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THE COMPARATIVE DEMOGRAPHY OF SEMELPAROUS *LOBELIA TELEKII* AND ITEROPAROUS *LOBELIA KENIENSIS* ON MOUNT KENYA

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SUMMARY

(1) Two species of rosette-forming *Lobelia* grow in the alpine zone of Mount Kenya. *Lobelia telekii* grows on dry rocky slopes and is usually semelparous (monocarpic); *Lobelia keniensis* grows in moist valley bottoms and is usually iteroparous (polycarpic). *Lobelia telekii* plants usually produce only a single rosette; *Lobelia keniensis* plants usually branch to produce multi-rosette individuals.

(2) In both species there was a minimum and a maximum rosette size at reproduction. Rosette size at reproduction was positively correlated with inflorescence size in both species. In *Lobelia keniensis* there was a minimum size at which single rosettes began to branch that was similar to the minimum flowering size.

(3) Distinct wet and dry periods of weather were identified, each about 15 months long. For both species, rosettes grew faster and had higher survivorship in the wetter sites and during the wetter period than in the drier sites or during the dry period.

(4) Predation by rock hyrax (*Procavia johnstoni*) of larger *Lobelia telekii* plants in the dry period resulted in a bimodal size-specific mortality pattern. During the dry period and immediately after it hyrax killed over half the larger *Lobelia telekii* rosettes in the study site.

(5) *Lobelia telekii* rosettes flowered at a larger size and produced larger inflorescences in the wetter sites than in the drier sites. *Lobelia keniensis* plants with more rosettes flowered more frequently than plants with fewer rosettes.

(6) In *Lobelia telekii* mortality before reproduction was higher than in *Lobelia keniensis* for all size classes, excluding the smallest seedlings. Mortality of multi-rosette *Lobelia keniensis* plants (death of all constituent rosettes) was very low and restricted to the drier sites.

(7) The evolution of semelparity in Mount Kenya *Lobelias* may have been favoured by the demonstrated higher adult mortality and greater time between reproductive episodes shown by *Lobelia keniensis* plants in drier sites.

INTRODUCTION

Several models for the evolution of semelparity and iteroparity rely on demographic variables (Charnov & Schaffer 1974; Bell 1977, 1980; Young 1981). Semelparity may be favoured by low adult survival, early senescence, increased time between reproductive episodes, high population growth rate, or high juvenile survival. However, there have been few published demographic comparisons of closely related semelparous (monocarpic) and iteroparous (polycarpic) plants (Hawthorn & Cavers 1975; Smith 1981).

This paper reports on 3·5 years of demographic data for a pair of long-lived herbaceous plants on Mount Kenya. *Lobelia telekii* (Scwheinf) is a primarily semelparous species of drier habitats between 3500 m and 5000 m and *Lobelia keniensis* (Fries & Fries) is a primarily iteroparous species of wetter habitats between 3300 m and 4600 m.

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Lobelia plants comprise from one to eighteen mutually attached rosettes through branching of the underground stem. Inflorescences of both are terminal, and a rosette invariably dies after flowering. The number of times that an individual flowers is equal to the number of its rosettes that survive to reproduce. Therefore growth form is intimately related to life history. Unbranched plants are semelparous, and branched plants are iteroparous. *L. telekii* is almost always unbranched, and *L. keniensis* is usually branched (Fig. 1).

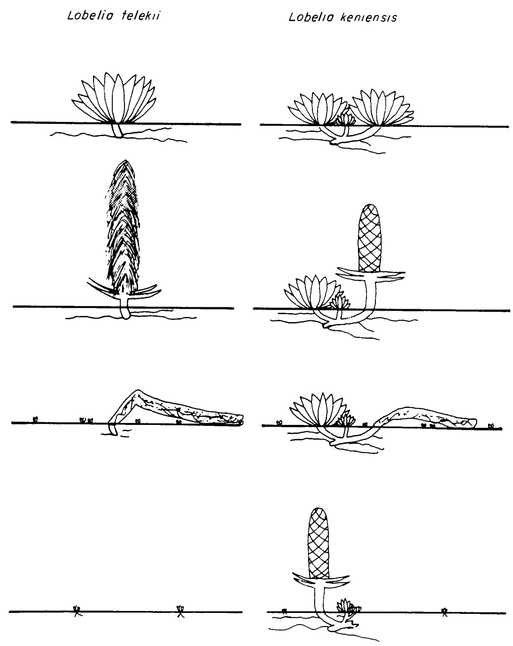

FIG. 1. Diagrams of life history stages of the semelparous (monocarpic) *Lobelia telekii* and the iteroparous (polycarpic) *Lobelia keniensis* on Mount Kenya. Successive stages follow down the columns.

STUDY SITES

The study sites are in the upper Teleki Valley on the western side of Mount Kenya 0° 10′S, 37° 17′E). For each species, three permanent plots were established. The *L. telekii* plots (T1, T2, T3) are at the head of the valley on north-facing slopes across from the Teleki Valley Ranger Station at 4200 m. The *L. keniensis* plots (K1, K2, K3) are along the south side of the valley bottom 1·0–1·5 km from the Ranger Station, between 3970 m and 4100 m.

The *L. keniensis* plots received 20–50% more rain than the *L. telekii* plots (Table 1). In the upper Teleki Valley, the percentage cover of the vegetation was strongly positively correlated with dry season soil-moisture (T. P. Young, unpublished), and the *L. telekii* plots were drier, had less vegetation cover, and lower concentrations of nutrient elements (except phosphorus) than the *L. keniensis* plots (Table 2).

There were parallel but less pronounced differences between the plots for each species. The soil-moisture estimates were not significantly different among the plots for a given species in June 1980. However, *L. telekii* plot T1 had significantly less vegetation cover

TABLE 1. Mean monthly rainfall (mm) in the upper Teleki Valley (Mount Kenya) between January 1978 and June 1981.

	February 1978– May 1979	June 1979– January 1980	February 1980– June 1981
Lobelia telekii Plot 3	80*	49	50
Ranger station	88	56	45
Lobelia keniensis Plot 1	120*	71	60

* Estimate from incomplete records.

