Journal of East African Natural History **109**(2)**:** 59–68 (2020)

GROWTH RATES IN THE GIANT ROSETTE PLANTS *DENDROSENECIO ADNIVALIS* AND *LOBELIA WOLLASTONII* ON THE RUWENZORI MOUNTAINS, UGANDA

Thomas T. Struhsaker
Department of Evolutionary Anthropology, Duke University,
Box 90383, Durham, North Carolina 27708-0383, USA
tomstruh@duke.edu

ABSTRACT

Stem lengths of *Dendrosenecio adnivalis* and *Lobelia wollastonii* were measured three times over 5.5 years in the Ruwenzori Mountains, Uganda. These are the only growth data for these two species. Both species had highly variable growth rates. Absolute growth rates in *D. adnivalis* were not related to the number of rosettes, inflorescences or initial height of plants. The *D. adnivalis* that were shorter at the beginning of the study grew proportionately faster than did taller individuals. Growth rate was positively associated with annual rainfall for *D. adnivalis* on the Ruwenzori Mountains, *D. keniodendron* on Mount Kenya, and *D. battiscombei* on the Aberdare Mountains. *Lobelia wollastonii* that were taller at the beginning of the study had greater absolute growth rates than did shorter plants. There was no significant relationship between the initial height and proportional increase in height for *L. wollastonii*. Growth rate and height are unreliable indicators of age for both species.

Keywords: *Dendrosenecio, Lobelia*, growth rates, Ruwenzori Mountains

INTRODUCTION

The giant rosette plants (*Dendrosenecio* and *Lobelia*) are among the most conspicuous features in the alpine zone of East Africa's mountains. They have been of particular interest to plant physiologists because of their equatorial location at high altitudes and the accompanying diurnal temperature extremes, warm days and freezing nights, and higher levels of ultraviolet light (*e.g.* Hedberg, 1964; Smith & Young, 1987). The growth rates of *Dendrosenecio keniodendron* (R.E.Fr. & T.C.E.Fr.) B.Nord., *Dendrosenecio battiscombei* (R.E.Fr. & T.C.E.Fr.) E.B.Knox and *Lobelia telekii* Schweinf. have been estimated, sometimes in the context of how these rates can be used to estimate the age of the plant. Most of these studies have been done on the dry western side of Mount Kenya. Aside from a single study on the Aberdare Mountains, which are much wetter than Mount Kenya, but not as wet as the Ruwenzori Mountains, there have been no systematic studies of plant growth on other wet mountains in East Africa or on other giant rosette species. Furthermore, previous systematic studies of growth in alpine *Dendrosenecio* and *Lobelia* have been based on growth in leaf length rather than growth in stem height, largely because most of these species are acaulescent

(Beck *et al.*, 1980; Beck *et al.*, 1984; Schmitt, 1991; Smith & Young, 1982, 1994; Young, 1985, 1994). I present here the only systematic growth rate data based on stem length measurements from two arborescent species over a 5.5- year period on the very wet Ruwenzori Mountains, Uganda, namely, the polycarpic *Dendrosenecio adnivalis* (Stapf) E.B.Knox and the monocarpic *Lobelia wollastonii* Baker f. *Dendrosenecio adnivalis* occurs only on the Ruwenzori Mountains and *L. wollastonii* only on the Ruwenzori and Virunga Mountains.

MATERIAL AND METHODS

The heights of *D. adnivalis* stems were measured from the base of the stem at ground level to the base of the tallest rosette, whereas stem heights of *L. wollastonii* were measured from the base of the stem to the base of the apical bud or the base of the floral spike. I had two study sites in the Ruwenzori Mountains, Uganda. One was in the vicinity of Kitandara Hut at 0°21'N, 29°53'E, ~4,027 m with an annual rainfall of ~2350 mm in the early 1960s (Osmaston & Pasteur, 1972). My sample dates for Kitandara were 24 August 1975, 17 July 1979, and 16 January 1981 for both plant species. The other site was in the vicinity of Bujuku Hut at 0°23'N., 29°53'E., ~3,993 m with annual rainfall of ~2000 mm in the early 1960s (Osmaston & Pasteur, 1972). My sample dates at Bujuku were 20 August 1975, 14 July 1979, and 18 January 1981 for *L. wollastonii* and 16 July 1979 and 18 January 1981 for *D. adnivalis*. All plants were marked with labeled flagging tape. Tape placed on *D. adnivalis* at Bujuku in 1975 were gone in 1979, so a new sample was measured and marked in 1979. No statistical analysis comparing growth rates between the two sites was done because of the great range in sizes and unequal distribution of plant heights sampled. All plants measured were in relatively close proximity to one another with similar soil, moisture, and light conditions. Latin names follow Knox (1993).

