

The Cost of Reproduction in *Senecio keniodendron*, a Giant Rosette Species of Mt. Kenya

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Summary. A three year study of *Senecio keniodendron* (Compositae), a giant rosette species of the alpine zone of Mt. Kenya, demonstrated that individuals which reproduce are more likely to die, and less likely to reproduce in the future if they do survive, than are vegetative individuals of the same size. However, if an individual reproduces, survives and reproduces again, then it produces more seeds during the second reproductive episode than does a plant of the same height reproducing for the first time, because reproduction is followed by production of lateral rosettes, increasing the number of potentially-reproductive rosettes per plant.

Slow-growing rosettes are less likely to reproduce than fast-growing rosettes. For rosettes which do reproduce, rosette size and rate of leaf production, measured before reproduction begins, are good predictors of fecundity.

Introduction

The effects of sexual reproduction on subsequent parental survivorship, growth and reproduction have been poorly documented for naturally-occurring plant populations (Bell 1980; Harper 1977; Law 1979; Schaffer and Schaffer 1980; Stearns 1976). Such data are needed for development of realistic models of life history, sexual selection, parent-offspring conflict and ecological energetics. A three-year study of *Senecio keniodendron* (Compositae), a giant rosette species common above treeline on Mt. Kenya, has provided a more detailed description of reproductive costs than previously reported.

Senecio keniodendron is endemic to the alpine zone of Mt. Kenya, latitude 0°, occurring from valley floors to ridges between approximately 3,700 m and 4,500 m elevation (Coe 1967; Hedberg 1964, 1969). The plants produce woody stems up to 8 m tall, with 1–15 terminal evergreen rosettes composed of large leaves; mean leaf longevity is 0.7 ± 0.01 years at 4,200 m (Smith and Young, unpublished data). A reproductive rosette produces a single terminal flower stalk as much as 2 m tall (Fig. 1). Flowers appear to be predominantly wind pollinated; the plumed achenes are wind-dispersed. The original rosette dies after seed maturation, and up to eight new lateral rosettes are produced around the flower stalk base. Up to five of these new lateral



Fig. 1. Flowering individuals of *Senecio keniodendron* at 4,200 m, Teleki Valley, Mt. Kenya, Februar 1979. Plant in foreground is approximately 3 m tall

rosettes survive (typically 2–3), each producing a new branch. Each flowering episode therefore typically results in new forks in the stem. Branching occurs only after flowering, and so provides a record of past reproduction. These branching patterns suggest that plants seldom reproduce more than 4 times before dying.

Reproduction occurs synchronously over the entire population on Mt. Kenya, at intervals of several years, so *S. keniodendron* can be considered a “mast year” species (Janzen 1976). Mast years are known to have occurred in 1979 (see below), 1974 (Phil Snyder, Vincent Fayad, personal communications), 1957 (M. Sapro, personal communication), 1929 (DeWatteville 1935), and may have occurred in 1922 and 1916, based on photographic evidence (O.

Hedberg personal communication). The long intermast intervals of 1929 to 1957, and 1957 to 1974, appear to be consistent with measurements of branching patterns (Smith and Young, unpublished data).

Materials and Methods

Senecio keniodendron flowered extensively throughout its range from January through April 1979. In March 1980 a survey of *S. keniodendron* was carried out on the floor of Teleki Valley, on the west side of Mt. Kenya, at an elevation of 4,180 m, in order to document postreproductive mortality. All plants at least 0.75 m tall, measured to the highest leaf tip, were recorded in the upper 1 km of the valley floor; for each plant, height, number of forks, number of living and recently dead vegetative rosettes, and number of living and recently dead reproductive rosettes were recorded ($n=691$ for rosettes and $n=471$ for individual plants). A reproductive rosette was classed as dead if all new lateral rosettes produced around the flower stalk were dead. Dead vegetative rosettes show characteristic changes in leaf color and form over time; observation of dead rosettes in permanently marked study populations provided a basis for estimating the approximate time at which such rosettes died in the valley floor population, so that rosettes which had died before 1979 could be distinguished and disregarded.