TABLE 2. Charactersitics and soil chemistry of plots containing *Lobelia telekii* and *L. keniensis* on Mount Kenya. Ranges of three samples are given for soil chemistry and mean 1 S.D. for ten estimates of slope, vegetation cover, and soil moisture. Chemical analyses were made by the National Agricultural Laboratories, Nairobi, Kenya.

Species	*Lobelia telekii*			*Lobelia keniensis*		
Plot	T1	T2	T3	K1	K2	K3
Altitude (m)	4190	4200	4190	4100	4000	3970
Vegetation cover (%)	26 ± 12	40 ± 15	39 ± 17	72 ± 10	63 ± 8	68 ± 12
Slope (°)	23 ± 5	26 ± 6	30 ± 5	13 ± 5	15 ± 4	11 ± 8
Soil moisture (%)	23·0 ± 1·5	24·9 ± 6·0	24·6 ± 4·0	74·5 ± 5·1	74·8 ± 4·0	64·8 ± 12·7
Soil elements						
N (g kg^{-1})	3·0–7·7	5·4–8·9	4·2–6·4	9·0–9·3	11·1–16·3	9·5–13·1
P (mg kg^{-1})	60–122	50–84	60–76	24–42	24–42	24–32
Na (g kg^{-1})	1·4–4·0	4·9–7·3	7·2–10·2	10·0–10·6	9·2–13·0	6·5–13·0
K (g kg^{-1})	0·5–1·5	1·3–2·0	1·0–3·0	7·8–16·3	7·9–11·3	9·9–12·4
Ca (g kg^{-1})	3–54	21–101	15–44	29–41	11–48	18–29
C (g kg^{-1})	37–79	43–84	34–75	91–99	116–155	94–133
Mg (g kg^{-1})	1–0·6	0·6–20·2	1–5·8	18·2–22·0	3·0–28·2	10·6–15·0
Mn (g kg^{-1})	1·5–2·0	3·5–3·9	1·5–2·2	5·0–7·2	0·4–1·1	6·6–10·6

and had generally lower elemental concentrations than plots T2 and T3. There were no clear soil-chemistry differences between the *L. keniensis* plots. However, a rain gauge maintained near plots K2 and K3 from March to September 1979 received 10% less rainfall than the gauge at plot K1 (533 mm *v.* 588 mm). The valley bottom rises relatively steeply in this region, and the observed increase in rainfall may be due to a local configuration associated with this rise. On these indications, the plots were tentatively divided into four groups of supposed increasing soil moisture: drier *L. telekii* plot (T1); wetter *L. telekii* plots (T2, T3); drier *L. keniensis* plots (K2, K3); and wetter *L. keniensis* plot (K1).

There was a pronounced wet period on Mount Kenya from 1977 to 1979 followed by a severe dry period from 1980 to 1981 (Table 1). The study period was divided into three: a wet period from February 1978 to May 1979 ; a transition period from June 1979 to January 1980; and a dry period from February 1980 to June 1981.

METHODS

Each *L. telekii* plot comprised four, and each *L. keniensis* plot five, 5 m × 5 m quadrats. One to several leaves of each *Lobelia* plant in each plot were marked with a waterproof ink, and an aluminium stake with a numbered tag was put in the ground nearby. On each multi-rosette plant, two rosettes were marked. Also 100–300 *Lobelia* plants of various sizes were marked and tagged near each plot. One thousand *L. telekii* single-rosette plants, 700 *L. keniensis* single-rosette plants, and 430 rosettes on 215 multi-rosette *L. keniensis* plants were marked and tagged.

In December 1979, ten 0·25 m × 0·25 m quadrats were randomly established in each plot. Seedlings arising in these quadrats were marked and tagged at 3–6 week intervals. New seedlings were always found in the cotyledon stage.

For each marked rosette, the length and width of the largest leaf were measured, and the total number of leaves counted. For multi-rosette individuals of *L. keniensis* the number of rosettes was counted. All plants were visited every 6 weeks. Cause of death was recorded where possible for rosettes that had died but were still present and included rock hyrax (*Procavia johnstoni mackinderi* Thomas), rodents, insect attack, bud damage of unknown origin, wilting, uprooting from solifluction, and burial under mudslides (a not infrequent fate of smaller *L. telekii* rosettes during rainy weather). Indications of damage or disease when they occurred were also recorded for living rosettes.

The length of the largest leaf was measured every 3 months on each marked rosette. Every 6 months the width of the largest leaf was measured and the total number of leaves counted on marked rosettes. The number of rosettes on marked *L. keniensis* plants were counted every 6 months. The flowering of marked rosettes was recorded and the length of the inflorescence measured. Reproduction of unmarked rosettes in tagged *L. keniensis* plants was also recorded.

Several rosettes of each species were dissected. All expanded and bud leaves were counted, and every tenth leaf measured. A single expanded leaf was taken from each of eighteen single *L. telekii* rosettes, eighteen single *L. keniensis* rosettes, and eighteen rosettes from multi-rosette *L. keniensis* plants. These leaves were measured on the plant, removed, and traced on paper. The area of each leaf was calculated using a digital planimeter.

RESULTS

The size of a rosette is a function of the length and width of its largest leaf, and the total number of leaves. Measured leaf area was very strongly correlated with the product of length and width for leaves of *L. telekii* ($r = 0{\cdot}99$, $n = 18$, $P < 0{\cdot}001$) and *L. keniensis* $r = 0{\cdot}99$, $n = 36$, $P < 0{\cdot}001$). Rosette dissections indicated that fully expanded leaves varied little in size within a rosette. Therefore the product of leaf length, leaf width, and total number of leaves is a good estimator of total leaf area. Leaf length very strongly correlated with the cube root of this product in *L. telekii* ($r = 0{\cdot}96$, $n = 35$, $P < 0{\cdot}001$) and in *L. keniensis* ($r = 0{\cdot}97$, $n = 37$, $P < 0{\cdot}001$) for randomly selected rosettes. Leaf length is therefore a reasonable measure of rosette size, and will be used as such. All values given are ± 1 S.E.

