Vegetation succession on Mt. Kenya in relation to glacial fluctuation and global warming

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Abstract

Question: 1) How has the plant community responded to recent glacial retreat? 2) Has the recent glacial retreat been affected by increases in temperature? 3) How have the number of plant clumps and the proportion of vegetation cover changed with the distance from the glacier edge (i.e., till age)?

Location: From Tyndall Tarn to the foot of Tyndall Glacier of Mt. Kenya (0°6' S, 37°18' E), Kenya.

Methods: The topography, soils, vegetation, and glacial distribution around the Tyndall Glacier of Mt. Kenya were investigated from 1992 to 2011. The effect of glacial retreat on the rate of movement of the leading edge (upper distribution limit) of plant species was examined. The distribution of vegetation was examined in a permanent plot that was surveyed in 1996 and 2011. The effects of temperature variation on glacial retreat were assessed by a least squares regression model.

Results: Tyndall Glacier retreated at a rate of ~3 m year^{-1} from 1958 to 1997. The rate increased to 7–15 m year^{-1} between 1997 and 2011. The leading edge of *Senecio keniophytum*, the first pioneer species to establish after glacial retreat, advanced with glacial recession. It was sparse in 1996. By 2011, the number of clumps and proportion of cover had increased. Clump size was affected by distance from the glacier edge (i.e., till age) in areas of recent deglaciation but not in deglaciated areas older than 15 years. Monthly mean minimum temperature at Mt. Kenya increased by >2°C from 1963 to 2011 and glacial retreat was related to increase in monthly mean minimum temperature.

Conclusion: The glaciers on Mt. Kenya have diminished rapidly in recent years, and pioneer plant species have advanced in response. The movements of some species do not appear to be directly spatially related to glacial retreat but may be related to increases in air temperature, soil development, seed dispersal limitation, and interval of masting. Recent unusually high temperatures and precipitation also likely caused the blooming during atypical seasons of some species.

Keywords: Glacier retreat; Global warming; Large woody rosette plants; Phenology; Pioneer species; Tyndall Glacier

Nomenclature: Coe (1967)

Introduction

Large changes are taking place on the high, glacier-covered mountains of Africa. The only African mountains still capped by glaciers are Mt. Kilimanjaro, Mt. Kenya, and Mt. Rwenzori. However, the retreat rate of theses glaciers has accelerated (Hastenrath 1984,1997, 2005, 2008) and are expected to disappear in the near future.

Numerous studies have been carried out on the dynamics of the glaciers of Mt. Kenya (Troll & Wien 1949; Charnley 1959; Hastenrath 1984, 1991, 2005; Kruss & Hastenrath 1983). Many of these studies have examined glacial fluctuations and deposits (Mahaney 1984, 1989, 1990; Mahaney & Spence 1989). Although plant succession has been well documented on glacier forelands in North America (Jones & del Moral 2005), Scandinavia (Robbins & Matthews 2009), other Arctic locations (Hodkinson et al. 2003), and the European Alps (Niederfriniger-Schlag & Erschbamer 2000; Raffl & Erschbamer 2004; Raffl et al. 2006a; Garbarino et al. 2010), little research has examined primary succession following glacial retreat on high, tropical mountains.

Worldwide, most studies have described vegetation changes on differently aged moraines and have chronicled centuries of change (Okitsu et al. 2004; Jones & del Moral 2005; Raffl et al. 2006b; Mori et al. 2008). However, few studies have involved real-time recordings of glacier recession and plant advance, in contrast to studies of community succession based on chronosequences and historical records of previous extensions of glaciers (Nagy & Grabherr 2009). Most studies have found that time, expressed as till age, is the main factor controlling species distributions (Whittaker 1987; Matthews 1992; Caccianiga et al. 2001). Previous research has demonstrated that succession requires several hundred years to reach the climax stage of alpine grasslands on ground moraines (Raffl & Erschbamer 2004). Low-cover pioneer communities grow on 20th-century deposits, whereas high-cover communities occur mainly on already stabilized moraines that date back to the 19th century (Caccianiga & Andreis 2004). Microbial functional diversity reaches stability within 50 years' succession (Tscherko et al. 2003). In the foreland of the Coleman Glacier, species richness and diversity were highest during early succession on small scales and during late succession on larger scales (Jones & del Moral 2005). However, in addition to till age, substratum stability may strongly influence vegetation patterns around glaciers on high, tropical mountains (Mizuno 1998, 2005a, 2005b). By examining patterns of larch establishment, Garbarino et al. (2010) found that the most influential factors determining stand density and age were proximity to the glacier terminus and seed sources as well as litter cover and elevation.

Coe (1967) described the distribution of vegetation, the colonization by plants, and the distribution of individual plant species on slopes below glaciers on Mt. Kenya. Spence (1989) analyzed the advance of plant communities in response to the retreat of the Tyndall and Lewis Glaciers from 1958 to 1984, and Mizuno (2005a, 2005b) examined the response of plant communities to more recent glacial retreats in 1992, 1994, 1996, 1997, and 2002.

In 2009, a previously unreported species was found in the outer areas of old glacial flow paths. Thus, some plant species have advanced regardless of glacial retreat. However, no studies have examined vegetation succession due to both recent glacial retreat and global warming, and their relationships have not been fully clarified.

In the present study, the following questions were investigated: 1) How has the plant community responded to recent glacial retreat? 2) Has the recent glacial retreat been affected by increases in temperature? 3) How have the number of plant clumps and the proportion of vegetation cover changed with the distance from the glacier edge (i.e., till age)? It was predicted that the invasion of new species to the study area in 2009 was affected by increases in temperature and that the atypical timing of the blooming of some species has been influenced by recent unusual temperatures or precipitation.

Methods

Study area – age, climate, and vegetation

The main study area was around Tyndall Glacier but, for comparison, the Lewis Glacier on Mt. Kenya and the glaciers on Mt. Kilimanjaro were also investigated.

Mt. Kenya is an isolated, extinct, denuded volcano that lies on the equator (0°6' S, 37°18' E), approximately 150 km north–northeast of Nairobi. The highest peak, Batian, is 5199 m above sea level. The mountain was formed between 3.1 and 2.6 million years ago (Bhatt 1991), and the volcanic plug has been dated to 2.64 million years ago (Mahaney 1990). Rocks of the volcanic massif consist of basalt, phonolite, kenytes, agglomerates, trachyte, and syenite (Mahaney 1990; Bhatt 1991).

There were 18 glaciers on Mt. Kenya at the end of the 19th century (Hastenrath 2008), but only a few, including the Lewis and Tyndall Glaciers, remain. Fluctuations in the sizes and movement of these glaciers have been recorded in detail (Hastenrath 1984, 1997, 2005, 2008; Mahaney 1990). Mahaney (1984, 1990) subdivided into the Tyndall advance (the Tyndall Moraine, ca. 900 yr BP) and the Lewis advance (the Lewis Moraine, ca. 100 yr BP), on the basis of several indirect measurements that included topographic position, weathering characteristics, and the degree of soil development (Spence & Mahaney 1988; Mahaney 1989, 1990; Mizuno 1998, 2005a).

The elevations in East Africa at which the annual minimum, mean, and maximum temperatures of the free atmosphere are 0°C are approximately 3500 m, 4750 m, and 6000 m, respectively (Hastenrath 1991). Annual precipitation is about 2500 mm year^{-1}

at 2250 m on the southeastern slopes of Mt. Kenya and decreases to less than 1000 mm year^{-1} at that altitude on the northern slope (Mahaney 1984; Hastenrath 1991). Annual rainfall is highest between 2500 and 3000 m on the south, west, and east slopes, and decreases towards the peak (<900 mm at 4500–4800 m). Above 4500 m, most precipitation falls as snow and hail.

