Mountain plants: their survival at high altitude.

Saussurea alpina, Britain.

Alpine saw-wort at left is a plant adapted to mountains of Western Europe, but without insulation against high altitude cold.

Snow-lily at right inhabits Himalayan mountains and has a thick downy insulation around its flower head.

Saussurea medusa, Himalaya,
Credit: B.Bartholomew, Harvard University.

www.alanrwalker.com

Mountain flowers are well studied by botanists and admired by people who visit hills and mountains. After ascending beyond the tree-line you pass rapidly through a series of ecological zones, each with a conspicuous flora characterized by adaptations to life on mountains. Similarly, traverse tundra lands polewards, but for hundreds of kilometres to see these changes.

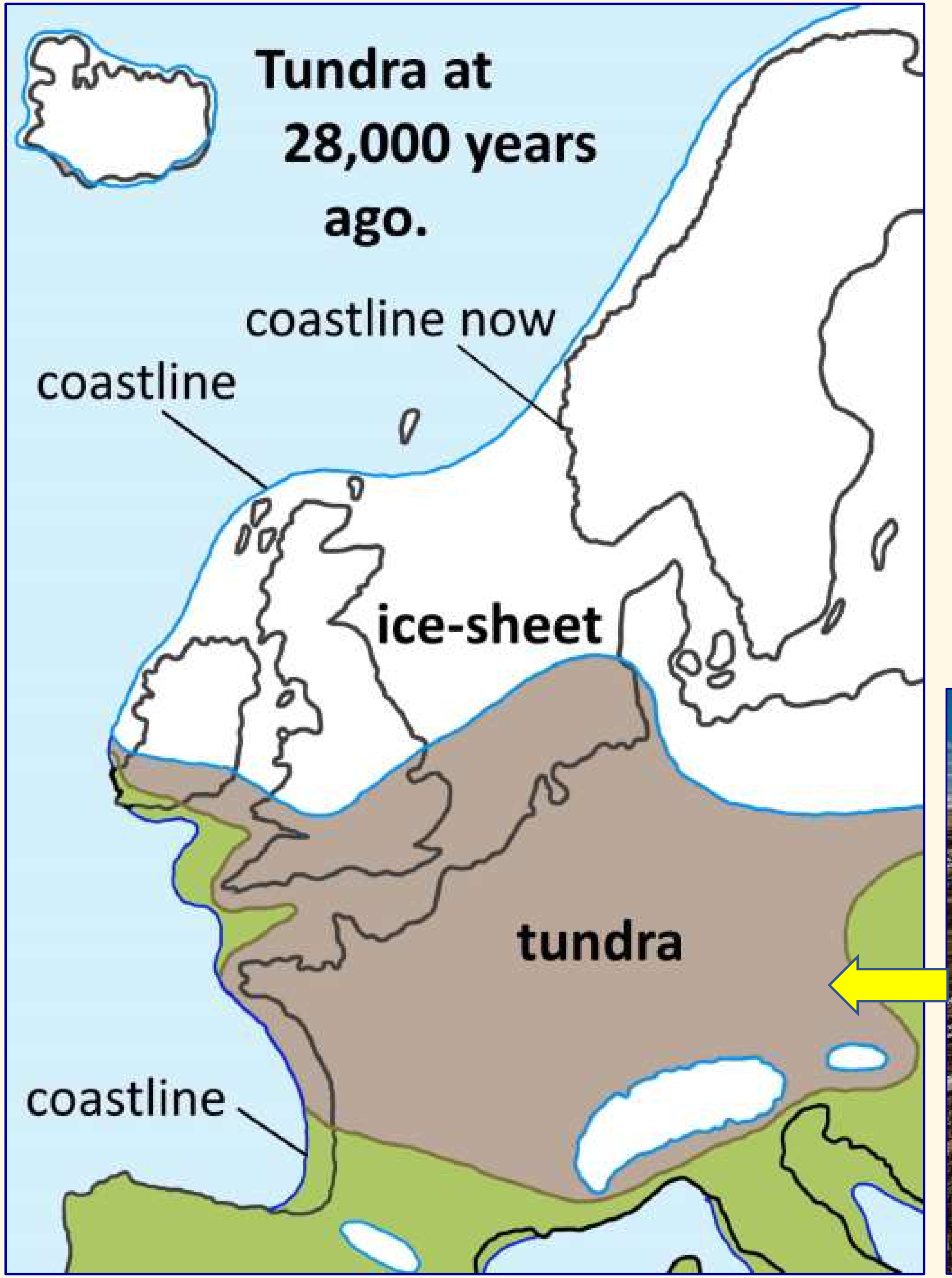
The physical environment of mountains is severe in most characteristics, more so than on lands close to the poles. For every 100 metres of vertical ascent, temperature drops by ~10^{o}C. As air gets thinner with altitude the concentration of the gases essential for plants, carbon dioxide and oxygen, decreases. Despite the drop in air temperature energy from intense sunlight through the thin atmosphere can heat plants excessively. Winds are often fierce in winter and carry crystals of ice that abrade the waterproof cuticle of leaves.

Nevertheless, flowering plants are able to colonize almost all land areas: purple saxifrage, *Saxifraga oppositifolia* is the most northerly vascular plant at Cape Morris Jesup, Greenland, at 80^{o}16′N. Saw-worts, *Saussurea* species, grow at 6000 metres or more in the Himalaya.

Purple saxifrage, *Saxifraga oppositifolia*, of typical prostrate growth form, is adapted to climate and soils of tundra and mountains and is distributed around north polar regions and mountains of Western Europe.

On a mountain rock face in Europe.

On stony ground in a tundra region.



Many montane plants evolved as pioneer species adapted to conditions on tundra.
Ice-sheets retreated leaving vast areas of ground to any plant that could adapt to become fit for this environment. Climate was severe but advantages here included:

* mineral nutrients plentiful.
* little competition from other plants.
* long daylight in summer season.

Tundra-like habitats also developed on isolated mountain tops.

Open ground left by a retreating icesheet in Spitzbergen.

Tundra vegetation in northern Norway.

Mountain top in Britain with tundra-like flora.