RESULTS

Dendrosenecio adnivalis

There was great variation in height growth rates between individuals and between sample periods for *D. adnivalis* (tables 1, 2). The longer the sample period, the smaller was the range in growth rates and the lower the standard deviation (table 3). The variation in height growth rates was not obviously related to the number of rosettes or the number of inflorescences. Height growth rates were approximately the same for plants with one rosette or plants with 21 rosettes. The absolute increase in height was not significantly related to the initial size of the plant when sampling began (Kitandara 1975–1981: $R^2 = 0.055$, $F = 0.40$, $p = 0.54$; Bujuku 1979–1981: $R^2 = 0.025$, $F = 0.25$, $p = 0.62$). However, shorter plants (presumably younger) grew proportionately faster than did taller (presumably older) plants for sample periods spanning more than 1.5 years, i.e. 4 to 5.5 years (figures 1, 2); Kitandara: (1975–1979: $R^2 = 0.42$, $F = 5.7$, $p = 0.043$, $n = 10$), (1979–1981: $R^2 = 0.37$, $F = 4.03$, $p = 0.085$, $n = 9$), (1975–1981: $R^2 = 0.57$, $F = 9.38$, $p = 0.018$, $n = 9$); Bujuku: (1979–1981: $R^2 = 0.20$, $F = 2.53$, $p = 0.14$, $n = 12$).

Lobelia wollastonii

As with the *D. adnivalis*, there was great variation in height growth rates between individuals and sample periods for *L. wollastonii* (tables 4, 5). During the two longer sample periods (1975–1979, 1975–1981) the *Lobelia* had smaller ranges in growth rates and lower standard deviations than the shorter sample period between 1979 and 1981 (1.5 years) (table 6). There

Table 1. Growth of Dendrosenecio adnivalis*, Kitandara, Ruwenzori Mountains, Uganda.*

Plant#	Ht.1975	R	FL	Ht.1979	R	FL	Ht.1981	R	FL
1	160	3	1D	192	3	0	193	3	0
2	153	10	3D	200	8	3L/1D	214	11	5D
3	96	8	2D	119	5	2L/2D	122	7	0
4	122	3	0	170	5	1D	183	5	1D
5	284	21	10D	333	19	2L/10D	333	23	14D
6	180	3	1D	228	3	1L/1D	229	4	0
7	80	1	0	110	1	0	123	1	0
8	190	4	1D	219	4	1D	237	4	1D
9	42	1	0	79	1	0	86	1	0
10	400	15	8D	460	2	5D	435D	D	5D

Ht = height cm, R = number of rosettes, FL = number of floral spikes, L= live, D = dead

Table 2. Growth of Dendrosenecio adnivalis*, Bujuku, Ruwenzori Mountains, Uganda.*

Plant#	Ht 1979	R	FL	Ht 1981	R	FL
1	313	1	0	318	1	0
2	227	1	0	254	1	0
3	109	1	0	120	1	0
4	235	2	1 D	244	2	1 D
5	160	1	0	160	1	0
6	330	2	0	331	2	0
7	130	1	0	139	1	0
8	450	1	1	475	1	0
9	87	1	0	104	1	0
1	208	1	0	208	1	0
11	332	2	1 D	337	2	1 D
12	176	1	0	178	1	0