Size distributions

The size distributions of pre-reproductive rosettes for both species are shown in Fig. 2. Only plants with initial largest leaf length greater than 1 cm are included because I am certain that all such rosettes present in the plots were found and tagged. The size distributions in Fig. 2 differ from those in Tables 3 and 4 because the latter include a large number of rosettes non-randomly sampled outside the plots in order to increase sample sizes in classes with few plants. The average *L. telekii* density in the drier plot (T1) was

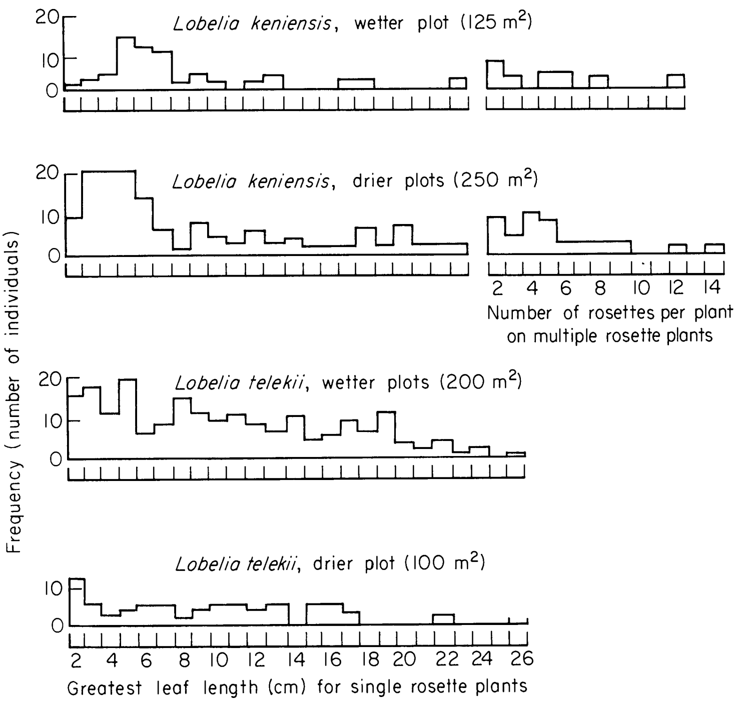

FIG. 2. Size-class histograms of *Lobelia telekii* and *Lobelia keniensis* single-rosette plants, and *Lobelia keniensis* multiple-rosette plants at sites on Mount Kenya.

$0{\cdot}66 \pm 0{\cdot}04$ m^{-2} ($n = 4$) and in the wetter plots (T2, T3) was $0{\cdot}99 \pm 0{\cdot}16$ m^{-2} ($n = 8$). There were no significant differences in plant density between *L. keniensis* drier plots (K2, K3) and the wetter plot (K1). The densities of single rosette plants were $0{\cdot}44 \pm 0{\cdot}10$ m^{-2} ($n = 10$) and $0{\cdot}42 \pm 0{\cdot}10$ m^{-2} ($n = 5$), respectively. The densities of multi-rosette plants were $0{\cdot}15 \pm 0{\cdot}02$ ($n = 10$) and $0{\cdot}14 \pm 0{\cdot}05$ m^{-2} ($n = 5$), respectively.

Seedling survivorship

Seedling survivorship in both species decreased exponentially (Fig. 3). Seven out of 360 marked, cotyledon-stage, *L. keniensis* seedlings survived for 13 months, with an average survivorship of 0·74 per month. Seedling survivorship in *L. telekii* was lower in the first 3 months (0·46 per month) than in the next 15 months (0·86 per month). Four out of 279 marked seedlings survived 18 months, with an average survivorship of 0·79 per month. The growth of seedlings was very slow. No seedling had added more than two new leaves in the first year after germination, and at least one seedling remained in the cotyledon stage for over a year.

Fate of Lobelia telekii *rosettes*

Size-specific fates of *L. telekii* rosettes are presented in Table 3. Growth rates, measured as the change in leaf length, were greater in the wetter sites than in the drier sites ($\chi^2 = 24{\cdot}0$, d.f. $= 1$, $P < 0{\cdot}001$), and greater in the dry period than in the wet period ($\chi^2 = 18{\cdot}0$, d.f. $= 1$, $P < 0{\cdot}001$). The average leaf length decreased for many size classes in the drier sites and during the dry period. This was due to rosettes producing smaller leaves.

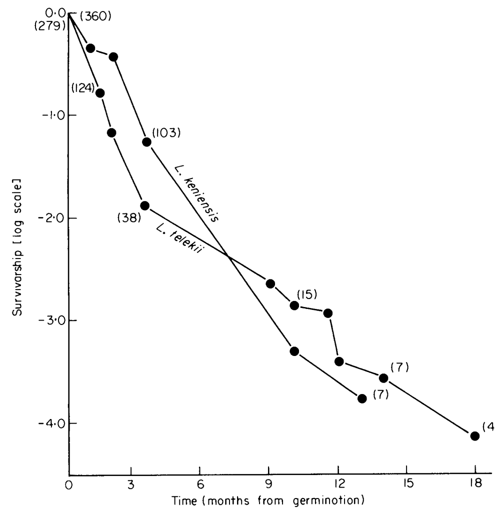

FIG. 3. Survivorship of seedlings of *Lobelia telekii* and *Lobelia keniensis* in ten $0{\cdot}25 \times 0{\cdot}25$ m^2 plots for each species on Mount Kenya. The numbers of seedlings surviving are given in parentheses. Seedlings germinating at different times are combined.

There was a minimum length of the greatest leaf prior to reproduction of 16 cm. Although one rosette with a greatest leaf length of 14 cm in February 1978 did flower eventually, it had grown to 16 cm before flowering. The largest flowering rosettes had a greatest leaf length of 27 cm. The average greatest leaf length at reproduction was significantly greater in the wetter sites ($20{\cdot}7 \pm 0{\cdot}4$ cm, $n = 56$) than in the drier sites ($18{\cdot}8 \pm 0{\cdot}6$ cm, $n = 10$, $t = 2{\cdot}14$, $P < 0{\cdot}05$). The probability of flowering and the average rosette size at reproduction were not significantly different between the wet and dry periods.