The vegetation of Mt. Kenya has been classified into the Alpine Belt (>3600 m), the Ericaceous Belt (3600–3400 m on the south slope, 2900 m on the north slope), and the Montane Forest Belt (<3400 m; Hastenrath 1984). The altitudinal distributions of *Senecio keniodendron* and *Senecio keniensis* (formerly *S. brassica*) are used to distinguish between the upper and lower alpine zones, although there is considerable overlap in their distribution (Hedberg 1951; Young and Peacock 1992). In the lower alpine zone, the tussock grasses *S. keniensis* and *Lobelia keniensis* occupy the wetter areas, and *Alchemilla* spp. predominate in dry areas. In the upper alpine zone, *S. keniodendron* is present up to 4500 m together with *Carex monostachya*, *Agrostis* spp., *Carduus platyphyllus*, *Arabis alpina*, *Senecio keniophytum*, and *Lobelia telekii*. In general, large woody rosette plants, including giant senecio (e.g., *S. keniodendron*) and giant lobelia (e.g., *L. telekii*), are characteristic of high, tropical mountain landscapes with large ranges in diurnal temperature (Hedberg 1964, 1968; Coe 1967; Smith & Young 1987; Rehder et al. 1988; Young 1991; Rehder 1992).

Data collection

Measurement of topography and glacier

Topography, soils, vegetation, and location of the glacial edge in several years around the Tyndall Glacier of Mt. Kenya were investigated from 1992 to 2011. A topographic profile was created, with distance and surface inclinations measured using a laser rangefinder (TruPulse 200). At the glacial margins, latitude and longitude were recorded using a global positioning system (GPS) unit, and the distances from the foot of Tyndall Glacier to a large rock constituting the northern part of the Tyndall Tarn were measured using both a measuring tape and the laser rangefinder. The length, width, and thickness of the glacier were measured in the same way.

Climate data

Temperature and precipitation data were acquired from the Meteorological Department of Nairobi. These data were recorded at the Nanyuki Meteorological Station (1890 m in altitude, 0.03°N, 37.02°E) on the north–northwest side of Mt. Kenya. Temperature data of the Mt. Kenya Global Atmosphere Watch (GAW) Station (3678 m in altitude, -0.06°N, 37.30°E) on the north side of Mt. Kenya were used for comparison with the data from Nanyuki. Because much of the data from the GAW Station were missing, data for months without missing data (July 2003, April 2004, and November 2005) were used to determine the temperature lapse rate. Based on comparisons between air temperature data at 1890 and 3678 m, the temperature lapse rate at Mt. Kenya was determined to be 0.63ºC/100 m (July 2003: 0.64, April 2004: 0.62, May 2005: 0.63). This was used to estimate the temperature at 4500 m altitude in the study area.

Temperature was recorded to assess the freeze–thaw environment of the land surface using an air temperature sensor and a data logger in the vicinity of the glacier edge from

31 August to 3 September 2011.

Soil profile

Typical soil profiles from various till ages (years after the disappearance of the glacier) were determined using soil profile data observed in 1992–2009. Till age (years) of the site was estimated from the glacial retreat rate and the distance from the glacier edge. In each soil profile, the texture, structure, and color of the soil were determined.

Vegetation sampling

Lines perpendicular to the direction of the slope were set in 2-m intervals from the end of the glacier, and individual plants inside the trim line (Fig. 1) were checked every 2 m. When the first specimen of a species was found, the distance from the glacial foot to that individual was measured.

The positions of the leading edge of each plant species to the foot of the glacier were measured. In August 2011, we were unable to determine the positions of the leading edges of pioneer species because the area in the vicinity of the glacier foot was covered with snow.

A permanent plot (80 × 20 m; Fig. 1) was established near the edge of the glacier in August 1996. All herbaceous individuals were mapped in August 1996 and August 2011. Quadrats (2.5 × 2 m) for statistical analysis were alternately selected in the permanent plot.

The number of clumps of *Helichrysum citrispinum* growing on the upper slope of Tyndall Tarn was surveyed in August 2009 and August 2011. A 30 × 50 m permanent plot (Fig. 1) was established in the area with a high population of this species in August 2011. All clumps of this species were mapped within this plot in August 2011.

Statistical methods

Differences in the number of plant clumps and the proportion of plant cover between 1996 and 2011 were examined using t-tests. Bonferroni post-hoc tests were used for comparisons of means among quadrats at different distances from the glacier edge.

A least squares regression model was used to examine the effect of glacial retreat on the rate of movement of the leading edge of each plant species. The effects of variation in temperature on the rate of glacial retreat were also assessed using a least squares regression model.

Results

Recent changes in temperature and glacial fluctuation at Tyndall Glacier

The Tyndall Glacier has been diminishing rapidly in recent years (Fig. 2), retreating approximately 250 m from 1958 to 2009 (Fig. 3). The average length of the main axis of the Tyndall Glacier, average width, area, and volume were estimated to be 175 m, 32 m, approximately 5600 m^2, and 19,600–22,400 m^3, respectively, in August 2009.

The Tyndall Glacier retreated at a rate of approximately 2.9 m $year^{-1}$ from 1958 to

1997, but the rate increased to 9.8 m year^{-1} from 1997 to 2002, 14.8 m year^{-1} from 2002 to 2006, 8.7 m year^{-1} from 2006 to 2009, and 7.5 m year^{-1} from 2009 to 2011 (Fig. 4).

Monthly mean minimum temperature at Nanyuki (1890 m altitude) on the western base of Mt. Kenya increased by >2°C in 48 years from 1963 to 2011 (Fig. 5). In contrast, precipitation did not significantly decline during the 55-year period starting in 1956, although annual fluctuations did occur (Fig. 6). Monthly mean maximum temperature also increased by >2°C during this period.

The rate of glacial retreat increased with increased monthly mean minimum temperature at 4500 m in altitude around the study area ($y = 5.882 x + 45.427$, $R^2 = 0.6625$; $P = 0.0085$).

Vegetation succession in relation to recent recession of Tyndall Glacier

The leading edge of *Senecio keniophytum* followed glacial retreat (Figs. 3, 4) at a rate of approximately 2.9 m year^{-1} from 1958 to 1997. This rate increased to 8.8 m year^{-1} from 1997 to 2002, to 14.0 m year^{-1} from 2002 to 2006, and to 10.3 m year^{-1} from 2006 to 2009. The rate of glacial retreat was significantly related to the movement of *S. keniophytum* ($y = 0.8635x + 1.5631$, $R^2 = 0.7205$, $P = 0.0047$). The movement of *Arabis alpina* may also have been influenced by the rate of glacial retreat at some level, but this is not significant ($R^2 = 0.3273$; $P = 0.080$). Other pioneer species, e.g. *Agrostis trachyphylla* and various mosses and lichens also advanced, and the rates of advance have also increased since 1997 (Fig. 4).

Although changes in the positions of the leading edges of the large woody rosette species *Lobelia telekii* and *Senecio keniodendron* were unrelated to glacial retreat through 1997, these species have since advanced (Fig. 4).

Vegetation succession in the permanent plot

The vegetation distribution in the permanent plot established near the glacier was measured in August 1996 and August 2011 (Fig. 7). *S. keniophytum* was only sparsely scattered in the plot in 1996 (Fig. 7a), but its distribution had expanded by 2011 (Fig. 7b). Although 55 clumps of *S. keniophytum* were found in the sampling quadrats in 1996, this number had increased to 217 clumps in 2011. Six clumps of *A. alpina*, two of *Agrostis trachyphylla*, and one of *S. keniodendron* were also encountered in the sampling quadrats in 2011 (Fig. 7b). Both the average number of plant clumps and the proportion of vegetation cover increased significantly ($P < 0.01$) between 1996 and 2011 (Table 1).

