

Biology of Afroalpine *Dendrosenecio* (Asteraceae)

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Abstract: The genus *Dendrosenecio* (“giant groundsel”), encompassing three species and 12 subspecies, is endemic to the high mountains of East and Central Africa where it constitutes the most conspicuous components of the afroalpine vegetation. Two lifeforms, the arborescent and the prostrate rhizomatous, are regarded as the results of evolution from forest-living woody or herbaceous ancestors. Due to the uninterrupted growth period in the tropics, there are no anatomical or morphological features which allow conventional age determination. However, stem elongation rates have been determined (3–5.5 cm per year) and indicate an age of about 250 years for the tallest arborescent *Dendrosenecios* which may reach a height of 10 m. 30 to 120 large leaves are clustered in an enormous terminal rosette, justifying the term “giant rosette” plants. A leaf bud, consisting of about as many developing leaves as the rosette contains, is found in the center. During the nocturnal frost period the adult rosette leaves form a so-called night-bud by nyctinastic upwards bending and thus protect the leaf bud from freezing by insulation. The stem is surrounded by a mantle of persistent dead leaves; this ameliorates the microclimate of the pith-cells which greatly contribute to water transport into the leaves. Below the leaf rosette a zone of putrefaction is found, from where the decay of the dead leaves apparently provides nutrients directly to the growing stem. The population dynamics of the arborescent *D. keniodendron* is characterized by a simultaneous inflorescence development at irregular intervals of up to more than twenty years. Due to sporadic flowering and a seedling survival rate of less than 1%, oscillations of the population size are to be expected.

Tropical alpine regions of the South American Andes are well known for their unique Páramo vegetation, the equivalent of which is represented by the so-called afroalpine vegetation on the East African high mountains. Plant life of the latter is characterized by several species of conspicuous giant-rosette plants belonging to the genera *Lobelia* (sect. *Rhynchopetalum* (FRES.) BENTH. & HOOK. f.) and *Dendrosenecio* (HAUMAN ex HEDB.) B. NORD. While previous authors have ranked *Dendrosenecio* as

a subgenus of *Senecio*, allied to the herbaceous sectio *Crociserides* (MABBERLEY 1973, 1976), NORDENSTAM (1978) in his new concept of the tribe *Senecioneae* has elevated this group into a genus of its own right.

Dendrosenecios ("giant groundsels") occur in the montane and alpine regions of the equatorial high mountains at elevations between 2 100 m and 4 600 m, however only on those mountains higher than 3 300 m (MABBERLEY 1976). According to a hypothesis put forward by WOOD (1971), former transitional climatic ameliorations could have forced the giant groundsels to higher elevations, from where they have again descended to their present habitats.

A character helpful for an understanding of the phylogeny of this genus is provided by its primitive, so-called "Dendrosenecio-branching" which appears to derive from a candelabriform construction (MABBERLEY 1973). Each stem or branch carries a terminal rosette of leaves, each up to 50 cm long and 20 cm wide which sometimes exceeds 1 m in diameter. A cone-shaped massy bud of folded and firmly appressed developing leaves indicates the center of the rosette and covers the apex of the stem. Upon formation of an inflorescence – which, e.g., in *D. keniodendron* is about 1.5 m long and 15 kg by weight – the terminal bud is consumed. Stem growth then continues by 1 to 8 lateral buds which originate at the base of the inflorescence and thus give rise to the typical *Dendrosenecio* architecture (Fig. 1). Groundsels from lower altitudes have a tendency for ample branching and the development of thin stems, and their leaves are caducous upon senescence. By contrast, species from higher zones tend to hyperpachycauly and pachycauly, producing thick-stemmed trees surrounded by persistent leaves or leaf-bases which finally form a marcescent frill.

As an interpretation of these tendencies, MABBERLEY (1976) suggests that the *Dendrosenecios* are derived from forest-living pachycaul and woody ancestors invading the tropical highlands. Hyperpachycauly and persistence of the marcescent leaves characterizes the evolutionary trait leading to the arborescent species, while becoming prostrate has been the other successful strategy for the colonization of wet places in the alpine regions. On the contrary, NORDENSTAM (1978) regards the extant *Dendrosenecios* as descending from herbaceous, tropical African ancestors. *D. johnstonii*, in his opinion, represents the type coming closest to the early, amply branched forms which might be characterized as forest-living woody herbs.