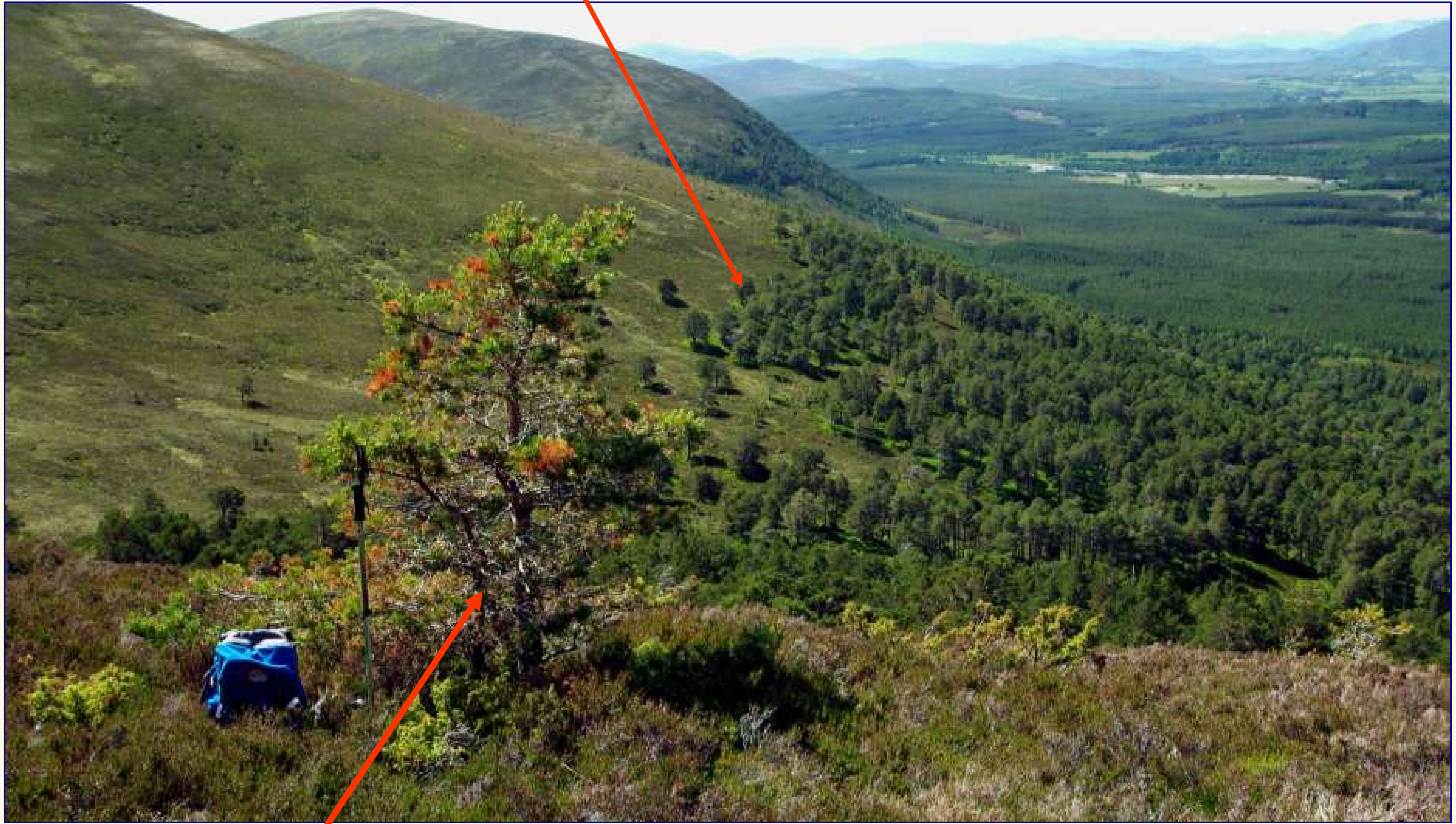
Some plants common high on mountains also thrive along rocky seashores or tundra. Can they be called mountain plants, or montane species? There is no simple answer. Species such as purple saxifrage, and thrift, *Armeria maritima*, are common in both habitats, but a useful definition of montane plants are those that are found above the tree-line rather than below it. The most important criterion for natural distribution is where the plant's population reproduces successfully, not where its seeds might be dispersed.

Trees are a distinct dividing line here simply because they are too tall for life during freezing conditions. Their growth zones of branches and reproductive buds (meristem tissues) are increasingly exposed to low temperature as trees advance uphill. Beyond an altitude with seasonal mean temperature between 5.5^{o} to 7.5^{o}C is the usual limiting level. In contrast to trees, montane plants grow low on the ground – the higher uphill the lower they tend to lie. Close to the ground they live in a sheltered boundary layer of still air.

On high mountains in the tropics there grow some plants of typical lowland genera that have adapted to severe montane conditions as giant forms. They grow above the distinct natural tree-line of typical genera of trees on these mountains.

Natural treeline as a boundary between montane and lowland plants.

Tree-lines on mountains in Britain are at ~500 to 600 metres; determined mainly by inability of trees to grow tall and reproduce where exposed to cold and wind.



Pinus sylvestris, stunted and frost-damaged at 600 metres, reproductively mature but only 1.8m tall.

Exposure to wind is one of the severest hazards for plants at high altitude. This tree-line of a Scots pine forest is characterized by trees stunted to a shape called *flagged*.

This is characteristic of mountains with a distinct prevailing wind direction. Branches facing into the prevailing wind are stunted.

These trees showed no development of cones.

Pinus sylvestris at treeline of same mountain massif as previous slide.

Physical constraints on leafy plants.

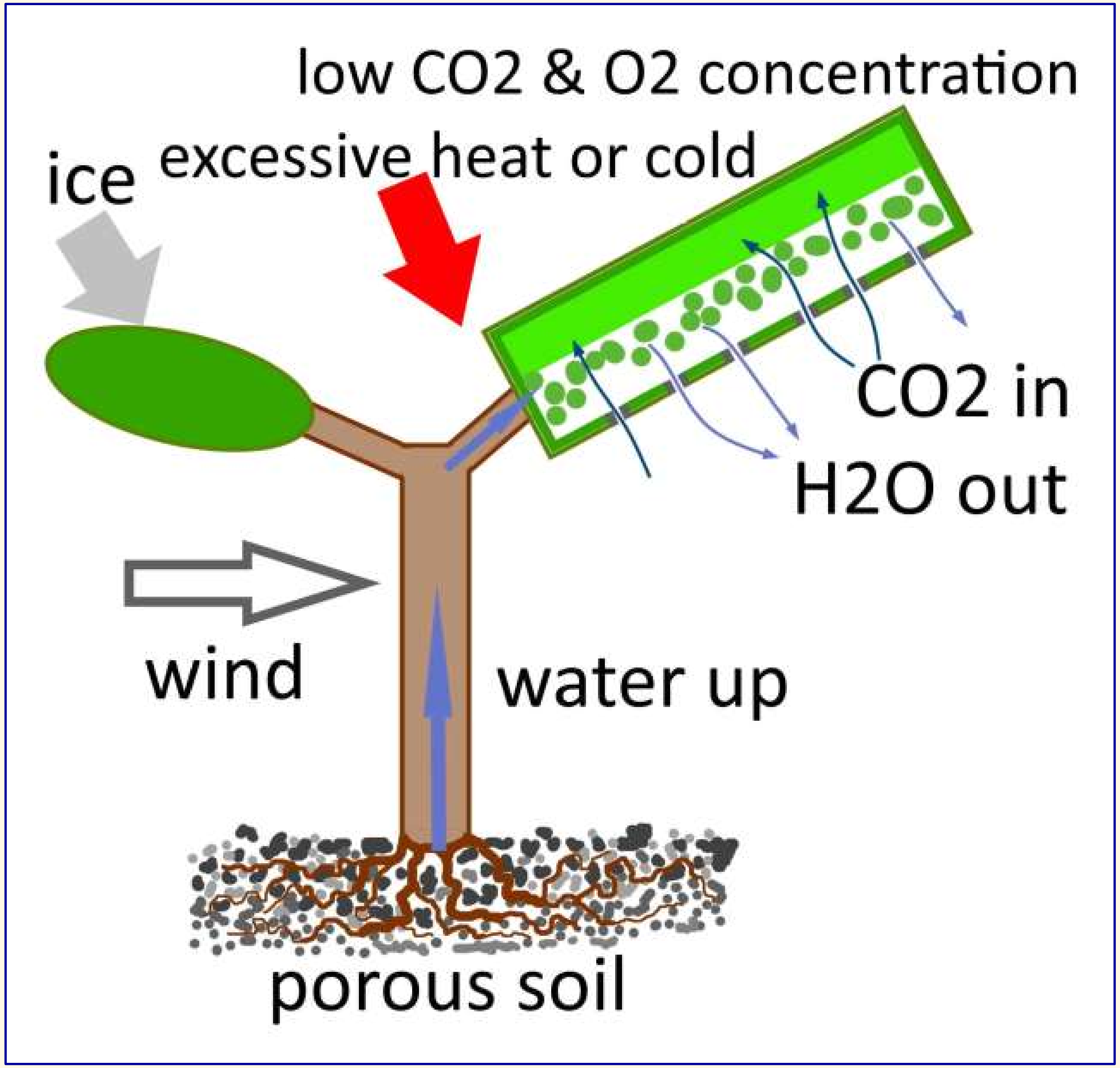
Dehydration is a typical problem for all life on land.