Size-specific *L. telekii* mortality was lower in the wet sites than in the drier sites ($\chi^2 = 17{\cdot}6$, d.f. $= 1$, $P < 0{\cdot}001$), and lower in the wet period, than in the dry period ($\chi^2 = 14{\cdot}2$, d.f. $=1$, $P < 0{\cdot}001$). During the wet period, mortality decreased with increasing rosette size. In contrast, during the dry period mortality was strikingly bimodal, with peaks in the smallest and the largest size classes. Most mortality of small rosettes was associated with wilting, bud damage, or unknown causes. Most of the large-rosette mortality (excluding flowering) was due to predation by rock hyrax. This predation continued beyond May 1981, and by November 1981 more than half of all the rosettes with greatest leaf length larger than 12 cm in the study sites had been killed. Hyrax only rarely killed smaller rosettes.

One of the *L. telekii* individuals in a wetter site (T2) branched before flowering. The single small rosette grew very quickly, but died within a year of the reproduction and death of the larger rosette.

Fate of Lobelia keniensis *single-rosette plants*

The above-ground size of an unbranched *L. keniensis* plant is the size of its single rosette. The above-ground size of a branched *L. keniensis* plant is composed of the size and number of its constituent rosettes. Three kinds of *L. keniensis* life table were produced: for immature single-rosette plants; for rosettes on multiple-rosette plants; and for entire multiple-rosette plants.

TABLE 3. Size-specific growth, mortality, and flowering rate of *Lobelia telekii* rosettes at sites on Mount Kenya. The wetter sites include plots T2 and T3 and the associated marked plants. The drier sites include plot T1 and associated marked plants. Growth rate ΔLL is measured as change in length of largest leaf. *T* is the total number of rosettes in a particular size class at the beginning of the period; *M* is the number of rosettes that died before flowering; and *F* is the number of rosettes that flowered and died. *n* values are given in parentheses.

Size class—greatest leaf length (cm)	Wetter sites						Drier sites					
				Annual rates						Annual rates		
	T	*M*	*F*	*M*(%*T*)	*F*(%*T*)	ΔLL ± 1 S.E.	*T*	*M*	*F*	*M*(%*T*)	*F*(%*T*)	ΔLL ± 1 S.E.
Overall period (February 1978–May 1981)												
⩽2·0	63	29	0	17	0	0·29 ± 0·04 (34)	34	21	0	26	0	0·19 ± 0·06 (13)
2·5–3·5	84	28	0	12	0	0·30 ± 0·04 (56)	24	13	0	21	0	0·14 ± 0·07 (11)
4·0–5·5	109	18	0	5	0	0·23 ± 0·03 (91)	23	7	0	11	0	0·06 ± 0·09 (16)
6·0–8·5	121	15	0	4	0	0·18 ± 0·04 (106)	41	8	0	6	0	−0·24 ± 0·09 (33)
9·0–11·5	112	16	0	5	0	0·23 ± 0·07 (96)	31	7	0	8	0	−0·32 ± 0·11 (24)
12·0–14·5	72	16	1	7	<1	0·38 ± 0·07 (55)	30	11	0	13	0	−0·40 ± 0·16 (19)
15·0–17·5	74	16	11	7	5	0·46 ± 0·08 (47)	30	16	2	21	2	−0·49 ± 0·15 (12)
18·0–20·5	63	3	18	1	10	0·46 ± 0·07 (42)	18	5	7	10	14	−0·44 ± 0·31 (6)
⩾21·0	40	7	26	6	28	0·11 ± 0·22 (7)	6	2	1	12	5	−0·05 ± 0·22 (3)
Wet period (February 1978–June 1979)												
⩽2·0	63	6	0	7	0	0·19 ± 0·06 (57)	37	7	0	15	0	0·09 ± 0·07 (30)
2·5–3·5	79	7	0	7	0	0·43 ± 0·05 (72)	25	3	0	9	0	0·02 ± 0·13 (13)
4·0–5·5	108	3	0	2	0	0·42 ± 0·06 (105)	23	4	0	13	0	0·26 ± 0·17 (19)
6·0–8·5	128	4	0	2	0	0·38 ± 0·06 (124)	42	1	0	2	0	0·16 ± 0·13 (41)
9·0–11·5	114	4	0	3	0	0·35 ± 0·07 (110)	31	1	0	2	0	0·18 ± 0·17 (30)
12·0–14·5	75	1	0	1	0	0·62 ± 0·10 (74)	28	1	0	3	0	0·03 ± 0·17 (27)
15·0–17·5	73	0	1	0	1	0·68 ± 0·09 (72)	30	1	1	3	3	−0·15 ± 0·13 (28)
18·0–20·5	63	0	4	0	5	0·63 ± 0·11 (59)	18	0	3	0	14	−0·05 ± 0·20 (15)
⩾21·0	41	0	11	0	21	0·46 ± 0·19 (30)	5	0	0	0	0	0·53 ± 0·37 (5)
Dry period (February 1980–May 1981)												
⩽2·0	26	10	0	32	0	0·18 ± 0·10 (16)	21	14	0	58	0	0·00 ± 0·20 (7)
2·5–3·5	64	17	0	22	0	0·09 ± 0·07 (47)	21	8	0	32	0	−0·15 ± 0·10 (13)
4·0–5·5	86	9	0	8	0	−0·06 ± 0·07 (77)	18	1	0	5	0	−0·19 ± 0·13 (17)
6·0–8·5	122	7	0	5	0	−0·22 ± 0·07 (115)	35	3	0	7	0	−0·75 ± 0·15 (32)
9·0–11·5	97	8	0	7	0	−0·31 ± 0·12 (89)	30	6	0	16	0	−0·95 ± 0·20 (24)
12·0–14·5	75	13	0	14	0	−0·17 ± 0·14 (62)	21	3	0	12	0	−1·89 ± 0·38 (18)
15·0–17·5	63	10	3	13	4	−0·17 ± 0·13 (50)	32	14	0	37	0	−1·46 ± 0·31 (18)
18·0–20·5	65	5	13	6	16	−0·03 ± 0·15 (47)	16	5	4	26	21	−0·91 ± 0·42 (7)
⩾21·0	41	5	11	10	22	−0·64 ± 0·26 (25)	4	2	0	43	0	−1·20 ± 0·20 (2)

The fates of single-rosette *L. keniensis* plants (Table 4) were similar to those for *L. telekii*, except for the absence of hyrax predation for hyrax do not normally occur in *L. keniensis* habitat. Size-specific growth rates were lower in the drier sites than in the wetter sites ($\chi^2 = 5{\cdot}5$, d.f. $= 1$, $P < 0{\cdot}05$) and lower in the dry period than in the wet period ($\chi^2 = 14{\cdot}2$, d.f. $= 1$, $P < 0{\cdot}001$).