Measurements of growth and reproduction were initiated in May 1977 for 16 permanently marked populations of *S. keniodendron* located throughout the species' range on Mt. Kenya. Each population had 60 adult plants. Number of newly expanded leaves was recorded for each plant every 4–6 weeks through August 1981. Newly expanded leaves were marked with ink; leaf size was recorded periodically; sample leaves from unmarked plants at the same elevation were measured, dried at 105°C and weighed to permit conversion from leaf size to leaf dry weight for study plants. Flower stalk size was recorded for every marked reproductive plant. Number of achenes per stalk and stalk dry weight were measured for five unmarked plants near each study population. Achenes were counted after they had expanded to nearly full size; there was a clear dichotomy between expanded and aborted achenes – the latter were small, shrivelled and lacked endosperm. Counts were made before achenes were fully mature to avoid underestimates of achene number due to dispersal. Each achene has one seed, so subsequent discussion will refer to seeds rather than to achenes. Germination tests were initiated in the field, but were accidentally destroyed.

Data on leaf production are presented for the period of 14 May 1977 to 4 August 1978 (434 days); transition to reproductive growth first became evident in August 1978. Growth data are presented for one representative population – a north-facing slope site at 4,200 m in Teleki Valley, located near the transects used for estimates for mortality. A complete analysis of the study plots will be presented elsewhere.

Results

Results are presented in Tables 1–3. Stalk dry weight was correlated both with rosette diameter, measured before reproduction began (Table 2c), and with total dry weight of leaves produced per rosette during 16 months preceding

Table 1. Leaf dry matter production for plants on a north-facing slope at 4,200 m. Means are followed by standard errors; n = sample size; df = degrees of freedom; F = F value from ANOVA; P = probability

a)	Mean annual leaf production per rosette = $1,154 \pm 81 \text{ g yr}^{-1}$, $n = 60$
b)	Total leaf production per rosette, May 1977 to August 1978 for: rosettes that flowered in 1979 = $1,955 \pm 123 \text{ g}$ rosettes that remained vegetative = $1,048 \pm 98 \text{ g}$ $F = 33.65$, $df = 64$, $P < 0.001$
c)	Total leaf production per rosette, May 1977 to August 1978 for: branched plants = $1,951 \pm 220 \text{ g}$ unbranched plants = $1,298 \pm 90 \text{ g}$ $F = 10.57$; $df = 62$, $P < 0.005$

Table 2. Reproduction for plants on a north-facing slope at 4,200 m. r = correlation coefficient; other symbols as in Table 1

a)	Number of seeds per stalk = $459,850 \pm 78,122$, $n = 5$
b)	Mean dry weight per stalk = $1,850 \pm 94 \text{ g}$, $n = 5$
c)	Stalk dry weight (y) vs. rosette diameter (x): $y = 1.26 \cdot 10^{-5} x^{3.94}$, $r = 0.972$, $n = 5$, $P < 0.01$
d)	Estimated stalk dry weight (y) vs. prereproductive leaf production per rosette (x): $y = 900 + 0.04 x$, $r = 0.521$, $n = 32$, $P < 0.01$
e)	Number of seeds per stalk (y) vs. stalk dry weight (x): $y = 172,818 + 174 x$, $r = 0.936$, $n = 5$, $P < 0.01$
f)	Estimated number of seeds per reproductive rosette for: branched plants = $449,800 \pm 20,500$ unbranched plants = $550,100 \pm 32,300$ $F = 10.78$, $df = 36$, $P < 0.001$
g)	Total estimated number of seeds per reproductive plant for: unbranched (single rosette) plants = $550,100 \pm 32,200$ branched (multiple rosette) plants = $861,700 \pm 121,100$ $F = 4.36$, $df = 30$, $P < 0.05$

reproduction (Table 2d). Stalk dry weight was closely correlated with estimated number of seeds per stalk (Table 2e). Knowledge of rosette size or rosette growth rate therefore permits prediction of fecundity (cf. Werner 1975).