Ht = height cm, R = number of rosettes, FL = number of floral spikes, D = dead

Table 3. Dendrosenecio adnivalis *height growth rates (cm/year).*

	$\bar{x}$	range	*SD*	*N*
Kitandara				
1975–1979	10.3	5.9–15.4.	±3.0	10
1979–1981	5.2	0–12.	±4.56	9
1975–1981	8.5	4.8–11.3	±2.12	9
Bujuku				
1979–1981	6.17	0–18	±6.2	12

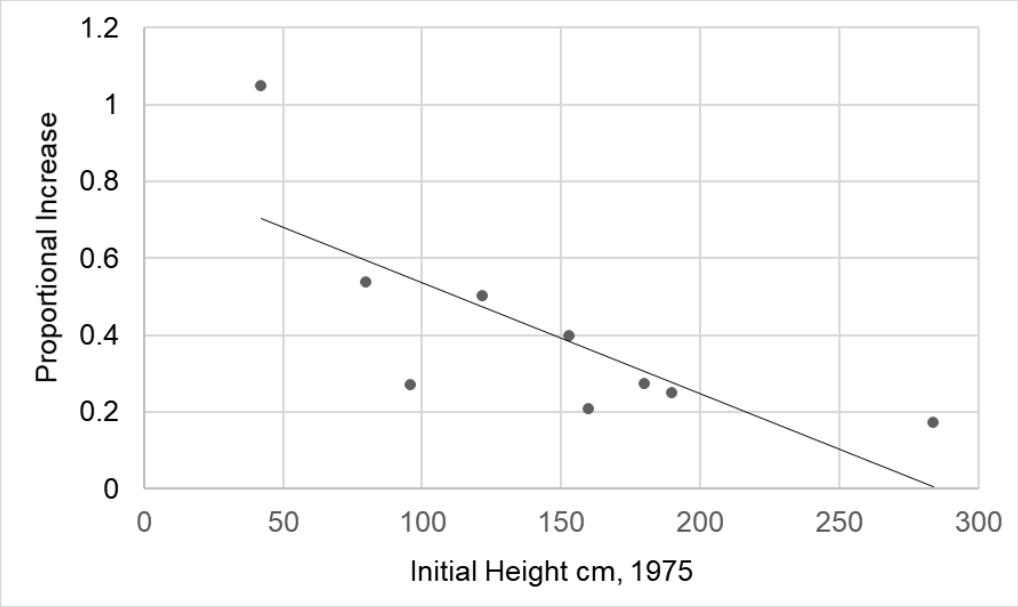

Figure 1. Dendrosenecio adnivalis*, proportional increase in height vs initial height in cm. 1975–1981. Kitandara.*