In *L. keniensis* single rosettes there was a minimum size at reproduction with greatest leaf length 16·0 cm, and a maximum at 27·5 cm. The probability of reproduction increased with size within this range. There were no significant differences in rosette size at reproduction between the wetter sites (21·2 ± 1·4 cm, $n = 6$) and the drier sites (21·2 ± 0·7, $N = 3$).

Size-specific mortality for single rosette *L. keniensis* plants was greater during the dry period than during the wet period ($\chi^2 = 8{\cdot}3$, d.f. $= 1$, $P < 0{\cdot}01$) were no significant differences in size-specific mortality between the drier sites and the wetter sites. Single-rosette *L. keniensis* plants began to branch at a minimum greatest leaf-length of

TABLE 4. Size-specific growth, mortality, and flowering rates of single *Lobelia keniensis* rosettes at sites on Mount Kenya. The wetter sites include plot K1 and associated marked plants. The drier sites include plots K2 and K3 and associated marked plants. Growth rate (ΔLL) is measured as change in length of largest leaf. *T* is the total number of rosettes in a particular size class at the beginning of the period; *M* is the number of rosettes that died before flowering; and *F* is the number of rosettes that flowered and died. *n* values are given in parentheses.

Size class—greatest leaf length (cm)	Wetter sites						Drier sites					
				Annual rates						Annual rates		
	T	*M*	*F*	*M*(%*T*)	*F*(%*T*)	Δll ± 1 S.E.	*T*	*M*	*F*	*M*(%*T*)	*F*(%*T*)	ΔLL ± 1 S.E.
Overall period (February 1978–July 1981)												
⩽2·0	40	24	0	23	0	0·16 ± 0·05 (16)	43	25	0	22	0	0·32 ± 0·04 (18)
2·5–3·5	39	6	0	5	0	0·40 ± 0·05 (33)	89	22	0	8	0	0·35 ± 0·04 (67)
4·0–5·5	91	9	0	3	0	0·27 ± 0·04 (83)	107	8	0	2	0	0·25 ± 0·03 (99)
6·0–8·5	69	8	0	3	0	0·36 ± 0·08 (61)	63	1	0	<1	0	0·22 ± 0·06 (62)
9·0–11·5	24	2	0	2	0	0·71 ± 0·11 (22)	17	1	0	2	0	0·49 ± 0·16 (16)
12·0–14·5	9	1	0	3	0	0·80 ± 0·12 (8)	11	3	0	9	0	0·46 ± 0·24 (8)
15·0–17·5	13	0	1	0	2	0·81 ± 0·10 (12)	26	0	0	0	0	0·65 ± 0·11 (26)
18·0–20·5	17	0	2	0	4	0·77 ± 0·12 (15)	24	0	2	0	2	0·48 ± 0·14 (22)
⩾21·0	6	0	3	0	18	0·86 ± 0·13 (3)	8	0	1	0	4	0·22 ± 0·15 (7)
Wet period (February 1978–June 1979)												
⩽2·0	40	16	0	33	0	0·13 ± 0·09 (24)	45	12	0	21	0	0·30 ± 0·06 (33)
2·5–3·5	39	0	0	0	0	0·37 ± 0·07 (39)	98	2	0	2	0	0·34 ± 0·05 (96)
4·0–5·5	89	0	0	0	0	0·36 ± 0·05 (89)	115	0	0	0	0	0·42 ± 0·09 (115)
6·0–8·5	69	0	0	0	0	0·50 ± 0·09 (69)	63	0	0	0	0	0·37 ± 0·11 (63)
9·0–11·5	24	0	0	0	0	0·71 ± 0·18 (24)	17	0	0	0	0	0·45 ± 0·19 (17)
12·0–14·5	10	0	0	0	0	1·00 ± 0·24 (10)	9	0	0	0	0	0·94 ± 0·29 (9)
15·0–17·5	11	0	0	0	0	1·15 ± 0·23 (11)	27	0	0	0	0	0·87 ± 0·17 (27)
18·0–20·5	19	0	0	0	0	1·15 ± 0·19 (19)	23	0	1	0	3	0·72 ± 0·19 (22)
⩾21·0	6	0	2	0	30	2·12 ± 0·33 (4)	8	0	0	0	0	0·43 ± 0·33 (8)
Dry period (February 1980–July 1981)												
⩽2·0	17	7	0	29	0	0·03 ± 0·08 (10)	4	2	0	36	0	0·32 ± 0·32 (2)
2·5–3·5	15	4	0	18	0	0·09 ± 0·10 (11)	65	20	0	21	0	0·26 ± 0·11 (45)
4·0–5·5	61	9	0	10	0	−0·12 ± 0·11 (52)	94	7	0	5	0	−0·09 ± 0·17 (87)
6·0–8·5	99	11	0	7	0	−0·55 ± 0·09 (88)	96	2	0	1	0	−0·15 ± 0·07 (94)
9·0–11·5	37	1	0	2	0	−0·08 ± 0·19 (36)	25	1	0	3	0	−0·08 ± 0·15 (24)
12·0–14·5	18	0	0	0	0	0·41 ± 0·17 (18)	11	1	0	6	0	0·32 ± 0·29 (10)
15·0–17·5	8	1	0	8	0	0·45 ± 0·23 (7)	19	0	0	0	0	0·32 ± 0·16 (19)
18·0–20·5	12	0	0	0	0	0·49 ± 0·26 (12)	21	0	0	0	0	0·43 ± 0·19 (21)
⩾21·0	10	0	1	0	7	0·29 ± 0·27 (9)	17	0	2	0	8	0·41 ± 0·28 (15)

16·0 cm (Table 5). The probability of branching increased with increasing rosette size. The probability of branching was consistently higher in the wetter sites than in the drier sites ($\chi^2 = 8{\cdot}0$, d.f. = 1, $P < 0{\cdot}01$), and consistently higher during the wet period than during the dry period ($\chi^2 = 6{\cdot}0$, d.f. = 1, $P < 0{\cdot}05$).