Plants lose water from leaves during respiration for growth and during transpiration for sucking water up

If soil is frozen but air is warm, and light is strong, then leaves may be damaged by dehydration.

Ice crystals blasted by wind erode the waterproofing cuticle of leaves

Also CO2 and O2 concentrations become low at high altitude.



Keys to survival as a plant on a mountain are to be able to withstand wind damage and freezing, to secure sufficient energy as photons of sunlight, the heat energy from sunlight, and to obtain sufficient mineral nutrients.

Adaptations of montane plants are of two types. A particular species of plant will have been adapted by evolutionary selection to have a genetic character of some shape, form, or growth pattern that fits the plant for life on mountains. This adaptation takes many generations to develop and work. An example is the bowl shape of flowers such as *Ranunculus* species that reflect sunlight onto the central reproductive parts to warm and activate the ovaries and nectaries and attract pollinators.

Another adaptation of some montane plants is to have variable growth forms, so that during the lifetime of the plant, as a perennial, it can grow short at high altitude or taller at low altitude. This is a flexible adaptation of growth, not one fixed genetically. An example is goldenrod, *Solidago virgaurea*, growing to 5cm on a mountain top, and other specimens to 50cm near the tree line. Within 10cm above ground high on a mountain there is often a boundary layer of relatively still air. Here during daytime the temperature can be up to 10^{o}C warmer than in windy air above.

Genetic adaptation to mountain environment.

Petals of glacier crowfoot are brightly reflective. The structure of the corolla of petals focusses heat energy of sunlight onto stamens, stigmas, and nectaries, attracting pollinators in search of sugars in nectar. Two flies are shown here, as common pollinators.

Glacier crowfoot, *Ranunculus glacialis*. Credit: R. Flogous Faust

Non-genetic adaptation as variable growth form.

Golden rod at **500m** in North Wales

Golden rod at **950m** in Scottish Highlands.

Solidago virgaurea

Montane plants have many types of adaptation to reduce risk of damage or death from freezing. This is a risk to not only plants on mountains at latitudes close the poles, as in Eurasia, North America, southern South America, and Australasia, but also mountains in the tropics.

A plant on a mountainside in the European Alps for example, at sunrise in midsummer might have its roots in soil that has frozen during the night because of radiation of heat energy into the clear mountain air. As the workings of the plant's leaves start in the morning sunshine they are likely to lack liquid water from their roots. The plant will suffer from frost-drought.

The highest mountains of Africa have a varied flora of montane plants that each 24 hours go through wide changes of temperature: -5^{o}C at night to +25^{o}C during daytime. Many of these plants have become adapted to these tropical conditions by becoming like trees (but above the normal tree-line) with stems to 3 metres or more tall, that are thickened and insulated with layers of dead leaves remaining from the apical rosette.

Temperature constraints on montane leafy plants.

Temperature inversion as: cold moist air sinks to leave clear sky above, then strong sunlight on plants in frozen soil leads to:-

frost drought at the higher altitude.

Temperature variation between night and day is large, it can be

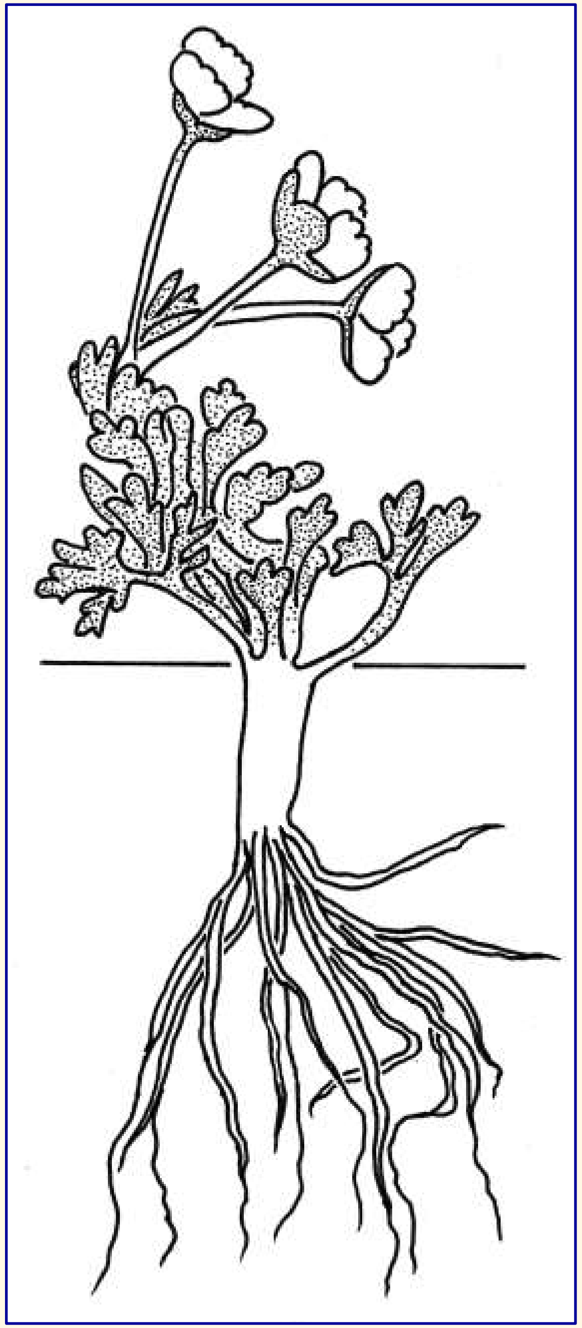
-5’ to +25’C,

and on tropical mountains this diurnal range occurs every day of the year. **(Mount Kenya)**

One adaptation to reduce the risk of such frost-drought is to have a thick main root and a growth form where the base of stem and leaves becomes drawn down below the surface of the soil. This will also aid the plant to grow well despite the effects of freezing water on the soil that causes frost-heave, as long ice-crystals grow vertically in the upper soil overnight.

Some plants have a type of anti-freeze in their tissues, as either a specific addition to their sap and cellular liquids or as a particular condition of these cellular liquids to remain liquid during freezing conditions. This is called super-cooling. Anti-freeze compounds are typically various kinds of sugars, which in solution increase the osmotic potential of the tissue liquids and resist freezing.

However, there are some distinct advantages of life on mountains. Herbivorous animals are often fewer in number and generally cannot reach plants that cling to cliffs. The soils of mountains may be rich in mineral nutrients associated with volcanic rock, or sedimentary rocks that have been finely frost-fractured during winter. Energy from sunlight is more intense at high altitude when the skies are clear of cloud.