The distance from the edge of Tyndall Glacier significantly affected the number of plant clumps and the proportion of vegetation cover in 1996 (Table 2). The number of plant clumps and the proportion of vegetation cover at 16–18 m from the glacier’s edge were significantly higher than values at 0–14 m (Table 2). We did not observe any plants in quadrats established at distances of 0–8 m from the edge of the glacier (Fig. 7a). Similar effects of distance on the number of plant clumps and the proportion of vegetation cover were not observed ($P > 0.05$, respectively) in 2011, when deglaciation exceeded 15 years (Table 3).

Vegetation and land surface stability

The range in daily temperature around the foot of Tyndall Glacier was around 10°C based on data from 31 August to 3 September 2011. During this time, temperatures fell to several degrees below zero by midnight, and temperature ranges were narrower during cloudy days. Ranges in diurnal temperature are generally wide on high-elevation tropical mountains, and freeze–thaw dynamics can render land surfaces unstable due to daily active solifluction. The maximum movement of unstable land surfaces was approximately 4 m year^{-1} (32 m over the 8 years from 1994 to 2002) on the Lewis Moraine. This movement was affected by particle sizes of the surface materials and topography (Mizuno 1998, 2005a, 2005b).

Vegetation succession in relation to recent global warming

Although *Helichrysu citrispinum* had not been found at altitudes above the Tyndall Tarn (4470 m) until 2006, 32 clumps of this species were identified on a lateral moraine of the Lewis Moraine (Fig. 1) on the west–northwest side of Tyndall Tarn above 4470 m in August 2009 (Fig. 4). This species was not found on the cirque bottom or the talus on the east side. Most of the clumps were blooming in August 2009. In August 2011, 36 of 49 clumps of *H. citrispinum* growing on the slope above Tyndall Tarn were found within the permanent plot (30 × 50 m)(Fig. 1), which had been established in an area with a high population of this species (Fig. 8). Only one clump was blooming in August 2011.

The monthly mean maximum temperatures estimated at 4500 m on Mt. Kenya in 2009 were 11.8°C (average from 2007 to 2011: 10.7°C) in March, 10.3°C (9.1°C) in April, 9.1°C (8.3°C) in May, 9.6°C (8.5°C) in June, 8.2°C (7.3°C) in July, 8.9°C (7.7°C) in August, and 10.1°C (8.7°C) in September. Temperatures from March to September 2009 were about 1°C higher than in an average year. *H. citrispinum* normally blooms from December to February. The monthly mean maximum temperature at 4500 m on Mt. Kenya is normally <8°C from July to November, increasing to >8°C from December, and *H. citrispinum* begins to bloom in December. The temperature in August 2009 was >8°C.

Senecio keniodendron rarely blooms, but when it does, it produces buds in mid-December and blooms as temperatures increase from January to February. However, in 2011, many individuals bloomed during August. The difference in temperature between 2011 and the average from 2007 to 2011 was <1°C. Precipitation during the dry season from June to August 2011 was much higher than normal. Precipitation in 2011 was 61.7 mm (average from 2002 to 2011: 36.3 mm) in June, 126.4 mm (54.7 mm) in July, and 100.4 mm (68.2 mm) in August. In contrast, precipitation from January to May 2011 was below normal, with values of 6.2 mm (average from 2002 to 2011: 18.7 mm) in January, 4.1 mm (16.9 mm) in February, 42.4 mm (54.3 mm) in March, 89.7 mm (117.1 mm) in April, and 57.8 mm (71.0 mm) in May.

Discussion

Vegetation succession in relation to recent global warming

The rate of glacial retreat has accelerated since 1997. The advances of pioneer species such as *Senecio keniophytum* and *Arabis alpina* have matched this rate of glacial retreat.

Seed sizes of *S. keniophytum* (3mm) and *A. alpina* (1-1.4mm) are very small, so these species can disperse seeds across relatively extensive area. Seed dispersal ability varies with species and the ability affects the plant community composition (Fuller & del Moral 2003). The characters of their seed dispersal may facilitate the invasion of these pioneer species in recent deglaciated area. The distributions of mosses, lichens, and *Agrostis trachyphylla* also advanced. Since 1997, these species advanced at a faster rate than years past as the glacier retreated. *S. keniophytum*, the first pioneer species to establish after glacial retreat, advanced at a rate similar to that of glacial retreat.

The distance from the glacier edge affects both the number of plant clumps and the proportion of vegetation cover in areas of recent deglaciation. Many seedlings of *S. keniophytum* were likely produced within 5–6 years after deglaciation. However, this effect of distance from the glacier edge was not verified in areas where deglaciation occurred at least 15 years ago. Therefore, the dynamics of plant advancement were substantially affected by the distance from glacier edge (i.e., till age) in areas of recent deglaciation.

The rate of retreat of Tyndall Glacier appears correlated to the increases in monthly mean minimum temperature. The movement of *S. keniophytum*, as well as that of *A. alpina* to some degree, could be explained by the rate of glacial retreat. The recent temperature increase is likely accelerating deglaciation and the expansion of these species onto upper slopes. If the glacier continues to retreat, these species should spread to the summit. Very sparse patches of *S. keniophytum* already occur around the Point Lenana summit (4985 m) of Mt. Kenya.

Changes in advance at the leading edges of *Loberia telekii* and *Senicio keniodendron*, common large woody rosette plants, appeared to be unrelated to glacial retreat up until

1997; since then, however, these species have advanced upslope. The succession of these species does not appear to be directly related to glacial retreat but may instead be linked to soil development from unstable slope to stable slope, and from poor soil to mature soil through humus deposition by pioneer species in a form of facilitation (Fig. 9).

Rare blooms of *S. keniodendron* typically occur from January to February. However, in 2011, many individuals bloomed during August. We believe that unusually high precipitation affected blooming during that month.

S. keniodendron is considered a “mast year” species with the masting interval estimated at between 5 and 29 years (Smith & Young 1982). The interval of masting may explain why the succession of this species does not directly relate to the glacial retreat.

Helichrysum citrispinum was first found on lateral moraines above 4470 m in 2009. During this year, the upper limit of the growing region for these species was estimated at around 4500 m in altitude. The expansion of *H. citrispinum* was likely favored by the increase of about 1°C during the growing season of 2009. In May 1995, four small open-top-chamber (OTC) greenhouses were set up to monitor the phenology and vegetation distribution on Mt. Kisokomagatake (2956 m) in the Central Japanese Alps using the International Tundra Experiment (ITEX) method (Nakashinden et al. 1997; Fukuyo et al. 1998; Zaiki et al. 2003). These OTC experiments demonstrated that such temperature increase can lead to the expansion of some species and to changes in their phenology (Nakashinden et al. 1997; Fukuyo et al. 1998; Zaiki et al. 2003).