Regardless of which of these two hypotheses is correct, it should be emphasized that none considers the giant afroalpine groundsels as the primitive woody ancestors of the extant herbaceous Eusenecios.

Taxonomy and Distribution. The subgenus or genus *Dendrosenecio*

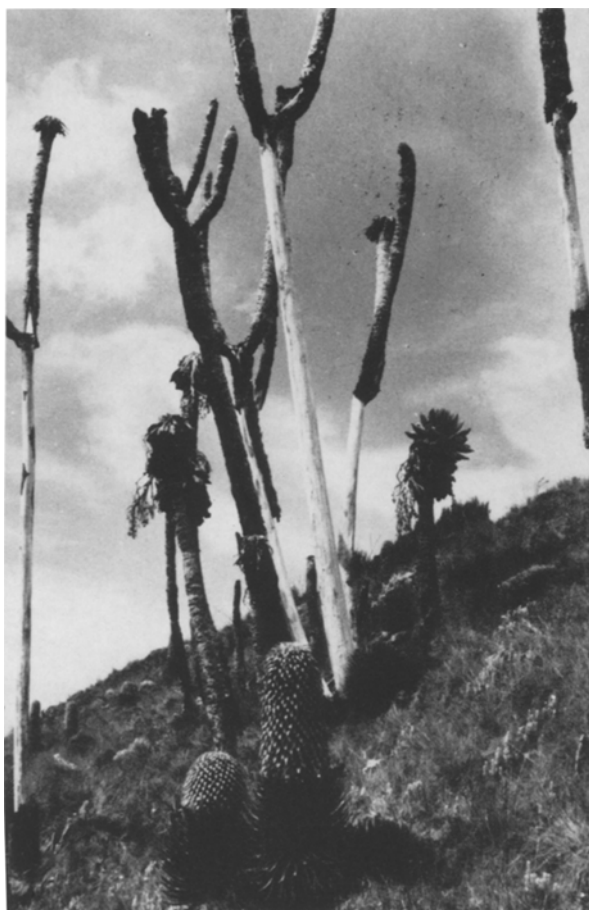


Fig. 1. *Dendrosenecio* branching, as illustrated by the skeletons of *D. johnstonii* subsp. *cottonii* after a fire. Three of the specimens in the background still show leaf rosettes, however only that on the right is yet alive. Note the marcescent inflorescences produced by the specimens which had survived the fire. Mt. Kilimajaro, Shira Needle, 3 750 m (Foto E. BECK, March 1985)

represents a striking example of adaptive radiation; still, according to MABBERLEY (1973) and NORDENSTAM (1978), it encompasses only three species. In contrast to previous treatments (FRIES & FRIES 1922, HEDBERG 1957) the main bulk of differentiation is related to a single variable arborescent species, viz. *D. johnstonii* (OLIV.) B. NORD. The other two species, *D. keniodendron* (R. E. & TH. C. E. FRIES) B. NORD. and *D. brassica* (R. E. & TH. C. E. FRIES) B. NORD., exhibit derived characters with respect to their synflorescences and \pm reduced woody stems.

Obviously, genetic barriers between the various *Dendrosenecio* taxa are low or completely absent, allowing for frequent hybridization (HEDBERG 1957). Polyploidy may have been of considerable importance for the origin of the recent taxonomic pattern. Although sufficient data are not yet available, the chromosome numbers (with respect to the basic number of $x = 10$) suggest various degrees of polyploidy, ranging from $2x$ to $10x$. So far, no correlation between polyploidy and altitude has been established (HEDBERG & HEDBERG 1977).