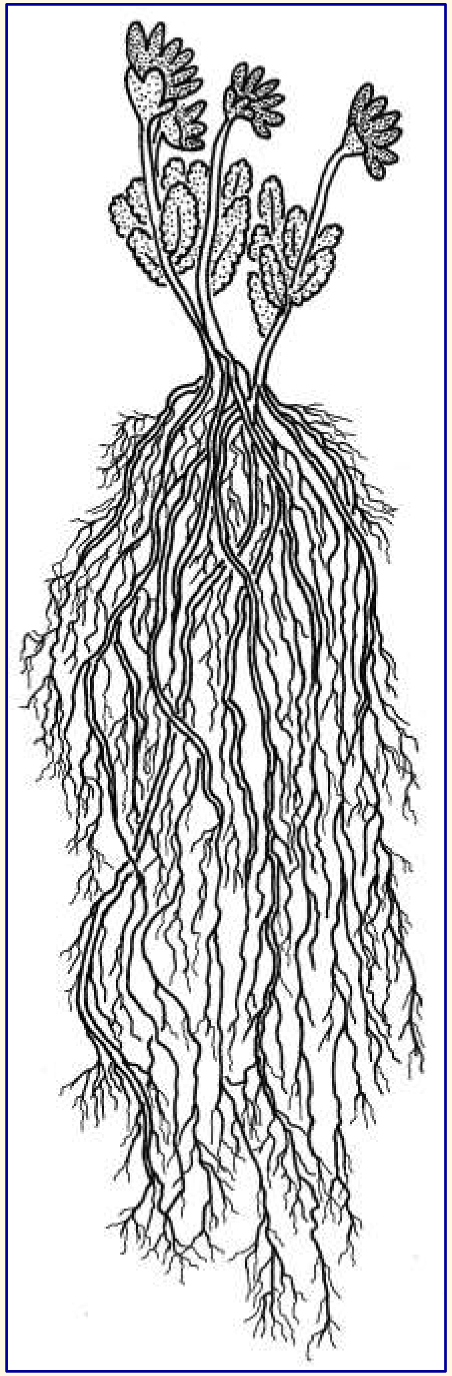
Roots of montane plants may be adapted as stores of nutrients. They may pull down the stem of the plant so that its meristem (growth zone) is below ground level and sheltered from frost. Roots can reach far in search of water and nutrients.

← **Ground level**

LEFT: Glacier crowfoot, *Ranunculus glacialis*.

RIGHT: Sticky primrose, *Primula glutinosa.*

Redrawn from photographs in C. Korner, *Alpine Plant Life*, 2021



Advantages of life on mountains.

Cliff hangers, such as these mountain avens and moss campions, avoid most herbivores.

Frost fracture and glaciers provide mineral nutrients and churn over the soil. Volcanic soils are rich in nutrients. Sunlight is strong.

Developing flower buds are very susceptible to frost damage. The upper (inner) surface of the bracts or sepals may be covered in a dense layer of fine hairs, a downy pubescence. The classic Alpine example of downy insulation is on the bracts of edelweiss, *Leontopodium alpinum.* Similarly, Himalayan snow-lotuses such as *Saussurea medusa* (see first page) have thickly pubescent bracts covering most of the plant except for tops of the minute florets. These florets remain accessible to their bumble-bee pollinators and the down retains heat to warm flower buds and florets.

Pubescence of leaves may also act as insulation for the mechanisms of photosynthesis but the evidence for this is unclear. However, leaves are separately well protected against the potentially damaging effects of ultra-violet light by the cuticle layer on top of the epidermis.

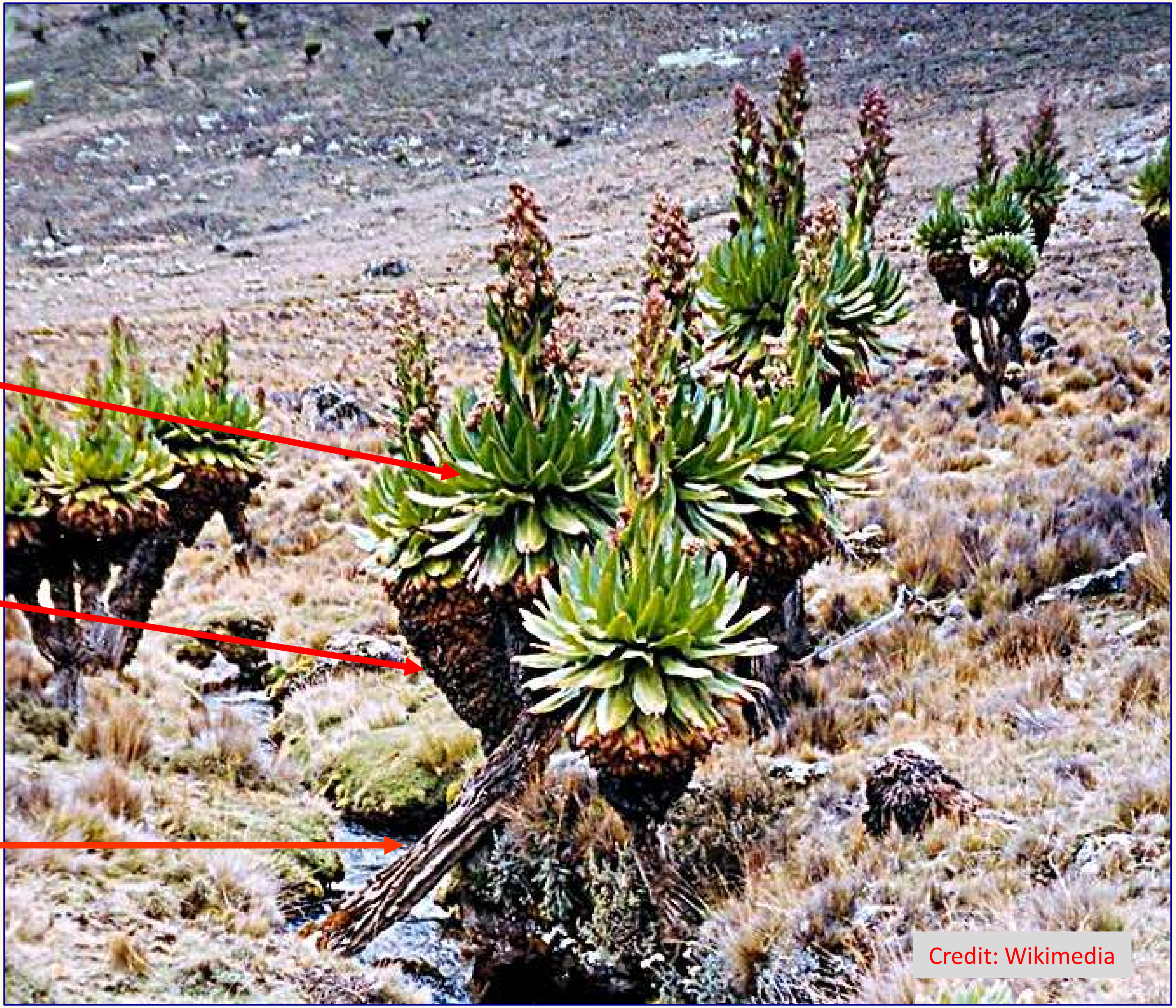
Some montane plants have a mechanism to protect flower buds: the bracts and sepals are able to change their shape during day and night so that they fold up over the bud to insulate it from cold air. The ability to move in this way is called nyctinasty. On the same plants dead leaves may remain on the growing stem as a layer of insulation (called marcrescent insulation) as on the giant senecios of African mountains.

Adaptations of leaves & stems of giant groundsels to protect against night-time frost.

Leaves can fold up over growing bud at night (nyctinastic).

Dead leaves remain on stem (marcrescent).

Thick stems (pachycaul).