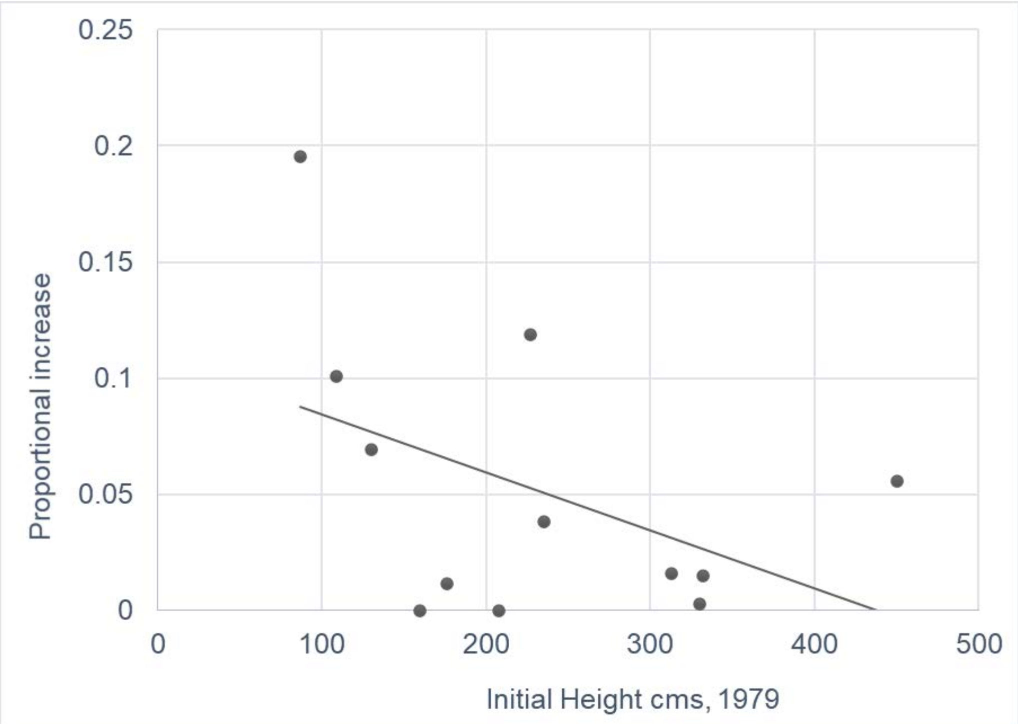

Figure 2. Dendrosenecio adnivalis*, proportional increase in height vs initial height in cm.1979–1981. Bujuku.*

Table 4. Growth of Lobelia wollastonii*, Kitandara, Ruwenzori Mountains, Uganda.*

Plant#	Ht. 1975	FL	Ht. 1979	FL	Ht. 1981	FL
1	245	1	D			
2	43	0	66	0	80	0
3	143	0	211	0	317	1
4	76	0	118	0	122	0
5	54	0	72	0	80	0
6	84	0	98	0	107	0
7	57	0	75	0	78	0
8	30	0	32	0	36	0
9	43	0	61	0	74	0
10	57	0	109	0	109	0

Ht= height cm, FL = floral spike, D=dead lying on ground

Table. 5 Growth of Lobelia wollastonii*, Bujuku, Ruwenzori Mountains, Uganda.*

Plant#	Ht.1975	FL	Ht.1979	FL	Ht.1981	FL
1	47	0	52	0	60	0
2	84	0	165D	DG	D	DG
3	5	0	5	0	D	0
4	56	0	142D	D	D	DG
5	52	0	118D	D	D	DG
6	79	0	107	0	109	0
7	90	0	220D	DG	D	DG
8	33	0	44	0	65	0
9	45	0	64	0	84	0
10	93	0	144	0	178	0
11	37	0	50	0	65	0
12	101	0	129	0	146	0
13	52	0	72	0	79	0
14	241	1	D	DG	D	DG
15	73	0	79	0	D	DG
16	72	0	112	0	130	0
17	14	0	16	0	23	0
18	63	0	72	0	87	0
19	161	1	D	DG	D	DG
20	160	1	164D	DG	D	DG

Ht = height cm, FL=floral spike; D=dead, DG = floral spike dead on ground

Table 6. Lobelia wollastonii *height growth rates (cm/year).*

	$\bar{x}$	range	*SD*	*N*
Kitandara				
1975–1979	7.3	0.51–17.4	±5.42	9
1979–1981	11.9	0–70.7	±22.24	9
1975–1981	8.6	1.1–32.2	±9.23	9
Bujuku				
1975–1979	4.6	0–13.1	±3.93	13[a]
1979–1981	9.9	1.33–22.7	±5.89	11
1975–1981	6.6	1.67–15.7	±3.9	11

a: If dead plants included in this period, then plant numbers 2, 4, and 7 grew at least 20–32.5 cm/year.

was a significant positive correlation between the height of a plant at the initial measurement and the absolute increase in height at the final measurement 5.5 years later (Kitandara, 1975–1981: $R^2 = 0.68$, $F = 14.94$, $p = 0.0015$, $n = 9$, figure 3) (Bujuku, 1975–1981: $R^2 = 0.48$, $F = 8.39$, $p = 0.018$, figure 4). Taller plants grew faster than did shorter plants in terms of absolute growth rate. In contrast, there was no significant relationship between the proportional increase in height and the initial height measurement from 1975–1981 (Kitandara, $R^2 = 0.29$, $F = 2.86$, $p = 0.14$, $n=9$) (Bujuku, $R^2 = 0.035$, $F = 0.33$, $p = 0.58$, $n = 11$).