Fates of rosettes on multiple-rosette Lobelia keniensis *plants*

The size-specific fates of rosettes on multiple-rosette *L. keniensis* plants are shown in Table 6. The growth rates were not significantly greater in the wetter sites than in the drier sites, but were significantly higher in the wet period than in the dry period ($\chi^2 = 12{\cdot}2$, d.f. = 1, $P < 0{\cdot}001$). Medium-sized rosettes (greatest leaf length 5·0–11·5 cm) grew rapidly in the wet period, but decreased in size in the dry period, with high variance in growth rate in both cases. There were no significant differences in mortality between sites or between periods. Growth and mortality rates were generally higher for smaller rosettes from multiple-rosette plants than for single-rosette *L. keniensis* plants.

TABLE 5. Branching patterns of initially unbranched *Lobelia keniensis* plants at sites on Mount Kenya. No rosettes with their greatest leaf length less than 16 cm branched. The number of rosettes per branched plant is averaged over all rosette size classes.

	Wetter sites				Drier sites			
Greatest leaf length (cm)	Total	Number branching	% branching per year	Rosettes per branched plant ± 1 S.E.	Total	Number branching	% branching per year	Rosettes per branched plant ± 1 S.E.
February 1978–May 1979 (Wet period)								
16·0–17·5	13	2	5	3·42 ± 0·48	26	2	2	2·75 ± 0·48
18·0–20·5	17	6	12		24	1	1	
⩾21·0	6	4	27		8	1	4	
June 1979–January 1980 (Transition period)								
16·0–17·5	11	2	14	3·38 ± 0·53	27	1	3	2·75 ± 0·48
18·0–20·5	19	4	17		23	1	3	
⩾21·0	6	2	27		8	2	20	
February 1980–July 1981 (Dry period)								
16·0–17·5	8	0	0	2·20 ± 0·20	19	0	0	3·00 ± 1·00
18·0–20·5	12	2	11		21	0	0	
⩾21·0	10	3	21		17	2	8	

Minimum size of the greatest leaf at reproduction for rosettes from multiple-rosette *L. keniensis* plants was 17·5 cm, and maximum was 28·0 cm. The probability of flowering increased with increasing rosette size within this range. The average greatest leaf-length at reproduction for plants in the drier sites was 22·1 ± 0·5 cm, ($n = 23$), and for plants in the wetter sites was 20·9 ± 0·5 cm ($n = 17$); no significant difference ($t = 1{\cdot}66, P \approx 0{\cdot}15$).

Fates of multiple-rosette Lobelia keniensis *plants*

The number of constituent rosettes varied greatly in multiple-rosette *L. keniensis* plants (Fig. 4). No less variation was obtained for observations covering 3·5 years than for that over shorter periods (Table 7). Despite this variation, the average number of rosettes per multiple-rosette plant was nearly constant with time in both the wetter and drier sites. The maximum number of rosettes per plant in any survey was eighteen, and no plant had more than fourteen rosettes in any two surveys reported here. Initiation of new rosettes did not coincide either in time or position with the flowering of rosettes on the plant. Only four multiple-rosette plants died between February 1978 and July 1981. All were in the drier sites (Fig. 4), and all but one died in the dry period; the exception died during the transition from the wet to the dry period.

The probability of a multiple-rosette *L. keniensis* plant reproducing in a particular period increased with increasing number of rosettes per plant, and the probability of a particular rosette flowering was independent of the number of rosettes on the same plant (Table 8). Plants with more rosettes flowered more frequently than plants with fewer rosettes.

Inflorescence size

In both species, the size of a rosette at reproduction was significantly correlated with the size of the inflorescence produced (*L. telekii*, $r = 0{\cdot}69$, $n = 22$, $P < 0{\cdot}001$; inflorescence length (cm) = 11·0 × [greatest leaf length (cm)] − 133; *L. keniensis*, $r = 0{\cdot}50$, $n = 25$, $P < 0{\cdot}01$; inflorescence length (cm) = 1·2 × [greatest leaf length (cm)] − 23. Inflorescences of *L. telekii* were larger and their size was determined more by rosette size than in the case

TABLE 6. Size-specific growth, mortality, and flowering rates of rosettes on multi-rosette *Lobelia keniensis* plants at sites on Mount Kenya. The wetter sites include plot K1 and associated marked plants. The drier sites include plots K2 and K3 and associated marked plants. Growth rate (ΔLL) is measured as change in length of largest leaf. *T* is the total number of rosettes in a particular size class at the beginning of the period; *M* is the number of rosettes that died before flowering; and *F* is the number of rosettes that flowered and died. *n* values are given in parentheses.