Dendrosenecio keniodendron growing at ~ 4000m on Mount Kenya.

Adaptations of leaves with pubescent upper surface?

Left: Common mouse ear, of lower altitudes, slightly hairy.

Right: Alpine mouse ear, of higher altitudes, pubescent.

A function for this pubescence of leaf surfaces is unclear. Also note that the arctic mouse-ear has leaves less hairy than the alpine mouse-ear.

Cerastium fontanum

Cerastium alpinum

Plants that grow in a low form, close to the ground as a cushion form, are typical of adaptations to severe conditions. The moss campion, *Silene acualis*, is a well studied example on mountains in Europe. Leaves of a single plant are small and numerous, forming a dense canopy that grows over many years up to half a metre diameter. In summer the bright red flowers cover the leafy canopy to attract pollinators. Botanists can probe into a cushion to measure its temperature and moisture. During summer in the European Alps, air temperature around a cushion may typically vary from 5^o to 10^oC, whilst temperature within increases as sunlight reaches the canopy, going from 8^o to 23^oC.

Also, within the cushion water is retained and there is an accumulation of general plant debris and blown dust that the roots of the plant can exploit for nutrients.

Another less common example of cushion plant is cyphel, *Minuartia sedoides.* Although the cushion grows to similar size as does moss campion, its flowers are small and greenish. Probably this species relies on smell of nectar to attract pollinators.

Adaptations as the cushion form.

Moss campion, with flowers more conspicuous than the mass of small leaves,

and Cyphel, with small apetalous flowers.

Cushions retain much heat from the sun, and act as a reserve of water. Organic debris collects on and within the cushion, providing nutrients.

Small leaves are typical of many montane plants, either forming the canopy of a cushion, or as a mat of leaves and roots lying low on the ground.

The trailing azalea, *Kalmia procumbens*, a prostrate creeping plant, has compact leaves with an oval cross section and two suture lines on the lower surface where exchange of carbon dioxide, oxygen and water vapour occurs in ways that reduce the risk of dehydration.

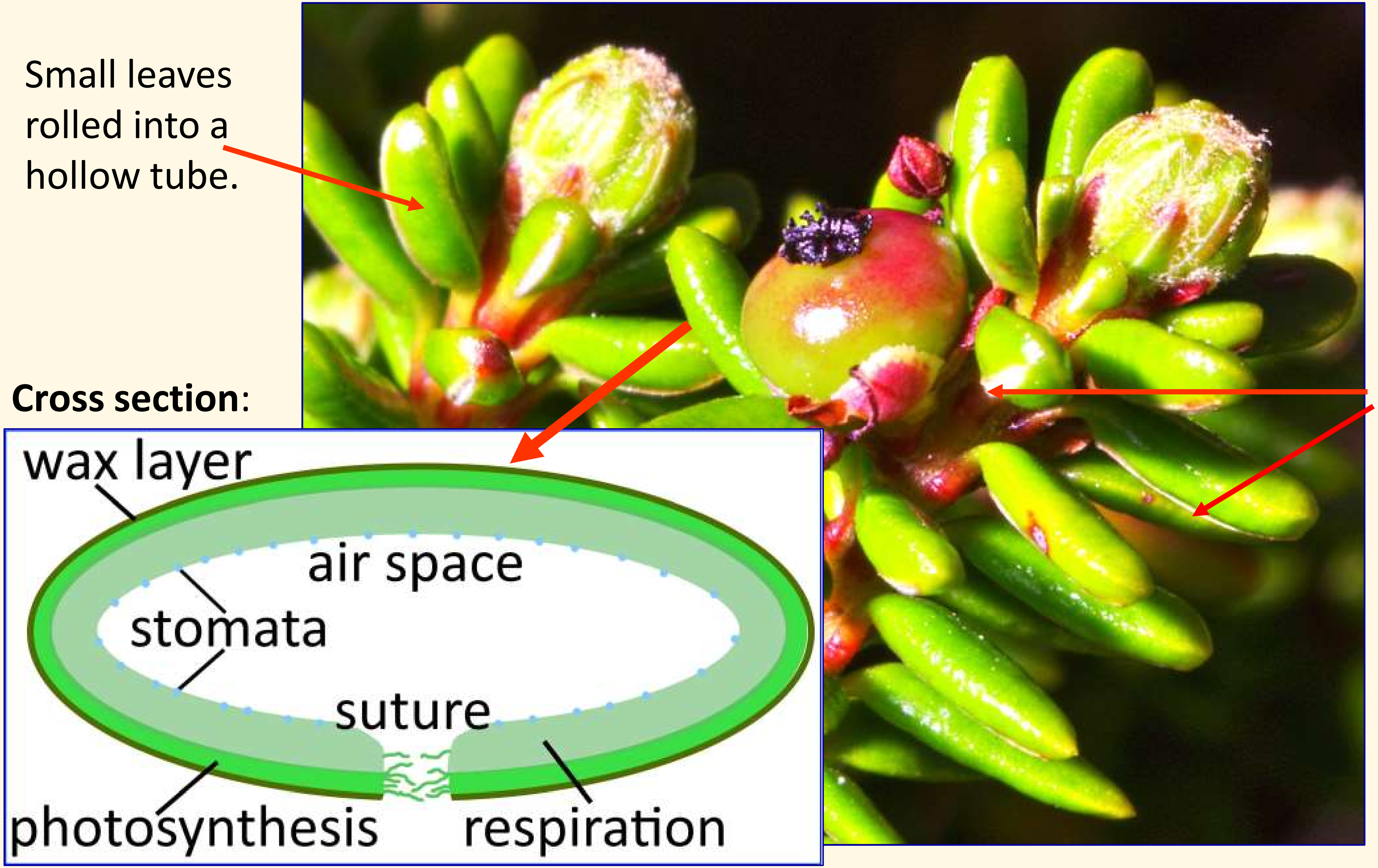
The crowberry, *Empetrum nigrum,* of low bush form, is one of the most widely distributed and conspicuous plants of tundra lands and lower slopes of mountains. Its small leaves are rolled up into a shape like a sausage, with a single suture line. Here is provided access to the stomata of the lower, now inner, surface of the leaf. It is at the stomata that exchange of atmospheric gases occurs. This is controlled by opening or closing of these openings into the central mesophyll region of the leaf where photosynthesis and respiration work.

Trailing azalea, *Kalmia procumbens*, lives on stony ground and rocks, forming low mats of thick rounded leaves that individually are ~5mm long and adapted to reduce water loss during transpiration.

Leaf structure of crowberry, *Empetrum nigrum*, to control transpiration.

Small leaves rolled into a hollow tube.

Cross section:



Suture lines.

Most montane plants are perennials, producing a new cohort of flowers and seeds each year, and often spreading as mats with woody stems over a cliff face or gravelly ground such as purple saxifrage, *Saxifraga oppositifolia*.

Some montane plants are annuals, such as alpine gentian, *Gentiana nivalis*, but are there are few montane species of this seasonal growth pattern (or phenology).

The constraints acting on a montane plant to flower and produce seed are strong. From flower bud-burst to dispersal of seed there may be only 60 days summer warmth for completion. One adaptation to lessen this constraint is found in glacier buttercup, *Ranunculus glacialis*. This species is adapted to survive under snow: cold but not enough to freeze the plant and protected from wind. The flower buds comprise up to three generations of pre-formed buds, the oldest of which matures rapidly into a flower attracting pollinators shortly after release from snow into sunshine.