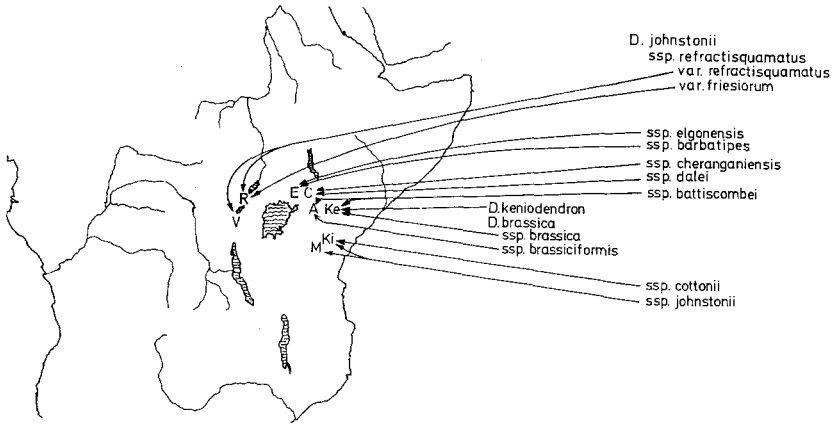


Fig. 2: Taxonomy and distribution of the genus *Dendrosenecio* which is endemic in equatorial East and Central Africa. Taxonomy follows MABBERLEY (1973) and NORDENSTAM (1978). *A* = Aberdare Mountains; *C* = Cherangani Hills; *Ke* = Mt. Kenya; *Ki* = Mt. Kilimanjaro; *M* = Mt. Meru; *R* = Mt. Ruwenzori; *V* = Virunga Volcanoes

The predominantly vicarious distribution of the species and subspecies of *Dendrosenecio* on the high mountains of tropical East Africa is shown in Fig. 2. No stringent evolutionary explanation of this phenomenon has been put forward up to the present.

Determination of Age. Arborescent *Dendrosenecios* eventually can attain a height of up to 10 m (BECK & al. 1983). Due to the rather weakly expressed seasons in the tropical alpine zone, annual rings or other rhythmical anatomical features usable for age determination, lack in these plants. Similarly, counting of stem forks or branching storeys does not provide an appropriate method, because flowering and subsequent branching takes place at irregular intervals of 5 up to 28 years (according to reports by local people). Therefore, other attempts have been made to evaluate stem growth rates and age of arborescent groundsel. HEDBERG

(1969) calculated an average annual stem elongation rate of 2.5 cm from photographs taken from the same specimen of *Dendrosenecio keniodendron* at an interval of 19 years. BECK & al. (1980) estimated a rate of 3 cm from the average annual leaf production and the number of marcescent leaf bases counted per length unit of stem. Both observations refer to juvenile, unbranched specimens. SMITH & YOUNG (1982), however, when investigating adult plants, found considerably higher rates of annual leaf production. Taking advantage of the persistence of the marcescent inflorescences, BECK & al. (1984 a) were able to directly measure length growth of branches which had developed subsequently to a known flowering event. They found an annual stem elongation rate of almost 6 cm subsequent to the first anthesis, while branching after the second or third flowering event resulted in lower rates of stem growth. This decrease of the stem elongation rate with increasing age was interpreted to reflect an enhanced consumption of assimilates by maintenance respiration of the growing non-photosynthesizing stem tissue (BECK & al. 1984 a). Relation of an average growth rate to the size of the giant groundsels indicates an age of about 250 years for the tallest specimens.

Biology of the Leaf Rosette. The leaf rosette of the various *Dendrosenecios* is composed of some 30 to more than 120 adult leaves. In the outermost leaves, senescence is easily recognized from chlorophyll disappearance and the spreading of dark lesions. While the arborescent groundsels of the lower alpine (and forest) zones usually drop their dead leaves, taxa which inhabit higher regions keep them as a dense frill of bract-like appendages around the stem or branch. In *D. keniodendron*, the size of the dead leaf may be less than one tenth of that of the adult one, indicating that other processes than merely drying up and shrivelling may be involved in marcescence. Indeed, a zone of putrefaction is found below the terminal leaf rosette, where the dead leaves stick together as a pulpy mass and from which they finally emerge in shrivelled bract-like form, consisting of little more than cell wall material. It is reasonable to assume that nutrients from the decaying leaves immediately enter the stem again, thus giving rise to a nutrient cycle which skips the soil. This unique internal nutrient turnover provides an explanation for the finding that leaves of aged specimens are as well supplied with nitrogen and phosphorus as those of juvenile plants.

As described above, a cone-shaped leaf bud terminates the rosette on its distal end. In *D. keniodendron*, the young leaves, firmly appressed and closely folded one into the other, grow in the bud until they have approached three quarters of their final size (BECK & al. 1980). At that time they form the outermost layer of the bud. The following developmental steps are greening, unrolling and spreading of the leaves from the cone.