There was little sign of leaves being browsed in my sample of either *D. adnivalis* or *L. wollastonii*. Among *D. adnivalis* only three plants (numbers 3, 4, and 5) in the Kitandara sample showed signs of leaves being browsed and in only one sample year (1981). None of this species sampled at Bujuku showed signs of browsing. There was a similarly low level of leaf browsing among the *L. wollastonii* sampled; one plant (number 5) in 1981 at Kitandara and two (numbers 1 and 4) in 1975 at Bujuku. The most likely browser was the tree hyrax (*Dendrohyrax arboreus* A. Smith, 1827), which I have observed eating the leaves of both species.

My data indicate that *L. wollastonii* stems must be at least 100 cm in height before they flower (tables 4, 5). More *L. wollastonii* flowered at Bujuku than at Kitandara despite the same sample period, similar elevation and precipitation. Seven of the eight plants that flowered at Bujuku did so between 1975 and 1979. The difference in flowering plants between these two sites cannot be attributed to differences in plant heights because there was no significant difference in heights between these two sites at the beginning of the study in 1975 (Mann-Whitney $U > 93$, $p > 0.10$, $F = 0.73$, $p = 0.27$).

DISCUSSION

Mean growth rate in stem height for *D. adnivalis* on the Ruwenzori Mountains was appreciably greater (>8.5 cm/year) than the estimates of stem height growth rate based on extrapolations from leaf-length growth rates for higher elevation *Dendrosenecio keniodendron* (2.3–5.3 cm/year) in the Teleki Valley on Mount Kenya (Beck *et al.*, 1980, 4100 m $n = 5$, 1984, 4180 m, $n = 11$; Hedberg, 1969, 4200 m $n = 1$; Smith & Young, 1994, 4200 m. $n = 196$), but similar to the estimates based on the leaf-length method for *Dendrosenecio battiscombei* (6.4–9.9 cm/year) on the Aberdare Mountains. (Schmitt, 1991 $n=9$) and *D. keniodendron* (11.6 cm/year) at a lower and wetter elevation site (3900 m) on Mount Kenya (Smith & Young, 1994). These differences in stem growth rate are even more pronounced when maximum rates are compared: Ruwenzori Mountains 18 cm/year, Aberdare Mountains 12.9 cm/year, Mount Kenya low and wetter elevation 20 cm/year versus the high elevation and drier site ~6 cm/year. Although different species are being compared, the most obvious explanation for these differences in growth rate is annual rainfall, which was much higher in the Ruwenzori Mountains (2000–2350 mm), Aberdare Mountains (~1500–1800 mm, Schmitt, 1991), and the lower elevation site on Mount Kenya (1048 mm) than at the 4200 m Mount Kenya site (~700 mm, Young, 1984,1985). Smith & Young (1994) came to a similar conclusion based on their Mount Kenya study, "...growth rate may be in part limited by rainfall." Temperature is an additional factor that may affect growth rate. In the mountains of East Africa temperature declines by about 0.56° C per 100 m elevation (East African Meteorological Department cited in Schmitt, 1991).