Forty-nine clumps of *H. citrispinum* were found on the lateral moraine above 4470 m (Tyndall Tarn) in 2011. Although the number of clumps in 2011 had increased since

2009, only one plant had flower buds. Flowering was likely depressed during August because temperatures during 2011 were within a normal cooler range. *Carduus platyphyllus* was also found above 4470 m. Although these species are not among the pioneers (such as *S. keniophytum*), they have advanced considerably in recent years. In 2009, the upper limit of the growing regions of these species was estimated at around 4500 m altitude. We postulated that their range expansions may not be directly related to glacial retreat, but rather their advance to upper slopes may be linked to increases in air temperature. Temperature may be involved because species such as *H. citrispinum* did not emerge on the cirque bottom where the glacier had recently disappeared and where the pioneer species are invading; rather they emerged on the old lateral moraine outside of old glacial flow paths (Figs. 1, 8). Furthermore, decreased movement of the land surface in the lateral moraine probably does not affect species emergence, because the conditions of deposits of comparable size have remained unchanged and movement has been constant (Mizuno 2005a, 2005b). Because the sediment has not changed, it was surmised that soil moisture has also remained constant. This species was not found in study area before 2006, but was in 2009. The annual maximum temperature of study area in 2009 was the highest and ~0.7°C higher than the average over 30 years from 1981 to 2011. Therefore, increasing temperature is likely the dynamic triggering of the recent advance of these species.

Environmental conditions affecting the vegetation around Tyndall Glacier

The expansion of pioneer species to higher altitudes is influenced by both glacial retreat and the stability of the land surface (Mizuno 1998, 2005a, 2005b). In the present study, areas where seedlings of *S. keniodendron* and *L. telekii* were growing in 2009 generally corresponded to the 1958 location of the Tyndall Glacier edge (Fig. 4). Thus, seedlings of these large woody rosette plants are able to grow in areas approximately 50 years after deglaciation (Fig. 9). These locations corresponded to stable land surfaces, with soils that changed over time from a coarse-grained grayish soil to a fine-grained brownish black soil through humus deposition by pioneer species such as *S. keniophytum* (Fig. 9) (Mizuno 1998, 2005a, 2005b). Plant distributions in the alpine zone on Mt. Kenya are significantly affected by movement of the land surface caused by frost action (Mizuno 1998, 2005a, 2005b).

These data indicate that most plants were unable to grow on unstable land surfaces for many years after deglaciation (Fig. 9). If the number of days during which temperatures at midnight fall below zero were to decrease through global warming, frost action would be reduced and vegetation distributions would shift.

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Fig. 1. Geomorphological map of the environs of Tyndall Glacier, Mt. Kenya. Margins of Tyndall Glacier in 1919 and 1926 are from Hastenrath (1983). The Lewis Moraine (Lewis Till) and the Tyndall Moraine (Tyndall Till) are from Mahaney (1990) and Mahaney and Spence (1989). The map is by Kazuharu Mizuno, based on Hastenrath et al. (1989).

Fig. 2. Tyndall Glacier in 1992 (**a**), 1997 (**b**), 2002 (**c**), 2006 (**d**), 2011 (**e**).

Fig. 3. Positions of the Tyndall Glacier front and the leading edge (upper distribution limit) of *Senecio keniophytum*, on the topographic profile.

Fig. 4. Glacial fluctuations and succession of alpine plants. Horizontal axis: distance (m) from the margin of the Tyndall Glacier to the leading edge (upper distribution limit) of each plant species. Vertical axis: date (the length of the vertical axis indicates years). Arrow: movement of the glacial margin or the leading edge of each plant species (the inclination of the arrow indicates speed of movement).

Fig. 5. Monthly mean minimum temperatures (a) and annual mean minimum temperature (b) at 1890 m (0.03 N, 37.02 E) on the Nanyuki side of Mt. Kenya.

Fig. 6. Precipitation at 1890 m (0.03 N, 37.02 E) on the Nanyuki side of Mt. Kenya.

Fig. 7. Vegetation distribution in 1996 (a) and 2011 (b) in a permanent plot (80 m × 20 m) established close to the foot of the glacier in August, 1996. Patch without letters: *Senecio keniophytum*; A: *Arabis alpina*; T: *Agrostis trachyphylla*; S: *Senecio keniodendron*.

Fig. 8. Distribution of the clumps of *Helichrysum citrispinum* in a permanent plot (30m ×50m) established in the area with the high population in August 2011.

Fig. 9. Typical soil profiles and till ages (years after the disappearance of the glacier). Till ages (years) of the plots are estimated from glacial retreat rates [3.8m/yr (-1958) (Charnley, 1959); 2.9m/yr (1958-1997); 9.8m/yr (1997-2002); 14.8m/yr (2002-2006); 8.7m/yr (2006-2009)] and distances from the ends of the glaciers. They were determined using soil profile data observed in 1992-2009.

Table 1. The average number of plant clumps (N) and the average proportion of vegetation cover (RC; %) on 80 quadrats (2.5m×2m) in 1996 and 2011.

Table 2. The average number of plant clumps (N) and the average proportion of

vegetation cover (RC; %) in quadrats (2.5m×2m) based on the distance (m) from the end of glacier in 1996.

Table 3. The average number of plant clumps (N) and the average proportion of vegetation cover (RC; %) in quadrats (2.5m×2m) based on the distance (m) from the end of glacier in 2011.

Table 1. The average number of plant clumps (N) and the average proportion of vegetation cover (RC; %) on 80 quadrats (2.5m×2m) in 1996 and 2011.

	N	RC (%)
1996	0.2±0.1	0.0±0.1
2011	2.7±0.3	3.6±0.5
	$P < 0.01$	$P < 0.01$

Table 2. The average number of plant clumps (N) and the average proportion of

vegetation cover (RC; %) in quadrats (2.5m×2m) based on the distance (m) from the end of glacier in 1996.

m	N	RC (%)
0-2	0.0±0.0a	0.0±0.0a
4-6	0.0±0.0a	0.0±0.0a
8-10	0.1±0.1a	0.0±0.0a
12-14	0.1±0.1a	0.0±0.0a
16-18	0.6±0.2b	0.1±0.0b

Different letters indicate statistically significant differences at the $P < 0.001$ level.

Table 3. The average number of plant clumps (N) and the average proportion of vegetation cover (RC; %) in quadrats (2.5m×2m) based on the distance (m) from the end of glacier in 2011.

m	N	RC (%)
0-2	2.3±0.4	5.4±1.6
4-6	3.0±0.6	2.6±0.5
8-10	2.4±0.5	2.3±0.5
12-14	2.7±0.8	3.4±1.1
16-18	3.3±0.5	4.4±1.0