Alpine snowbell, *Soldanella alpina,* similarly shelters under late-lying snow beds until summer warmth comes. Some of these plants that survive winter under snow can photosynthesize enough whilst so buried to start their seasonal activity early.

Snow can provide a more sheltered site than bare mountain tops exposed to freezing winds.

Glacier crowfoot at 4000m.

Ranunculus glacialis Credit: Wikimedia

Snowbell at 2000m.

Soldanella alpina

Pollination of montane plants is mostly by insects. Some are pollinated by wind. The splendid displays of brightly coloured flowers on mountainsides in summer are to attract insects, not us. Large flowers, or masses of small ones attract insects from a distance. For these alpine plants to invest so much energy and material into making big floral displays there needs to be a reproductive reward, in a cost to benefit relationship.

The butterflies that are so conspicuous in alpine regions are just one of many different types of insects that fly up mountains in search of nectar as high energy, sugary food.

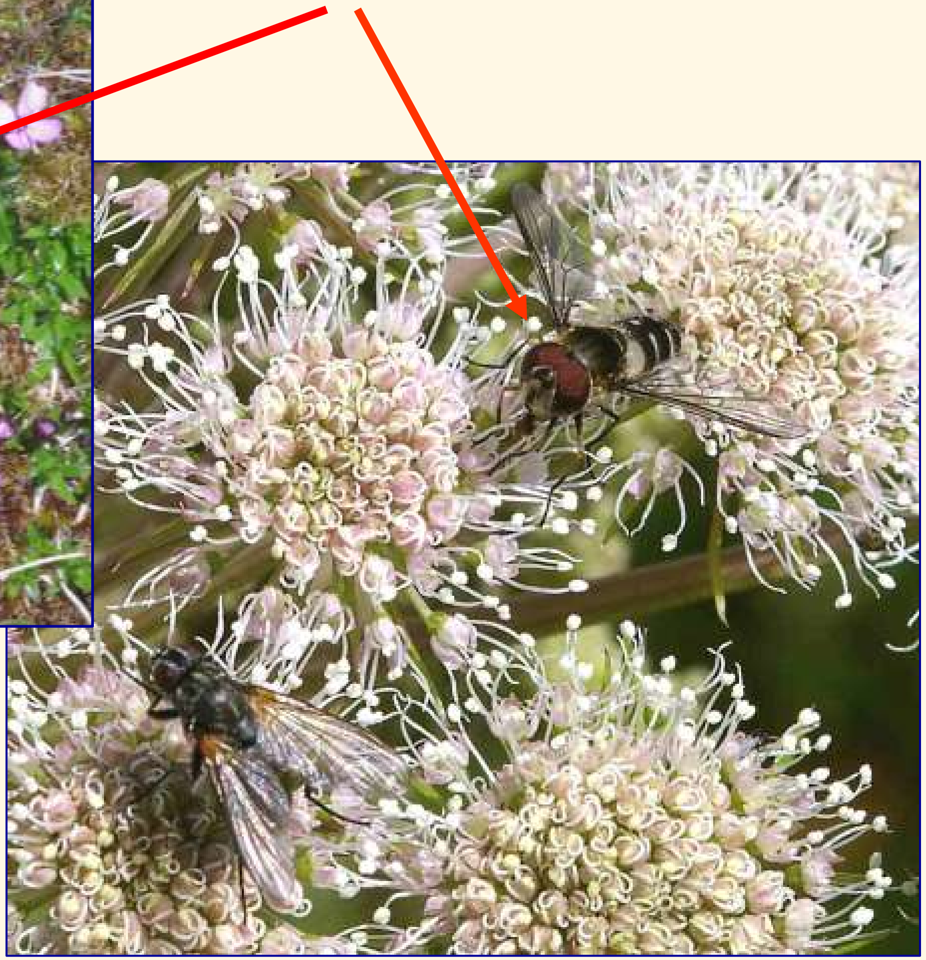
Edelweiss has been recorded as attractive to species of insects that come from as many as 27 families, and of these the commonest are two-winged flies, the dipterans of the house-fly, mosquito and midge type. The males of most species of blood-sucking flies feed only on nectar. Bumblebees are common here, and beetles can often be found crawling over the surface of inflorescences in search of nectar.

Adaptations of flowers to attract pollinators: butterflies, moths, flies, bees, beetles . . .

The energy cost of large flowers is balanced by genetic benefit of sexual reproduction.

Alpenrose

Moss campion



Angelica

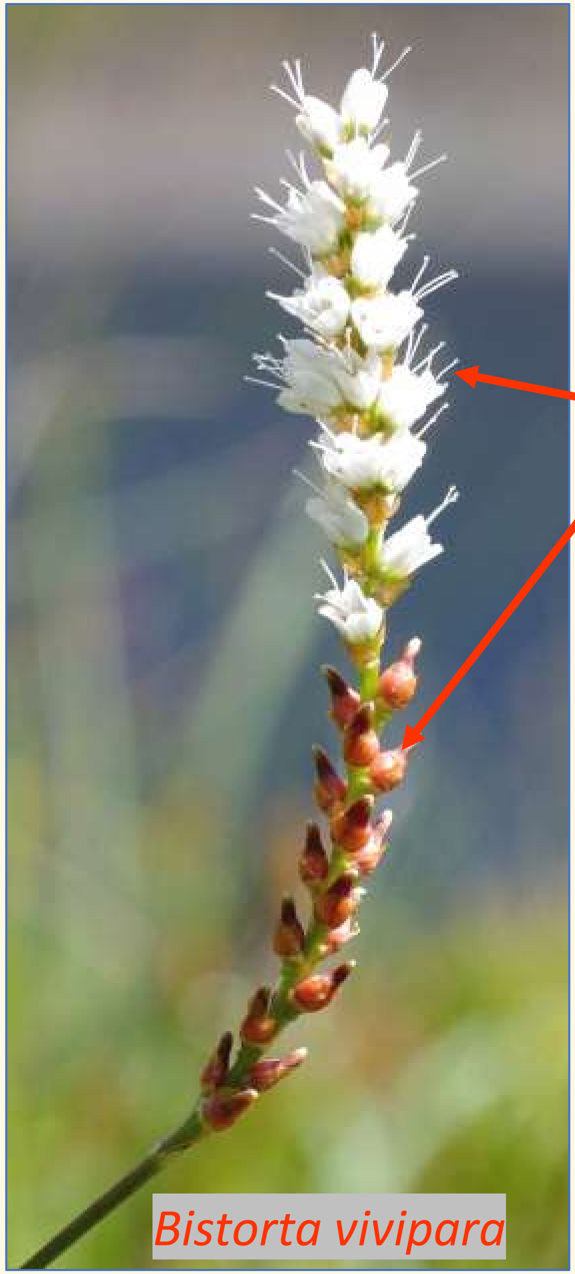
Pollination is fundamental for sexual reproduction and this form of producing offspring is crucial for species of plants and animals to maintain advantages of high genetic diversity. However, sexual reproduction is complex and risky for plants. There are other ways for a species to maintain local populations, known collectively as asexual reproduction.

Alpine bistort is an example of a montane species that is simultaneously sexual with ordinary flows, and with a budding process. They have small flowers at the top of the single stem, and simple bulbils lower down. Mature bulbils detach and take root in the ground.

Vegetative spread is a way of maintaining a vigorous population that remains ready to reproduce sexually when conditions are good. Cloudberry is an example.

Crowberry has tiny flowers that are wind pollinated. Most populations of this species have just one sex on each individual plant (dioecious character). Populations in more severe sites may have bisexual individual plants. Each has flowers with both anthers producing pollen and receptive stigmas that will provide the route for pollen to the ovaries for fertilization. Both ways of fertilization produce seeds within black berries that birds will eat and so disperse this species widely.