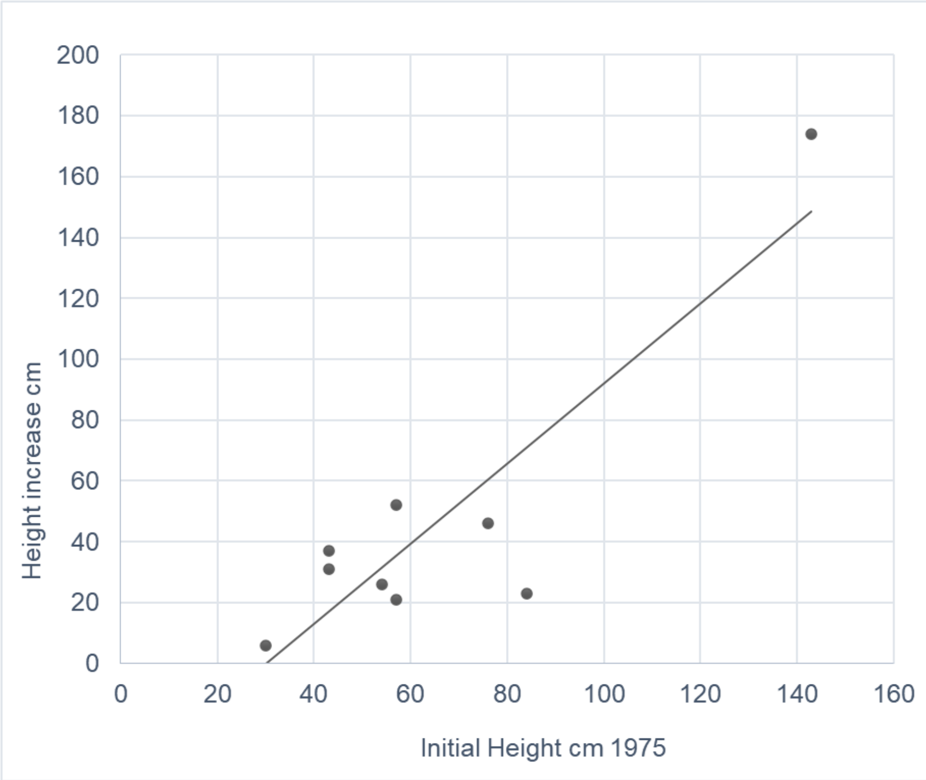

Figure 3. Lobelia wollastonii*, height increase in cm vs initial height in cm. 1975–1981. Kitandara.*

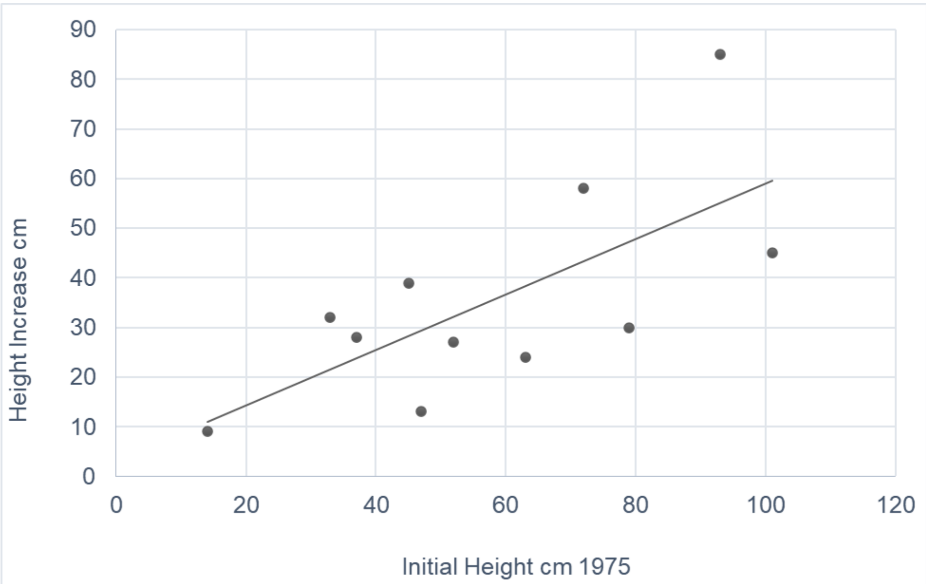

Figure 4. Lobelia wollastonii*, height increase in cm vs initial height in cm. 1975–1981. Bujuku.*

Height divided by the mean annual growth rate in height does not appear to be an accurate way to estimate the age of an individual *D. adnivalis* because of the appreciable variation in growth rates. For example, the tallest *D. adnivalis* was 460 cm tall before it died sometime between my 1979 and 1981 samples. Depending on which mean value of growth rate used (5 to 10 cm/year, table 3), this specimen would have been somewhere between ~46 and 92 years old. Furthermore, because shorter and presumably younger *D. adnivalis* grow proportionately faster than taller and presumably older plants, it appears that growth rates in *D. adnivalis* are not constant through time but vary with age. Consequently, absolute height is a poor indicator of absolute age. It is clear, however, that *D. adnivalis* can attain considerable age. Smith & Young (1987) reached similar conclusions for giant rosette plants in general. Schmitt (1991) suggested that some of the tallest (up to 7 m) *D. battiscombei* on the Aberdare Mountains might have been 100–150 years old.