Fast growing rosettes were more likely to reproduce than slow-growing rosettes in the study population (Table 1b). Plant height did not differ significantly between vegetative and reproductive rosettes ($229 \pm 15 \text{ cm}$ versus $246 \pm 20 \text{ cm}$, $df = 64$, $F = 0.43$, not significant). Seven marked plants had both vegetative and reproductive rosettes in 1979. Leaf production per rosette between May 1977 and August 1978 was $1,558 \pm 148 \text{ g dw}$ for rosettes that flowered in 1979, and $1,060 \pm 112 \text{ g dw}$ for rosettes on the same plants that remained vegetative ($df = 12$, $F = 7.14$, $P < 0.025$).

Leaf production per rosette between May 1977 and August 1978 was lower for branched plants than for unbranched plants (Table 1c). Branched plants had an average of 2.6 ± 0.8 rosettes per plant. Estimated number of seeds produced per reproductive rosette (based on stalk size) was lower for branched plants than for unbranched plants (Table 2f). However, branched plants which repro-

Table 3. A For plants with two rosettes, the number of plants in which 0, 1, or 2 rosettes flowered; **B** similar analysis for plants with three rosettes; **C** For plants with two rosettes, the number of plants in which 0, 1, or 2 rosettes died; **D** similar analysis for plants with 3 rosettes. Classes were pooled in C and D to eliminate small expected values

(A) # Reproductive	2	1	0		
Actual number	12	12	30	$X^2 = 13.50, P < 0.005$	
Expected	6.0	24.0	24.0		
(B) # Reproductive	3	2	1	0	
Actual number	18	4	15	27	$X^2 = 116.35, P < 0.005$
Expected	2.7	18.4	27.6	13.8	
(C) # Dead	0 or 2	1			
Actual number	16	3			$X^2 = 0.54, P > 0.40, N.S.$
Expected	14.6	4.4			
(D) # Dead	0 or 3	1 or 2			
Actual number	8	7			$X^2 = 0.15, P > 0.90, N.S.$
Expected	8.8	6.2			

duced had an average of 1.9 ± 0.2 reproductive rosettes per plant. Consequently, total estimated number of seeds per reproductive plant was greater for branched than for single-rosette plants (Table 2g). Multiple rosette plants are produced only as a result of branching following reproduction. Plants which reproduce at time 1 and survive to reproduce at time 2 therefore produce more seeds at time 2 than do plants of the same height which did not flower earlier.

For plants on the Teleki Valley floor surveyed in March 1980, 4% of all vegetative rosettes and 17% of all reproductive rosettes died after January 1979 ($X^2 = 38.7, P < 0.001, n = 691$). For entire plants, 3% of all nonreproductive individuals and 18% of all reproductive individuals died in this period ($X^2 = 11.8, P < 0.001, n = 471$).

Sixty-five % of unbranched plants reproduced in 1979, while only 40% of the branched plants reproduced ($X^2 = 238, n = 238, P < 0.001$). Analysis is for plants between 1.5 m and 2.5 m tall only, because less than 5% of plants under 1.5 m tall were branched, and less than 5% of plants over 2.5 m tall were unbranched. Thus, a given reproductive episode, with associated branching, reduces the probability of subsequent reproduction. This result is consistent with the observations, above, that vegetative growth rate per rosette is lower for branched than for unbranched plants, and that slow growing rosettes are less likely to reproduce than fast growing rosettes.

On plants over 1.5 m tall with two or three rosettes, all rosettes were reproductive or all were vegetative significantly more often than expected by chance (Table 3a and b), suggesting that flowering tends to be an all-or-nothing response. However, for these same plants, the numbers of living and dead rosettes per individual approximated a binomial distribution (Table 3c and d), suggesting that rosette mortality is generally not an all-or-nothing response.