Reproduction on mountains may be difficult: manage without sex.



Bistorta vivipara

Alpine bistort with flowers and bulbils.

Cloudberry in Britain is common on uplands, but flowers are uncommon and ripe fruits rare. Vegetative spread seems common.

Rubus chamaemorus

Adaptive flowering strategy.

Crowberry is usually dioecious as shown here with:

* pollination by wind,
* vegetative spread.

But a bisexual sub-species occurs in tundra and montane habitats.

Female plant: tiny petals, no nectar.

Empetrum nigrum

Male plant: prominent anthers.

The definition of the term species is a complex problem for biologists. The most often used definition of species is a population of one type living thing, all of which can freely interbreed to produce fertile offspring adding to that population. This interbreeding in populations living in severe environments may be sufficiently flexible for hybrids between species to form populations that are reproductively self-sustaining.

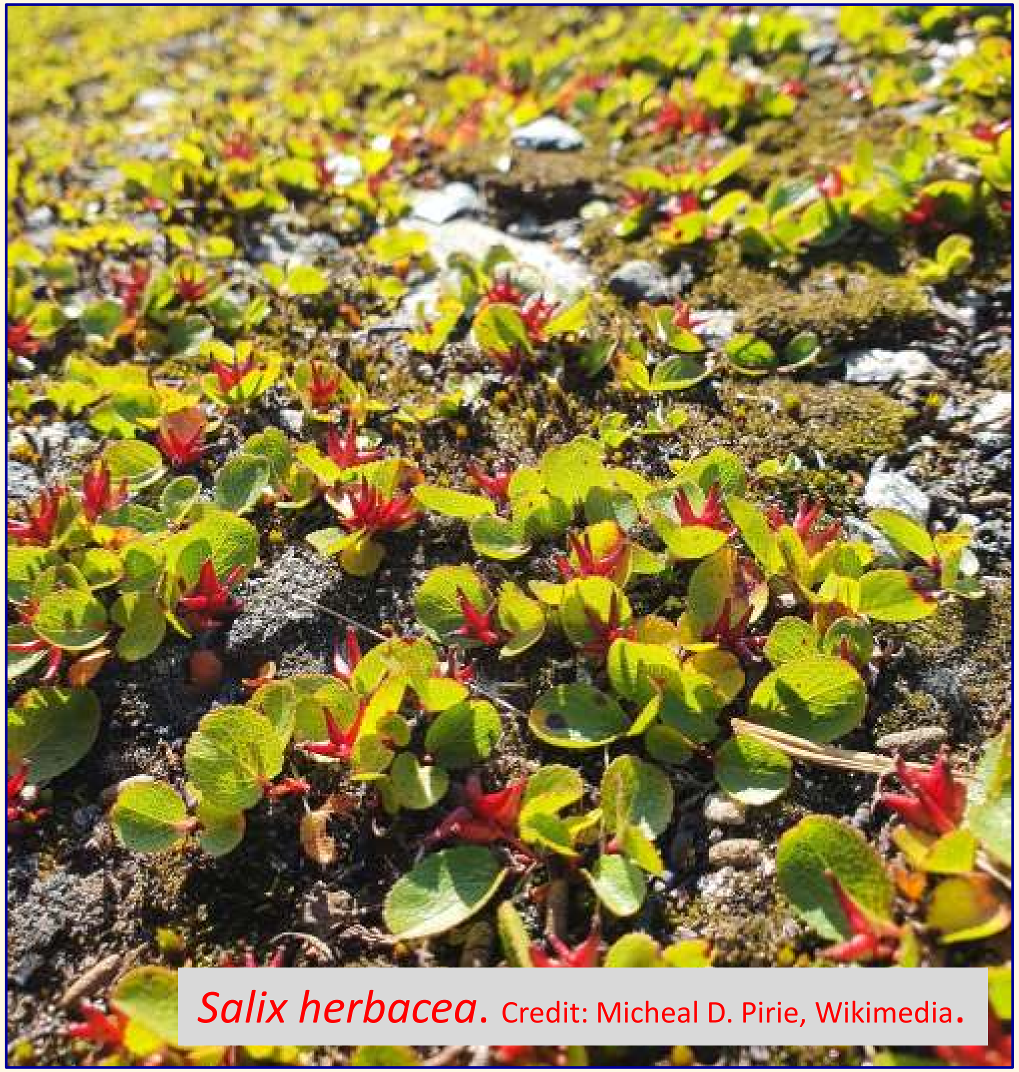
This is found commonly in the species of birches, *Betula*, and willows, *Salix*, that live on tundras and mountains. The silver birch, *Betula pendula*, is not a tree of mountains but the closely similar downy birch *Betula pubescens* is a pioneer species capable of advancing over fairly empty tundras and uplands, if not mountains. These two species readily hybridize to produce fertile offspring. Dwarf birch, *Betula nana*, is a montane species of shrub that grows a few centimetres above ground level to no more than 1 metre high. Downy and dwarf birches form hybrids.

The willows, *Salix* species, are similar, with more species, all difficult to differentiate and many have distinctly montane habit and form. Genetic flexibility seems to be an advantage to these life-forms making a living under severe conditions.

Birch and willow species, of genera *Betula* and *Salix*, are usually trees but some species have evolved as adapted to mountains and tundra, with prostrate forms, creeping stems, and small rounded leaves.

Betula nana. Credit: Kim Hansen, Wikimedia

Dwarf birch



Salix herbacea. Credit: Micheal D. Pirie, Wikimedia.

Least willow

Some montane plants provide good insights into the evolution of new species. Well studied and conspicuous examples are the strange plants found high on the mountains of East Africa, from Kilimanjaro in the east to the Ruwenzori range in the west. People who study them often call these mountains ‘sky-islands’ with isolated flora and fauna of intriguing form and habit.

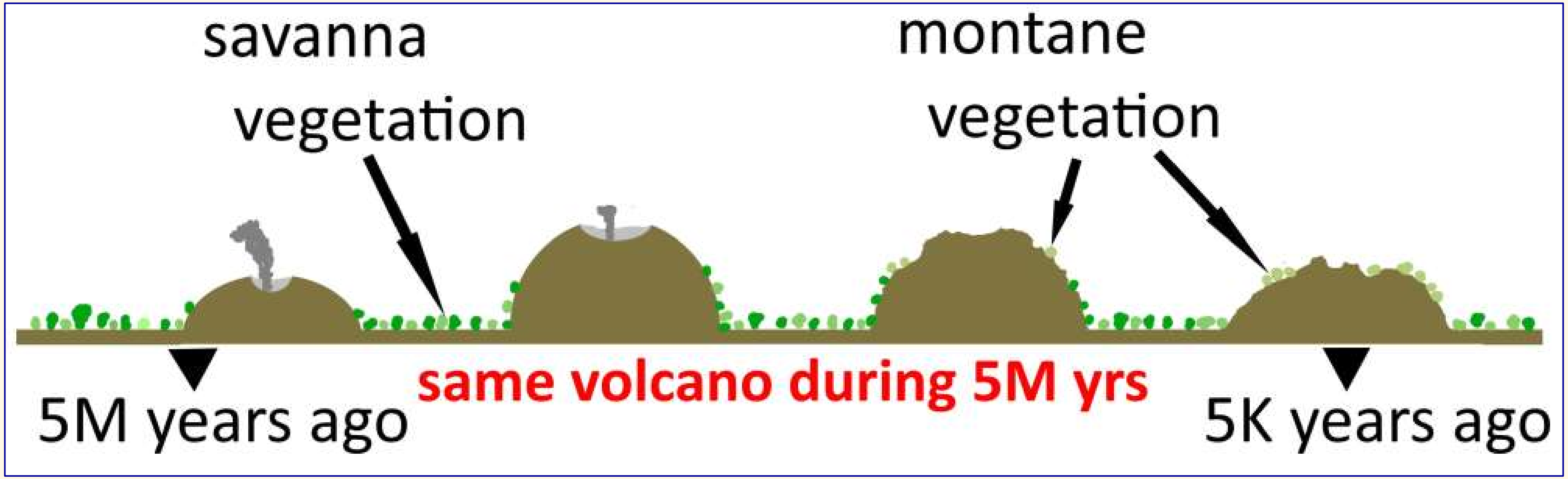
These mountains are of recent origin in geologic time, arising as volcanoes or uplift blocks, associated with tectonic plates of the East African Rift System. High on their slopes grow species of *Senecio,* also *Lobelia,* that evolved here into tree forms rather than the ordinary groundsel plants of lowlands.