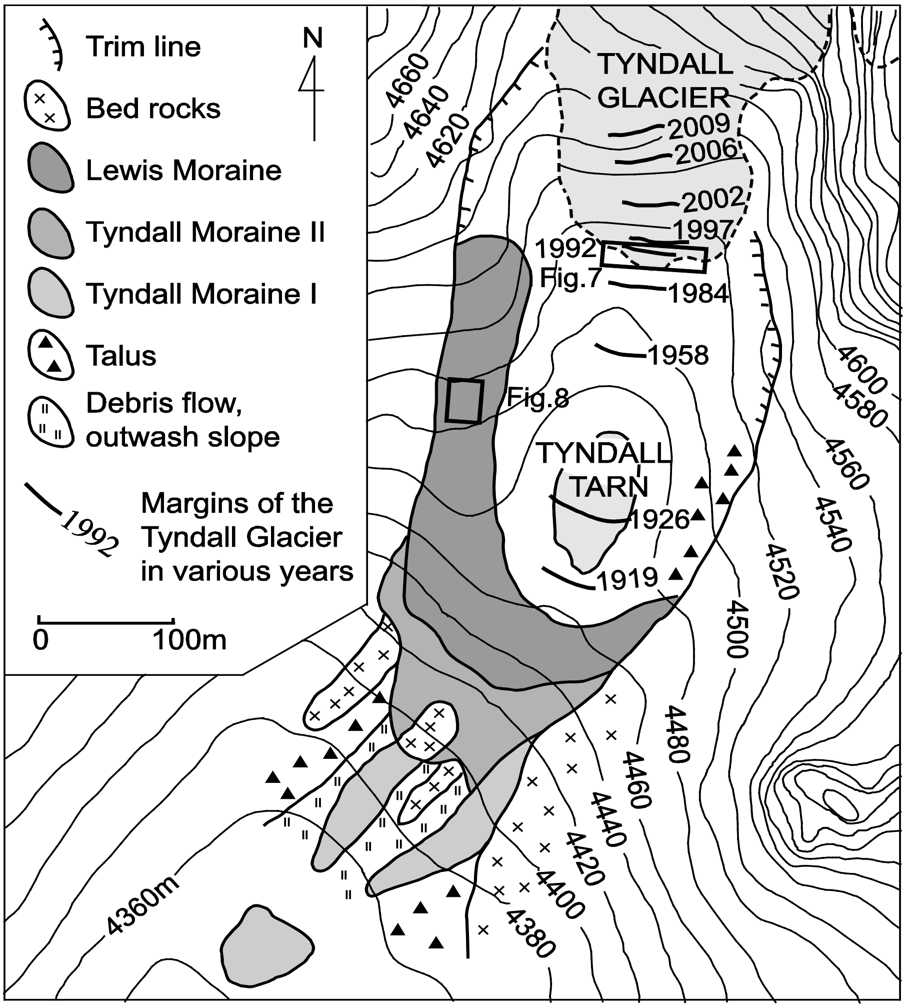

Trim line
Bed rocks
Lewis Moraine
Tyndall Moraine II
Tyndall Moraine I
Talus
Debris flow,
outwash slope
1992
Margins of the
Tyndall Glacier
in various years
0
100m
N
TYNDALL
GLACIER
2009
2006
2002
1997
1992
Fig.7
1984
1958
Fig.8
TYNDALL
TARN
1926
1919
4660
4640
4620
4600
4580
4560
4540
4520
4500
4480
4460
4440
4420
4400
4380
4360m

Fig. 1

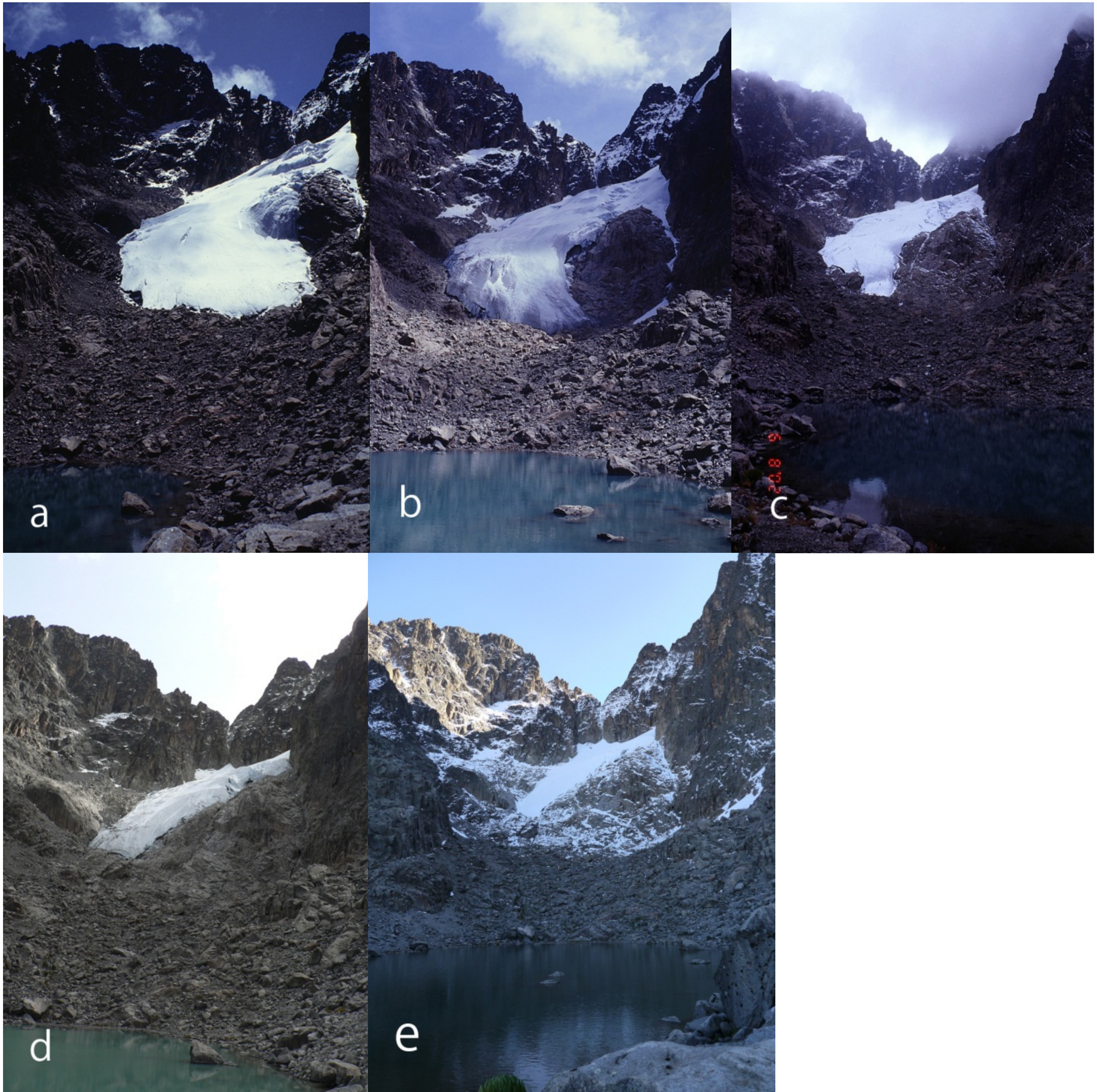


Fig. 2

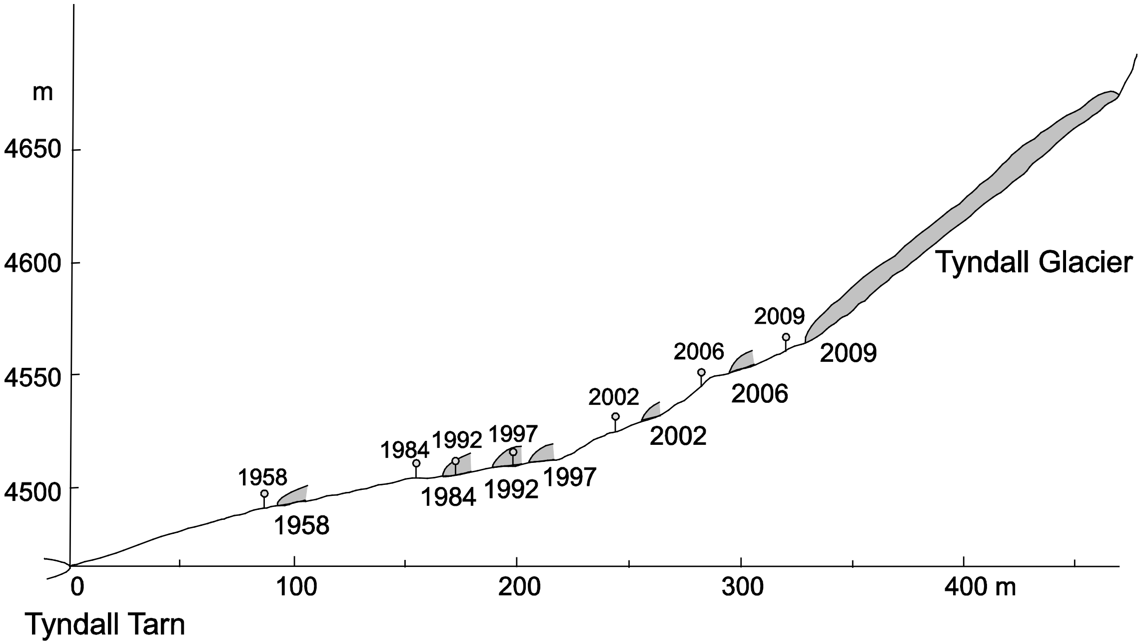

m
4650
4600
4550
4500
Tyndall Glacier
2009
2009
2006
2006
2002
2002
1984
1992
1997
1997
1992
1984
1958
1958
0
100
200
300
400 m
Tyndall Tarn