Size class—greatest leaf length (cm)	Wetter sites						Drier sites					
				Annual rates						Annual rates		
	T	*M*	*F*	*M*(%*T*)	*F*(%*T*)	ΔLL ± 1 S.E.	*T*	*M*	*F*	*M*(%*T*)	*F*(%*T*)	Δll ± 1 S.E.
Overall period (February 1978–July 1981)												
⩽2·0	10	9	0	48	0	0·29 (1)	5	3	0	23	0	0·57 ± 0·29 (2)
2·5–3·5	7	2	0	9	0	0·69 ± 0·22 (5)	11	9	0	39	0	1·36 ± 0·36 (2)
4·0–5·5	8	5	0	24	0	0·56 ± 0·37 (3)	20	13	0	26	0	1·10 ± 0·29 (7)
6·0–8·5	17	11	0	26	0	0·86 ± 0·43 (6)	25	7	0	9	0	0·69 ± 0·25 (18)
9·0–11·5	19	5	0	8	0	1·47 ± 0·21 (14)	26	8	0	10	0	0·90 ± 0·29 (18)
12·0–14·5	20	5	0	8	0	1·36 ± 0·12 (15)	18	6	0	11	0	0·40 ± 0·16 (12)
15·0–17·5	38	1	2	1	2	1·04 ± 0·11 (35)	28	2	0	2	0	0·40 ± 0·15 (26)
18·0–20·5	24	0	4	0	5	0·86 ± 0·10 (20)	53	0	6	0	3	0·61 ± 0·07 (47)
⩾21.0	21	0	11	0	17	0·66 ± 0·08 (10)	70	0	18	0	8	0·56 ± 0·05 (52)
Wet period (February 1978–June 1979)												
⩽2·0	10	6	0	51	7	0·77 ± 0·47 (4)	4	2	0	42	0	0·38 ± 0·38 (2)
2·5–3·5	9	1	0	8	0	0·96 ± 0·63 (8)	9	1	0	8	0	0·34 ± 0·56 (8)
4·0–5·5	7	0	0	0	0	0·93 ± 0·36 (7)	18	3	0	13	0	1·10 ± 0·47 (15)
6·0–8·5	17	1	0	5	0	2·28 ± 0·63 (16)	23	4	0	13	0	0·83 ± 0·44 (19)
9·0–11·5	18	1	0	5	0	1·36 ± 0·50 (17)	28	1	0	3	0	1·62 ± 0·49 (27)
12·0–14·5	31	3	0	11	0	1·60 ± 0·23 (18)	15	0	0	0	0	0·41 ± 0·32 (15)
15·0–17·5	38	0	1	0	2	1·16 ± 0·20 (37)	28	0	0	0	0	0·58 ± 0·31 (28)
18·0–20·5	23	0	2	0	9	1·21 ± 0·19 (21)	53	0	4	0	6	0·96 ± 0·13 (49)
⩾21·0	20	0	5	0	20	1·23 ± 0·18 (15)	64	0	8	0	10	0·72 ± 0·14 (58)
Dry period (February 1980–July 1981)												
⩽2·0	0						0					
2·5–3·5	3	0	0	0	0	0·22 ± 0·11 (3)	7	5	0	55	0	0·46 ± 0·46 (2)
4·0–5·5	7	4	0	42	0	0·43 ± 0·29 (3)	8	4	0	36	0	0·77 ± 0·93 (4)
6·0–8·5	9	5	0	41	0	0·00 ± 0·75 (4)	19	8	0	30	0	−0·07 ± 0·33 (11)
9·0–11·5	9	4	0	31	0	−1·30 ± 0·43 (5)	13	1	0	5	0	−0·48 ± 0·62 (12)
12·0–14·5	16	4	0	17	0	0·92 ± 0·32 (12)	23	5	0	15	0	0·17 ± 0·44 (18)
15·0–17·5	29	2	0	5	0	1·06 ± 0·18 (27)	30	3	0	7	0	0·04 ± 0·40 (27)
18·0–20·5	30	0	2	0	5	0·75 ± 0·15 (28)	42	1	0	2	0	0·88 ± 0·21 (41)
⩾21·0	43	0	9	0	14	0·33 ± 0·13 (34)	85	0	12	0	9	0·41 ± 0·13 (73)

of *L. keniensis*. The fitted regression lines indicate that, on average, *L. telekii* inflorescence size tripled from the smallest to the largest flowering rosettes in this study. In contrast, *L. keniensis* inflorescence size increased by only 25% over the observed range of flowering rosette sizes.

DISCUSSION

Inflorescence size and rosette size at reproduction

Plant size has been shown to be a good predictor of fate in several herbaceous species. In particular, a minimum size at reproduction has been demonstrated repeatedly (Werner 1975; Inouye & Taylor 1980; Gross 1981; Thomson & Beattie 1981). In addition Thomson & Beattie have shown a minimum size at which *Viola blanda* L. plants begin to produce stolons, and this size is similar to the minimum size for flowering. There seems to be a threshold which may be either the accumulation of a minimum amount of stored

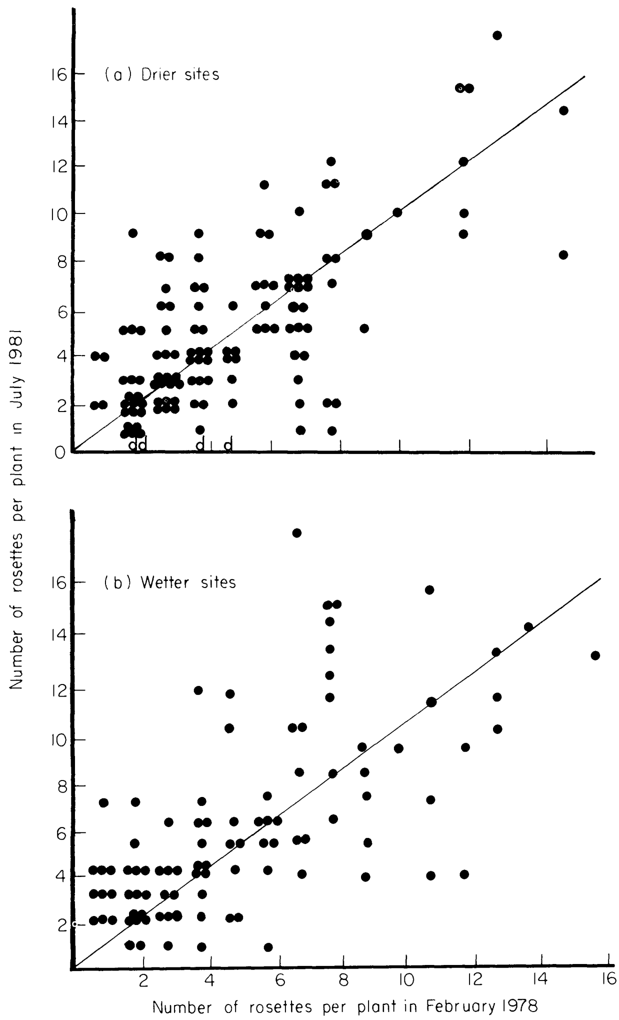

FIG. 4. Changes in the number of rosettes per plant for multiple-rosette *Lobelia keniensis* plants at sites; (a), drier sites and (b), wetter sites on Mount Kenya between February 1978 and July 1981; (d), plants that died during this period; (——), position of no change between dates.

reserves, or a point at which production first exceeds maintenance by an amount sufficient for flowering or stolon production.

Both *L. telekii* and *L. keniensis* rosettes have a minimum size at flowering, and *L. keniensis* plants have a minimum size at which they begin to branch. All of these minimum sizes are similar in Mount Kenya alpine *Lobelias*. Because all the resources of the plant go into reproduction in the semelparous *L. telekii*, it is not surprising that inflorescence size is more sensitive to rosette size at reproduction than in the iteroparous *L. keniensis*, which apportions its resources between flowering and new rosette production.