In their study of *D. keniodendron* on Mount Kenya, Beck *et al.* (1984) concluded that unbranched plants elongated slowly, but growth rate nearly doubled after the first flowering and the subsequent branching, then declined with increasing age. No such pattern was apparent for *D. adnivalis* on the Ruwenzori Mountains, where absolute increase in height was unrelated to apparent age, number of rosettes, or floral stalks. However, as pointed out above for *D. adnivalis*, proportional increase in height is inversely related to age, assuming height is a rough indicator of age. Using stem growth rates to estimate age is further complicated by the finding that estimated growth rate depends to some extent on the duration of the sample period. In general, longer sample periods show less variation.

There was no obvious synchrony of flowering among *D. adnivalis* when the data from my two study sites are combined. This is contrary to that reported for *D. keniodendron* on Mount Kenya (Smith & Young, 1982). However, there may be some degree of flowering synchrony within each of my two study sites (compare tables 1 and 2). There were other important differences between the Ruwenzori Mountains and Mount Kenya study sites that might account for differences in growth and reproductive rates and survivorship of *Dendrosenecio*. Browsing by hyrax was not uncommon on Mount Kenya (Smith & Young, 1987; Young & Smith, 1994) and elephants occasionally killed adult plants by eating the central pith (Mulkey *et al.*, 1984). Such events were rare or absent in the Ruwenzori Mountains This is because Mount Kenya was protected against hunting as a national park, whereas there was no such protection on the Ruwenzori Mountains during my studies. Elephants had been eliminated and poaching of hyrax was common and widespread. Fire was reported to occur periodically at the Mount Kenya site (Smith & Young, 1982), but there was no indication that fire ever affected my two study sites on the Ruwenzori Mountains.

The only other study on growth rates in a monocarpic species of *Lobelia* is that of Young (1984, 1985) who studied *Lobeli telekii* on Mount Kenya. However, because Young's study used leaf length as a measure of growth, it is not directly comparable to my study of *L. wollastonii*, which measured stem length. As with my study, Young (1985) found great variation in growth rates and concluded, as I do, that size alone is not necessarily a good indicator of age. He estimated that *L. telekii* flower and then die somewhere between the age of 40–70 years. This large range in age estimates was due in part to the fact that slower growing and smaller plants were more subject to herbivory by hyrax, more likely to die, and tended to flower at a smaller size than faster growing individuals. Consequently, some of the larger flowering *L. telekii* may be younger than smaller flowering plants (Young, 1985). My sample size is not sufficient to conduct analyses similar to those made by Young (1985). However, crude age estimates can be made for *L. wollastonii* at the Bujuku site by dividing the last measured height of the seven plants that flowered and died there between 1975 and

1979 by the mean growth rate estimated during the same period for the sample of 20 plants (tables 5 and 6). These calculations suggest that the *L. wollastonii* at Bujuku were between the ages of 22 and 56 years old when they died. This wide range in age, if correct, suggests that the *L. wollastonii* may be like the *L. telekii* on Mount Kenya, with fast and slow growing individuals in the same population. It is of interest that much earlier Hauman (1934), in describing *L. wollastonii* on the Ruwenzori Mountains, guessed, in the absence of data, that they might live to 40–50 years.

The stem height growth rates and estimates in my studies and those of others on related species on Mount Kenya and the Aberdare Mountains were made 35 to 45 years ago. Since then there have been changes in climate and in human activities in these areas. Temperatures have risen and glaciers have receded (*e.g.* Taylor *et al.*, 2006). The Ruwenzori Mountains are now a national park, which presumably means there is better protection against poaching, particularly the trapping of hyrax. This in turn means that hyrax populations may have increased resulting in an increase in browsing and mortality of the giant rosette plants. The impact of these changes on growth and survivorship of giant rosette plants should be examined through long-term studies of these fascinating plants throughout Africa's mountains.