Fig. 3

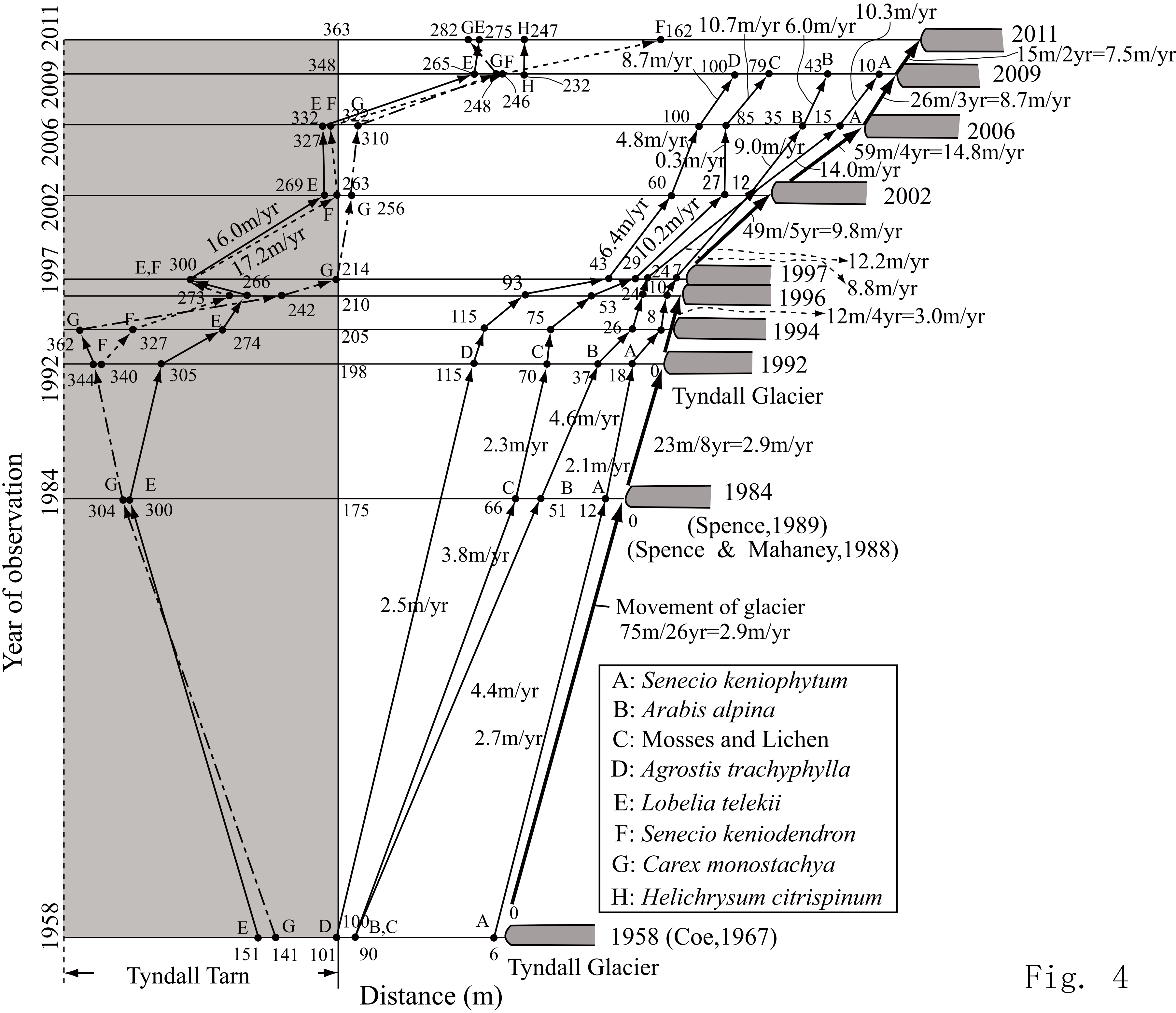
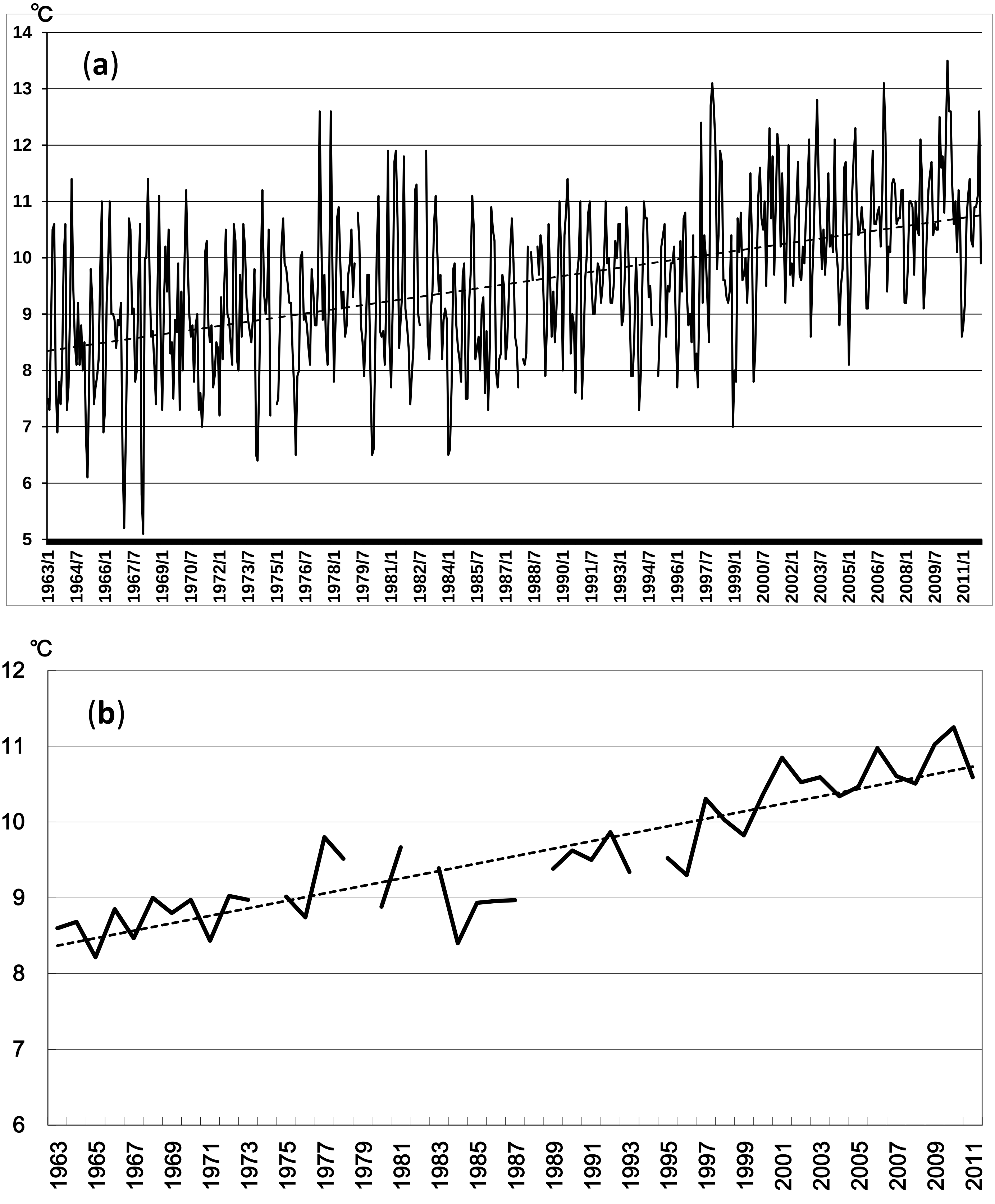