Clonal growth in Lobelia keniensis

The number of rosettes that mature to reproductive size, and therefore reproductive success in *L. keniensis*, depend on clonal growth. Multiple-rosette *L. keniensis* plants have

TABLE 7. Mean number of rosettes per plant of *Lobelia keniensis* at specified times, and changes in the number of rosettes per plant in wetter and drier sites over different periods on Mount Kenya. Size classes were chosen arbitrarily. *n* values are given in parentheses.

	Wetter sites			Drier sites		
	Mean number of rosettes per plant ± 1 S.E.	Size class	Change in number of rosettes per plant year^{-1}	Mean number of rosettes per plant ± 1 S.E.	Size class	Change in number of rosettes per plant year^{-1}
February 1978–July 1981	5·94 ± 0·37 (86)	⩽8 rosettes	+0·27 ± 0·10 (68)	5·15 ± 0·27 (118)	<6 rosettes	+0·17 ± 0·07 (77)
	(February 1978)	⩾9 rosettes	−0·64 ± 0·21 (17)	(February 1978)	>7 rosettes	−0·37 ± 0·51 (38)
February 1978–February 1980	5·93 ± 0·37 (86)	⩽8 rosettes	+0·40 ± 0·12 (74)	5·15 ± 0·29 (117)	<6 rosettes	+0·31 ± 0·15 (85)
	(February 1980)	⩾9 rosettes	−1·04 ± 0·32 (15)	(February 1980)	>7 rosettes	−0·42 ± 0·24 (37)
February 1980–July 1981	6·03 ± 0·39 (87)	⩽8 rosettes	+0·41 ± 0·18 (75)	5·34 ± 0·31 (113)	<6 rosettes	+0·03 ± 0·11 (89)
	(July 1981)	⩾9 rosettes	−0·60 ± 0·10 (18)	(July 1981)	>7 rosettes	−0·14 ± 0·25 (28)

TABLE 8. Number of inflorescences produced by multiple-rosette individuals of *Lobelia keniensis* with different numbers of rosettes between May 1978 and May 1980 on Mount Kenya.

Number of rosettes per plant	Number of individuals	Total number of inflorescences	Inflorescences per individual	Inflorescences per rosette
2–4	69	8	0·12	0·04
5–7	54	9	0·17	0·03
8–10	20	4	0·20	0·02
11–13	14	7	0·50	0·04
14–16	5	3	0·60	0·04

(i) large changes in the number of constituent rosettes over relatively short periods of time, (ii) rapid and highly variable growth of small and medium rosettes, and (iii) high mortality of medium rosettes, when compared with single *L. keniensis* rosettes of the same size.

Multiple-rosette plants can adjust their size by varying either the size or the number of their constituent rosettes. Such changes in *L. keniensis* appear to be associated with changes in local conditions. Medium-sized rosettes grew very quickly during the wet period, and decreased in size during the dry period. Variation in the number of rosettes was independent of wet and dry weather. This variation may be due to the local success or failure or rosettes in finding favourable sites within a clone. Medium-sized rosettes that died were usually severely crowded by a larger rosette on the same plant, often were 'buried' under the old leaves of the larger rosette. Rosettes free of such crowding usually survived.

I interpret these patterns as evidence for an exploratory nature of clonal growth in *L. keniensis*. Rosette buds are initiated throughout the year and grow quickly when conditions are favourable. When conditions for the plant deteriorate, or the prospects of good growth for a particular rosette are not high, the plant can reduce the size of rosettes or allow them to die. The cost of rosette death can probably be offset by recovery of resources from the rosette by the plant. In contrast, rosettes that find themselves in favourable sites within a clone will survive continue to grow. Such an exploratory tactic may maximize the number of rosettes that a particular *L. keniensis* plant matures to reproductive size.

Differences in demography between sites

In the semelparous *L. telekii*, inflorescence size was positively correlated with soil moisture, while in the iteroparous *L. keniensis*, inflorescence size was relatively constant, and clone size was positively correlated with soil moisture (T. P. Young, unpublished). This suggests that demographic features of these plants may also vary in response to soil moisture or other factors correlated with soil moisture. The small edaphic differences between 'wetter' and 'drier' plots for each species may not, by themselves, justify such a separation. However, there were significant differences in *Lobelia* growth and mortality between 'wetter' and 'drier' sites for both species, and these differences paralleled significant demographic differences between the wet and dry weather periods on Mount Kenya during this study. It appears, therefore, that the separation of wetter and drier sites for each species was appropriate. Demographic variation associated with these between-site differences may have important consequences for the study of life history evolution in these *Lobelia* species, because the semelparous *L. telekii* occurs in drier habitats whereas the iteroparous *L. keniensis* occurs in wetter habitats.

Size-specific mortality was higher in *L. telekii* than in *L. keniensis* single-rosette plants. Size-specific growth rates of *L. telekii* rosettes were generally lower than those of *L.*

keniensis rosettes. However, the overall growth rates and average size at reproduction in *L. telekii* wetter-sites were similar to those in *L. keniensis* drier-plots, despite significantly lower soil moisture and nutrient concentrations and lower rainfall of the *L. telekii* wetter-sites compared with the *L. keniensis* drier-plots. This implies that each of these species has adapted physiologically to its local conditions.

A distinction between semelparity and iteroparity is made by differential investment in present and future reproduction. *L. telekii* rosettes produce significantly larger inflorescences than *L. keniensis* rosettes of the same size. In *L. keniensis*, present reproduction is apparently reduced in favour of future reproduction. The relative advantage of this future reproduction is strongly affected by demographic variables (Charnov & Schaffer 1974; Bell 1976, 1980; Young 1981).

Of particular interest here are the predictions that semelparity will be favoured by relatively increased time between reproductive episodes and decreasing adult survivorship (Young 1981). Because the number of rosettes per plant decreases with soil moisture in *L. keniensis*, plants in drier habitats reproduce less frequently than plants in wetter habitats. In addition, *L. keniensis* adult mortality is greater in drier sites than in wetter sites. I suggest that these demographic differences make iteroparity less and less profitable for *L. keniensis* in drier and drier habitats, and that semelparity is, therefore, favoured in the drier habitats where *L. telekii* occurs. Of course, this does not preclude the possibility that other factors have been involved in the life history evolution of Mount Kenya *Lobelia* species.

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