ACKNOWLEDGMENTS

I thank Lysa Leland for assistance in measuring plants and recording data, Professor Truman Young for valuable comments on the manuscript, Professors Erwin Beck and Klaus Schmitt for providing relevant literature and two anonymous reviewers for comments. Funding was from the author. I thank the Uganda National Research Council and Uganda Forest Department for permission to study in Uganda.

REFERENCES

Beck, E., R. Scheibe, M. Senser, & W. Muller (1980). Estimation of leaf and stem growth of unbranched *Senecio keniodendron* trees. *Flora* **170**: 68–76.

Beck, E., I. Schlutter, R. Scheibe & E.-D. Schulze (1984). Growth rates and population rejuvenation of East African giant groundsels (*Dendrosenecio keniodendron*). *Flora* **175**: 243–248.

Hauman, L. (1934). Les *Lobelia* géants des montagnes du Congo Belge. *Institut Royal Colonial Belge, Section des Sciences Naturelles et Médicales, Mémoires* 8° **II** (1): 1–52.

Hedberg, O. (1964). *Features of Afroalpine Plant Ecology*. Almqvist & Wiksells Boktryckeri AB, Uppsala.

Hedberg, O. (1969). Growth rate of the East African giant *Senecios*. *Nature* **222**: 163–164.

Knox, E.B. (1993). The species of giant *Senecio* (Compositae) and giant *Lobelia* (Lobeliaceae) in Eastern Africa. *Contributions from the University of Michigan Herbarium* **19**: 241–257.

Mulkey, S.S., A.P. Smith & T.P. Young (1984). Predation by elephants on *Senecio keniodendron* (Compositae) in the alpine zone of Mount Kenya. *Biotropica* **16**: 246–248.

Osmaston, H.A. & D. Pasteur (1972). *Guide to the Ruwenzori, The Mountains of the Moon.* West Col Productions, Reading, U.K.

Schmitt, K. (1991). The vegetation of the Aberdare National Park, Kenya. Association for Comparative Alpine Research, Munich. *Hochgebirgsforschung, High Mountain Research* **8**: 1–259.

Smith, A.P. & T.P. Young (1982). The cost of reproduction in *Senecio keniodendron*, a giant rosette species of Mt. Kenya. *Oecologia (Berl)* **55**: 243–247.

Smith, A.P. & T.P. Young (1987). Tropical alpine plant ecology. *Annual Review of Ecology and Systematics* **18**: 137–158.

Smith, A.P. & T.P. Young (1994). Population biology of *Senecio keniodendron* (Asteraceae)-an Afroalpine giant rosette plant. In P.W. Rundel, A.P. Smith & F.C Meinzer. (eds), *Tropical Alpine Environments, Plant form and function*. Cambridge University Press. Pp. 273–293.

Taylor, R.G., L. Mileham, C. Tindimugaya, A. Majugu, A. Muwanga & B. Nakilieza (2006). Recent glacial recession in the Rwenzori Mountains of East Africa due to rising air temperature. *Geophysical Research Letters* **33**: 1–4.

Young, T.P. (1984). The comparative demography of semelparous *Lobelia telekii* and iteroparous *Lobelia keniensis* on Mount Kenya. *Journal of Ecology* **72**: 637–650.

Young, T.P. (1985). *Lobelia telekii* herbivory, mortality, and size at reproduction: variation with growth rate. *Ecology* **66**: 1879–1883.

Young, T.P. (1994). Population biology of Mount Kenya lobelias. In P.W. Rundel, A.P. Smith & F.C. Meinzer (eds), *Tropical Alpine Environments, Plant form and function*. Cambridge University Press. Pp. 251–272.

Young, T.P. & A.P. Smith (1994). Alpine herbivory on Mount Kenya. In P.W. Rundel, A.P. Smith & F.C. Meinzer (eds), *Tropical Alpine Environments, Plant form and function*. Cambridge University Press. Pp. 219–235.