Discussion

The high fecundities recorded for *S. keniodendron* are not unusual for higher plants (Harper 1977), especially for species which have high seed and/or seedling mortality, and which reproduce only once or a very few times during their lifespan. Survivorship of *S. keniodendron* seedlings is very low except in occasional moist, protected microsites (Smith, ms. in preparation, cf. Smith 1980, 1981). For example, on the level valley floor used for surveys of adult mortality, the average density of cotyledon stage seedlings of *S. keniodendron* in 12 permanent 25 cm by 25 cm plots was 15.6 ± 3.2 (equivalent to 250 seedlings per m^2) on 16 January 1980. When resurveyed on 16 February 1981, after portions of two dry seasons, there were no seedlings remaining. Successful establishment of offspring seems to depend on production of abundant, wind dispersed achenes in order to increase the probability of encountering favorable sites. Intensive studies during future flowering years will deal with the relationships between seed production, viability, dormancy and seedling recruitment.

Only one other study has dealt with leaf production in *Senecio keniodendron*. Beck et al. (1980) estimated leaf production rates for five prereproductive plants between 0.5 m and 1.3 m tall in the Teleki Valley, within one km of our study site, during a single 6 week period (28 March to 8 May 1979). Extrapolating from this period, they calculated annual leaf production per plant of $369 \pm 59 \text{ g yr}^{-1}$, far lower than our figure of $1,154 \pm 81 \text{ g yr}^{-1}$. There are two reasons for this discrepancy. First, the size distribution of plants in our sample of 60 individuals reflects the pre-dominance of large adults in this region; only 8 of our plants were 1.3 m or less tall, Beck's upper size limit. Continuous leaf expansion data from 14 May 1977 to 4 August 1978 for these 8 short plants in our study yield an average annual rate of $577 \pm 160 \text{ g yr}^{-1}$, much closer to that obtained by Beck et al. A second problem with their annual estimate is that only $1/4$ of their 6 week sampling period was rainy, while in general, rainy weather on Mt. Kenya occurs during at least $3/4$ of the year (Smith and Young, unpublished data). Thus, lower dry season growth rates are over-represented in their estimate of annual productivity. One of our consecutive sampling intervals (2 March to 3 May 1979) is roughly comparable to Beck's study period of 28 March to 8 May 1979. Applying their method of calculating annual leaf production to our data for 8 short plants during this period, we obtain a rate of $486 \pm 119 \text{ g yr}^{-1}$, an even closer approximation to their estimate.

The data presented in Tables 1–3 imply that *S. keniodendron* plants are resource-limited, and that high allocation of resources to reproduction results in decreased allocation to vegetative growth and maintenance, increasing the risk of mortality. Production of multiple rosettes on a given plant following reproduction apparently is not associated with proportional increase in resource base, because per rosette rates of growth and reproduction are lower for multiple-rosette plants than for single-rosette plants. The stimulus for flowering appears to be systemic in nature, with all or none of the rosettes on a multi-rosette plant flowering more often than expected by chance. However, rosette mortality appears to be a more individualistic response, perhaps resulting in part from competition for resources among interconnected rosettes (White 1979). There are three possible

Table 4. The impact of current reproduction on expected future reproduction, for two cohorts of equal age, each with initial n of 100 individuals. Calculations are based on values of mortality, flowering and seed production given in the tables and text. Mortality in intervening non-mast years is assumed to be equal for vegetative and surviving reproductive plants, and so is ignored. AEF = average expected fecundity in mast year # 2 for each of the original 100 individuals

A		B
100 Individuals All reproduce	Mast year # 1	100 Individuals No reproduction
↓		↓
18 Deaths		3 Deaths
↓		↓
82 Individuals 33 Reproduce	Mast year # 2	97 Individuals 63 reproduce
↓		↓
28, 436, 760 Total seeds in mast year 2 (AEF = 284,400 Seeds)		34, 653, 780 Total seeds in mast year 2 (AEF = 346,500 Seeds)

causes of post-reproductive rosette mortality that are not related to resource limitation: new lateral rosettes produced after reproduction are initially much smaller and therefore less buffered against rapid diurnal freeze-thaw cycles than are established rosettes (cf. Smith 1974); rock hyrax (*Procapra johnstoni*) frequently feed on inflorescences, and often damage new lateral rosettes in the process, although hyrax-related mortality has not yet been documented; terminal inflorescences can be 2 m tall, and appear to increase susceptibility of plants to windthrow, but this appears to be a minor source of mortality.