Year of observation
1958
1984
1992
1997
2002
2006
2009
2011
Distance (m)
Tyndall Tarn
Tyndall Glacier
1958 (Coe,1967)
1984
(Spence,1989)
(Spence & Mahaney,1988)
1992
1994
1996
1997
2002
2006
2009
2011
Movement of glacier
75m/26yr=2.9m/yr
23m/8yr=2.9m/yr
12m/4yr=3.0m/yr
12.2m/yr
8.8m/yr
49m/5yr=9.8m/yr
14.0m/yr
59m/4yr=14.8m/yr
26m/3yr=8.7m/yr
15m/2yr=7.5m/yr
10.3m/yr
10.7m/yr
6.0m/yr
8.7m/yr
4.8m/yr
0.3m/yr
9.0m/yr
6.4m/yr
10.2m/yr
16.0m/yr
17.2m/yr
2.5m/yr
3.8m/yr
4.4m/yr
2.7m/yr
2.3m/yr
4.6m/yr
2.1m/yr
E 151
G 141
D 101
100
B,C 90
A 6
0
G 304
E 300
175
C 66
B 51
A 12
0
G 344
F 340
305
198
D 115
C 70
B 37
A 18
0
G 362
F 327
E 274
205
115
75
26
8
273
266
242
210
93
53
24
10
E,F 300
G 214
43
29
24
7
269 E
F 263
G 256
60
27
12
332 E F 327
322 G 310
100
85
35 B
15
A
348
265 E
248
G F 246
H 232
100 D
79 C
43 B
10 A
363
282 G E 275
H 247
F 162
A: Senecio keniophytum
B: Arabis alpina
C: Mosses and Lichen
D: Agrostis trachyphylla
E: Lobelia telekii
F: Senecio keniodendron
G: Carex monostachya
H: Helichrysum citrispinum

Fig. 4


℃
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1966/1
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2011/1
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2009
2011

