Mr. Alexis Peltier, our aircraft pilot and Mrs. Chiaki Hayakawa, our adviser for taking photographs of glaciers on Kilimanjaro. The expenses for the field research were supported by a Grant-in-Aid for Scientific Research (Project No. 13371013 headed by Dr. Kazuharu Mizuno, Kyoto University) from the Ministry of Education, Science, Sports, Culture, and Technology of the Japanese Government.

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