Fig. 3. A colony of the cabbage groundsel (*D. brassica*) in the upper Teleki valley of Mt. Kenya (4200 m). Due to the early morning hour, the specimens in the foreground had just started to open the night-bud, while most of the leaf rosettes in the background are already in the day-position. (Foto E. BECK, February 1985)

Location and size of the leaf-bud may be interpreted in terms of an adaptation to the unique climate: Tropical alpine regions are subjected to a so-called “Frostwechselklima” (TROLL 1943) which has been characterized by HEDBERG (1964) as “Summer every day and winter every night”. At elevations above 4000 m nocturnal frost may regularly occur. This type of a climate, where the diurnal temperature oscillations by far exceed those of the seasons (which are merely characterized by changes in humidity) requires another principle of bud protection than is suitable for plants passing through a prolonged period of suspended growth, i.e., for plants of temperate climatic zones. Upon onset of the nocturnal frost period, the adult leaves of the afroalpine giant rosette plants nyctinastically bend upwards and inwards, giving the whole rosette a globular shape. This so-called night-bud (Fig. 3) provides a more or less sealed and insulated air space around the bud-cone during the night, but rapidly opens upon warming by the first rays of sunshine in the morning. Since BECK & al. (1984 b) have shown that the developing leaves are almost as frost resistant as the adult ones, protection of the leaf-bud from subfreezing temper-



Fig. 4. Flowering giant groundsels (*D. keniodendron*) at 4 150 m altitude on Mt. Kenya (Teleki valley). Some of the trees in the background show the complete mantle of dead leaves around the stems, while the specimen in the foreground has lost the lower parts of these insulating cylinders probably due to the action of animals (e.g., buffalos) or man. The “naked” parts of the stem have produced an extraordinary thick bark (Foto E. BECK, March 1985)

atures in the night-bud may be interpreted rather as a means to prevent nocturnal stand-still of leaf growth due to freezing than to avoid cryo-injury.

Similarly, insulation of the stem by the thick mantle of leaf remnants (Fig. 4) may not be a requirement for frost protection but for the maintenance of water flow through the stem. In the Andean equivalents of the *Dendrosenecios*, the caulescent frailejones (e.g., *Espeletia timotensis*), GOLDSTEIN & MEINZER (1983) have shown that water flow predominantly takes place via the living pith cells and hence would be stopped by frost. This, in turn, must result in an embolus in the leaf vessels when transpiration commences upon rapid thawing and warming of the leaves in the early morning (HEDBERG & HEDBERG 1979).

Thus, adaptation to the afroalpine “Frostwechselklima” requires frost tolerance by the plants. Referring to the leaf bud and the stem tissue this is achieved by mechanisms of freezing avoidance (BECK & al. 1982), while freezing tolerance is practiced by the adult leaves (BECK & al. 1984 b).

Population Dynamics. Whereas the prostrate and rhizomatous cabbage groundsel (*D. brassica*) at Mt. Kenya is capable of producing inflorescences continuously, flowering of the arborescent *Dendrosenecios* appears to take place at irregular intervals and, with respect to certain areas, more or less synchronously. On Mt. Kenya, 1979 was one of the so-called "mast years", when more than 50% of the specimens of *D. keniodendron* produced inflorescences (BECK & al. 1984a). 1974, 1957 and 1929 have been reported as former "mast years" (SMITH & YOUNG 1982) and 1985 was the most recent one (Fig. 4). However, then, the percentage of flowering rosettes was relative low (about 10%).

The flowering event of 1979 was used to obtain some insight into the population dynamics of *D. keniodendron*. SMITH & YOUNG (1982) have counted about half a million achenes per inflorescence, providing an enormous potential for regeneration. According to germination studies, about 18% of the seeds were capable of germination (BECK & al. 1984 a), a figure which correlated fairly well with field studies by SMITH & YOUNG (1982) who found 25 000 seedlings per 100 m² in spring 1980. Despite the relative rare flowering of the giant groundsel, such a yield would still be far beyond that required for an efficient regeneration of the population. However, only between 0.2% and 0.6% of the seedlings survived the subsequent three years, while from 1983 to 1985 their number remained constant. Since the seedlings of *D. keniodendron* are as frost resistant as the adult plants, infra- and interspecific competition, uprooting by soil movement due to frost heaving, and destruction by the considerable populations of mice and other rodents may be regarded as the main reasons for the disappearance of more than 99% of the seedlings during the period of establishment. Because seed production took place again five years later, the regeneration of 1979 can be assumed to guarantee population stability for the next few years. However, due to the irregularity of flowering, constancy of the population size may be rather the exception than the rule.

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