It is not immediately clear from the data presented above whether a current reproductive episode will, on the average, increase or decrease the average expected seed production per individual during the next mast year: reproduction increases a plant's potential future fecundity because post-reproductive branching results in more rosettes per plant, each of which can flower if the plant survives. However, this same reproductive episode both increases the risk of post-reproductive mortality, and decreases the probability of future reproduction among survivors. In order to provide some insight into how these three factors might interact to determine average expected fecundity during the next reproductive episode, we provide a simple hypothetical example: two cohorts each have 100 individuals; those in cohort A all reproduce during mast year number 1, while those in cohort B, although mature by mast year 1, delay reproduction until the second mast year (Table 4). This example suggests that, with respect only to expected fecundity per individual in a future mast year, the benefits of having reproduced in the past are, on the average, outweighed by the costs of past reproductions: for each of the initial 100 individuals in cohort A, average expected fecundity in mast year # 2 is 284,400 seeds, compared with 346,500 seeds in cohort B. We cannot yet estimate the effect of delayed reproduction on longevity and total number of reproductive episodes, and so cannot calculate total potential lifetime seed production for cohorts A and B.

There are two extrinsic factors which might favor delayed reproduction in *S. keniodendron*. First, destruction of inflorescences by hyrax is more common on short than on tall plants. In Teleki Valley at 4,200 m, mean height of 30 plants with hyrax-damaged inflorescences was 174 ± 7.0 cm; mean height of the 30 nearest undamaged reproductive plants was 274 ± 23.2 cm. Typically, 50% to 100% of the flowers were eaten on damaged plants. Plants which delay reproduction until they are older, and thus taller, may therefore have greater effective fecundity. A second factor is that minimum nighttime temperature at 3 m above the ground can be as much as 3.8° C warmer than at ground level (Smith unpublished data, cf. Smith 1979, 1980) so inflorescences on tall plants may be less susceptible to frost damage. Lower branches of flower stalks on short plants occasionally appear wilted after particularly cold nights, suggesting that frost damage may be a significant factor. Stem tissue near the ground is protected from low temperature by thick bark and often by dead leaves retained on the stem (cf. Smith 1979), but flower stalk tissue lacks such protection.

These potential advantages of delayed reproduction must be weighed against both the demographic advantages of beginning reproduction early (Stearns 1976), and at least two potential costs of delayed reproduction. Elephants occasionally leave the montane forests and feed on stands of *S. keniodendron* at the species' lower elevational limit. They kill large numbers of plants over approximately 1 m tall, possibly in order to obtain the protein-rich central pith. This feeding has eliminated most adult plants below approximately 3,800 m in two major valleys (Liki North and Teleki) with less intense damage in other valleys (Mulkey, Smith and Young, ms. in preparation). Greatly delayed reproduction in the face of such periodic herbivore pressure will presumably be selected against. However, elephant feeding may be a recent phenomenon, and in any event affects only a small portion of the total Mt. Kenya population. A second factor is that fires periodically kill large numbers of *S. keniodendron*, especially on the drier northern slopes of the mountain, again near the species' lower elevational limit. Frost and hyrax damage are both less common at these lower elevations, suggesting that selection for delayed reproduction may be reduced here, while selection against it may be greater due to higher incidence of fire and elephant damage. Our estimates of age in these plants are as yet too imprecise to permit comparisons among elevational populations with respect to age of first reproduction.

Cost of reproduction has been measured in terms of mortality and fecundity – currencies relevant to Darwinian fitness. Field studies now in progress will permit more precise estimates of the impact on fitness of variation in reproductive schedules.

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