Fig. 5

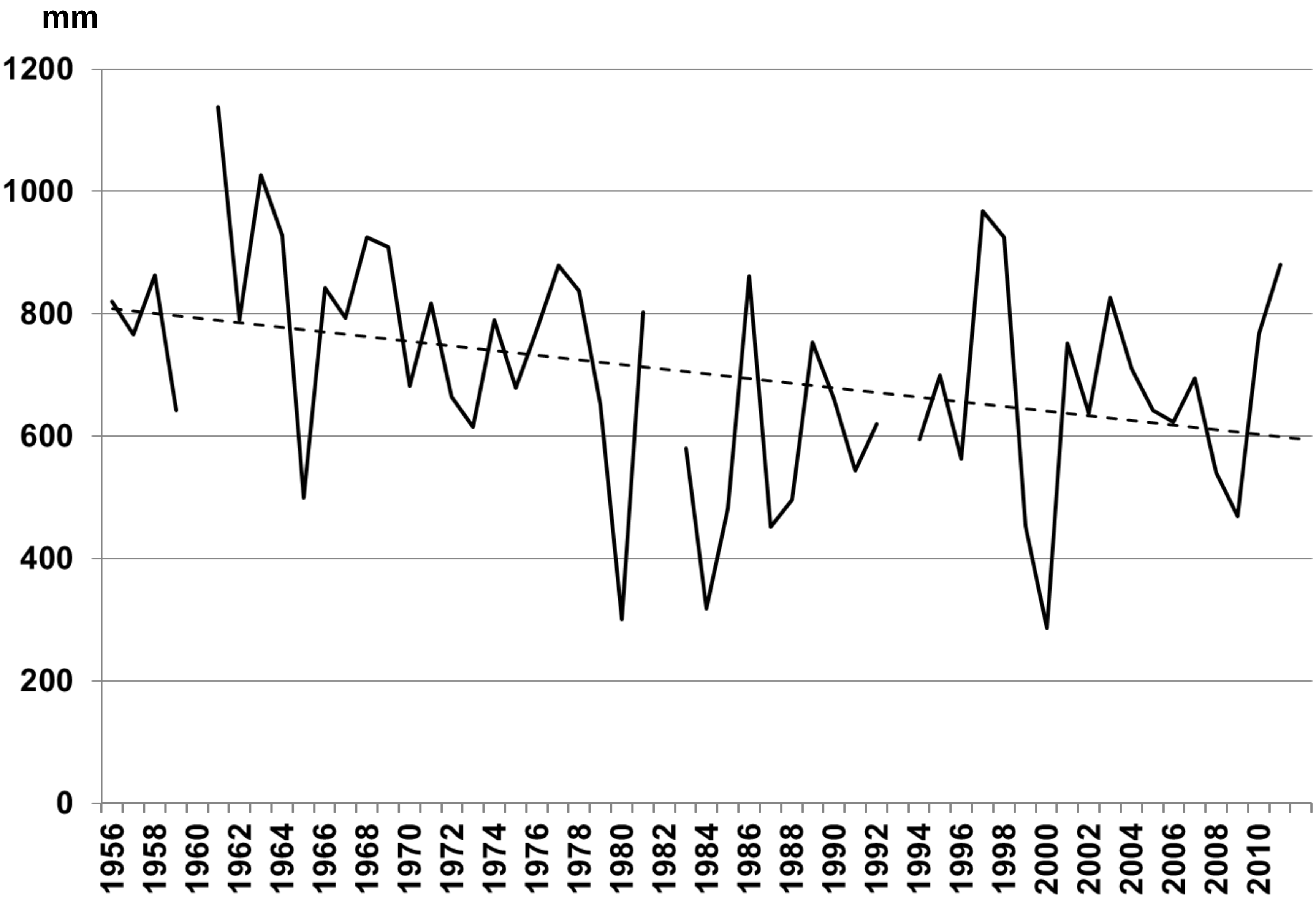

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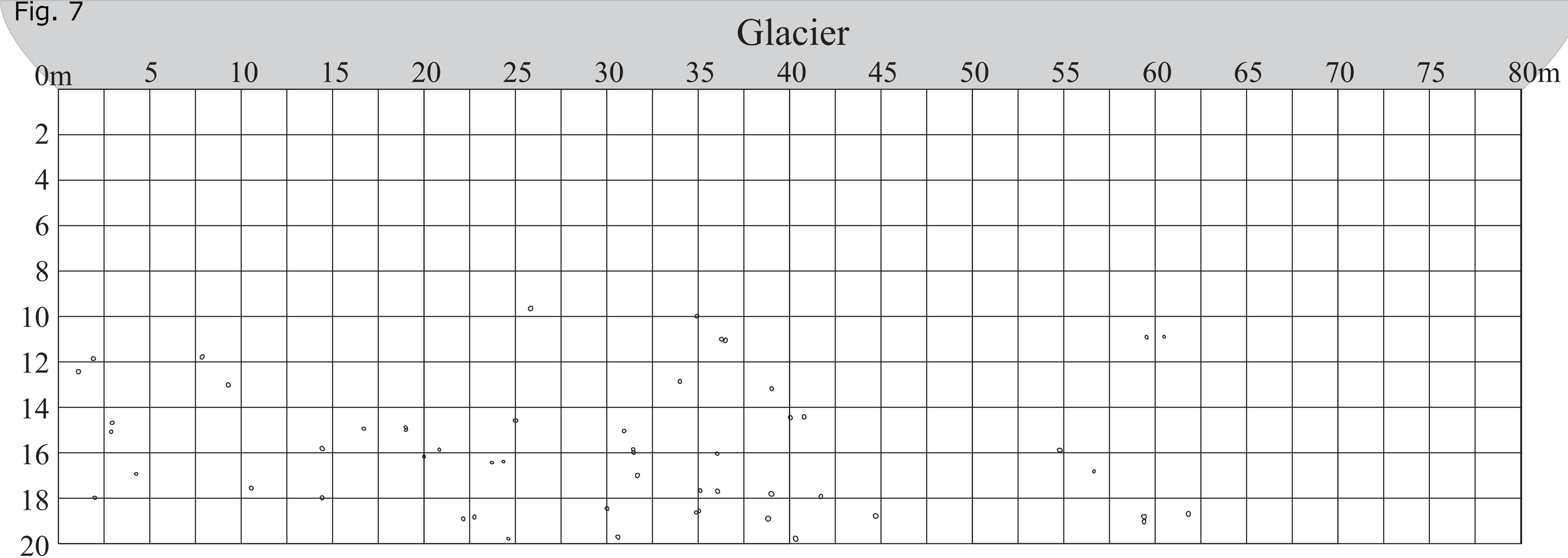
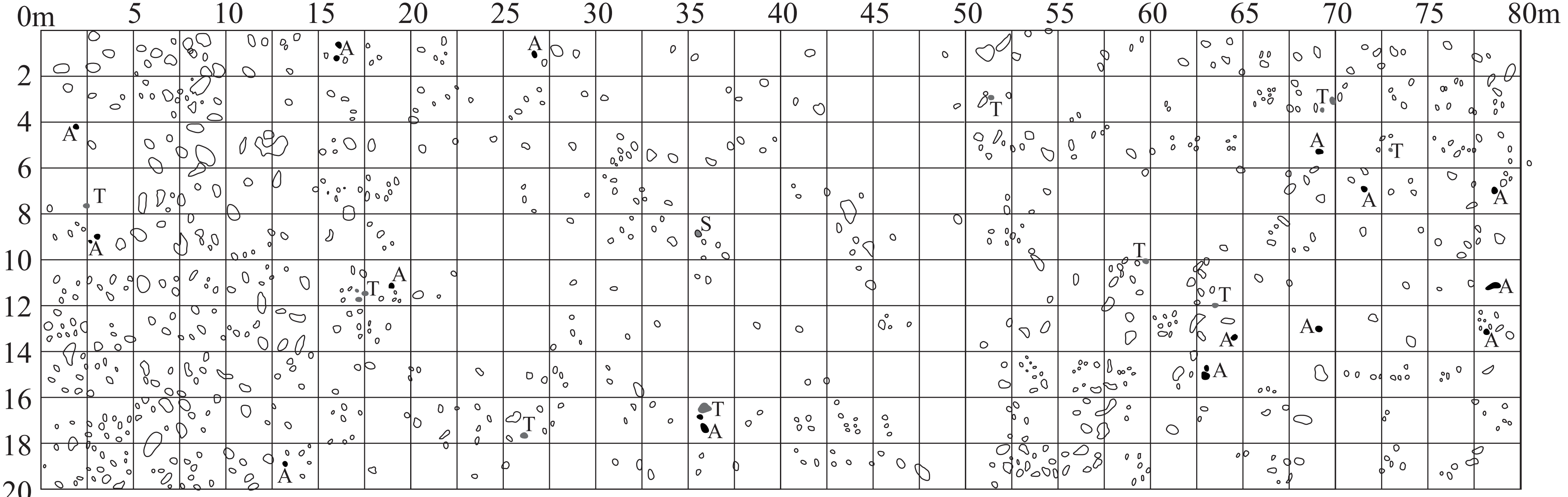
Fig. 6

Fig. 7



(a) 1996



(b) 2011

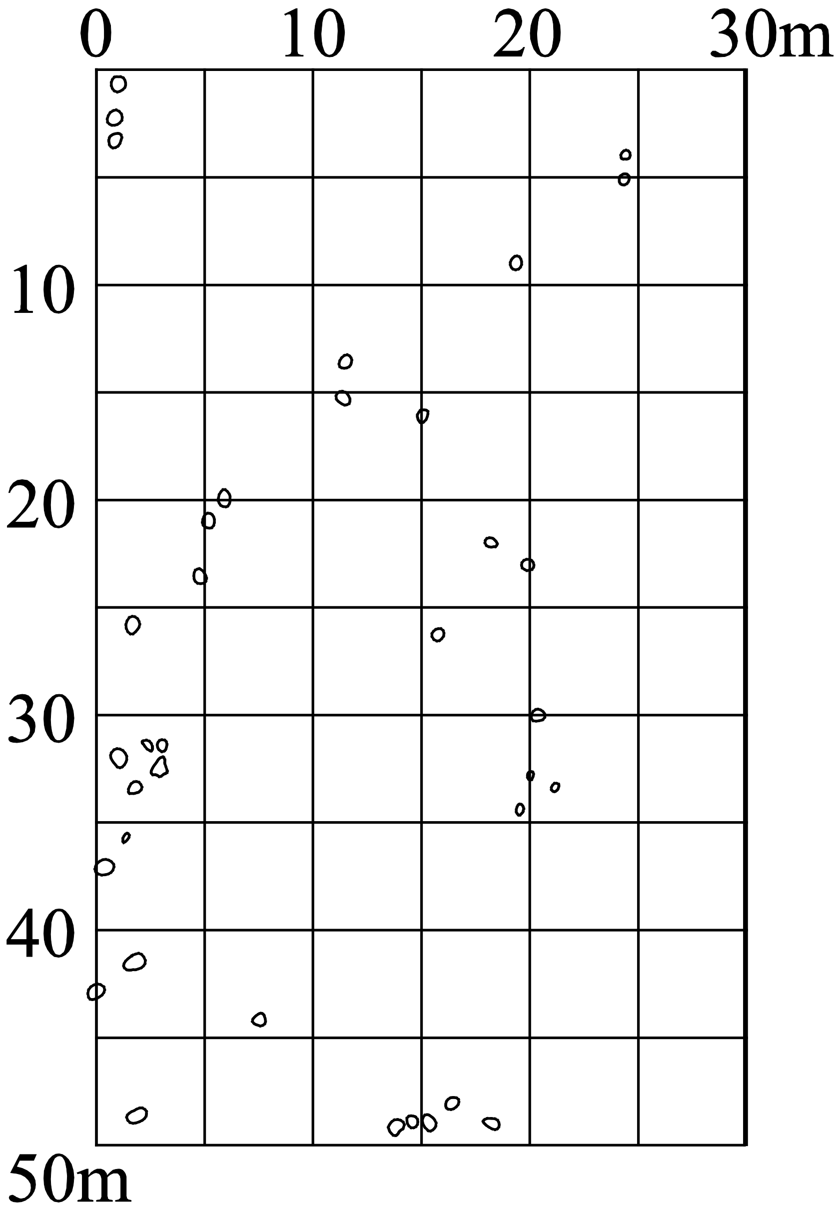


Fig. 8