Here each individual mountain or range has one or more similar but clearly separate species that are fully endemic to that location. How these populations evolved has long been studied, and now by using modern methods of molecular genetics to compare the floras of many isolated mountains.

Origin of montane giant groundsels within savanna lands.

Some species of ordinary groundsels survived on rising active tropical volcanoes, then adapted variously to montane conditions.

African savanna. Credit: Wikimedia



The distances between these East African mountains are from 310km to 525km. In between there are no species of plant that resembles these tree forms: the natural vegetation is grassy savanna to lowland forest. Evidence now available from detailed genetic studies of these high altitude plants reveals a type of evolution known as geographic (allopatric or vicariant). As the mountains grew taller they lifted up the savanna flora with them. The species that flourished high up there were those that adaptated to the severe climate for plant life high on tropical mountains.

Although average yearly temperature and light are highly favourable, and the soils that developed are rich in mineral nutrients, the daily variation in temperature and the risk of freezing damage is severe. These plants have adaptations that include nyctinastic leaves that fold can fold up each night to insulate the large central inflorescence. The leaves on some species are not shed from the stem as they age so a thick insulating layer of dead leaf is formed, a characteristic called marcresence. Most species have stems thickened with deep bark as insulation, the pachycaul condition.

Origin of montane flora on tropical mountains.

Three volcanos and one mountain range (Ruwenzori) all with similar montane floras but different species. Did they originate from a single source species?

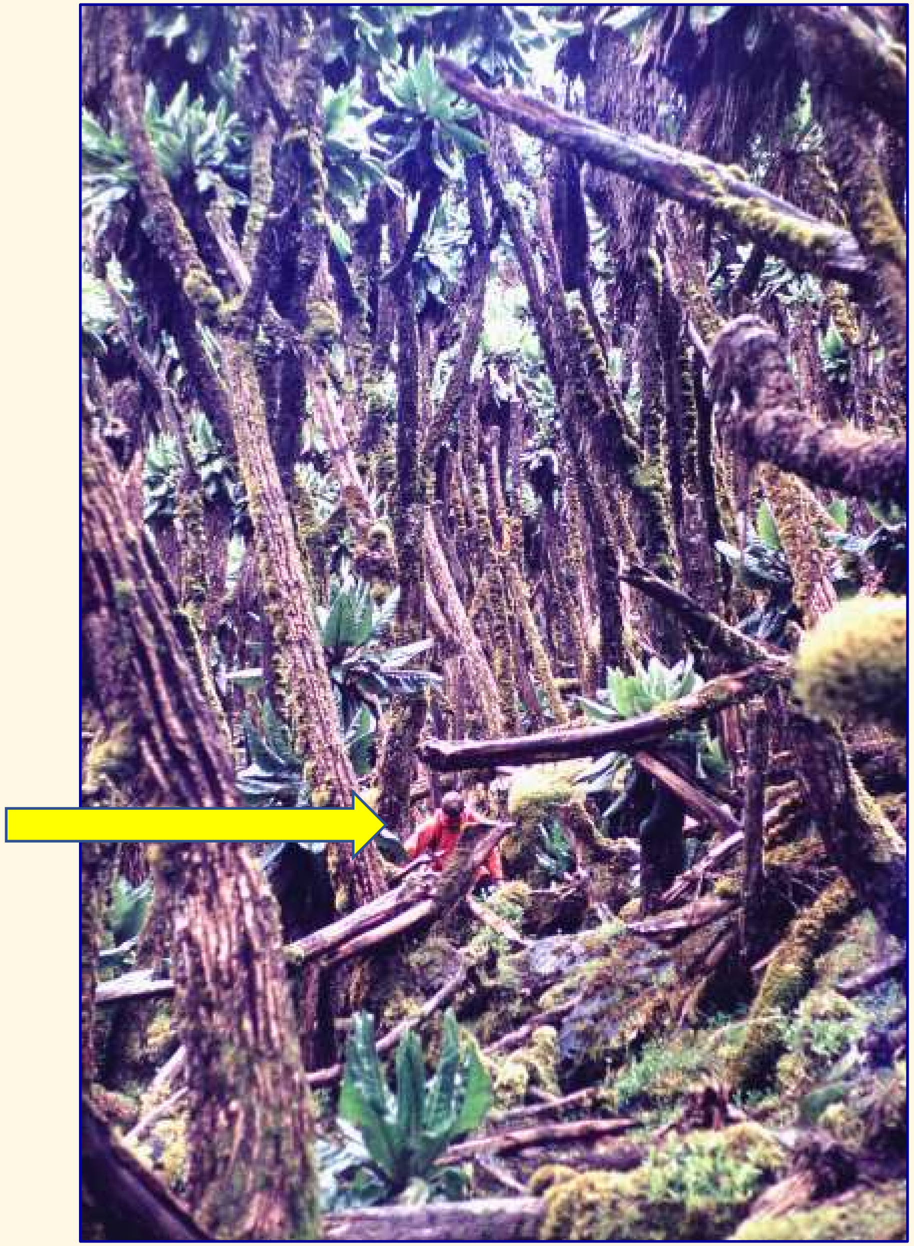
Similar flora of isolated mountains in the tropics.

Giant groundsels (Asteraceae) with major adaptations to montane conditions and also demonstrating convergent evolution between different genera.

Dendrosenecio in Kenya.

Espeletia in Ecuador Credit: Wikimedia

Climates and plant size on these mountains vary greatly.



Ruwenzori, the wet eastern approach route

Kilimanjaro, the dry north east slope access path

Species of giant groundsels on African mountains:

as highly endemic ***Dendrosenecio*** species
(also *Lobelia* species)

Ruwenzori range (**wet**)

Kilimanjaro (**dry**)

Mount Kenya (**moist**)

We live in an ice-age – it will end when the ice-sheet on Greenland melts away. Our climate naturally warms, slowly but now accelerating because of our use of fossil fuels, adding to the natural greenhouse effect. Glaciers on mountains retreat rapidly and the plants of tundra in regions such as Alaska and Siberia migrate polewards.

Here some of the same species we know as mountain plants are able to flourish and advance: mountain avens, *Dryas octopetala*; purple saxifrage; dwarf species of birches and willows.

For those of use who find mountains easier to visit than tundras, an important botanical enquiry is what will happen to our local montane flora. Some of the highest growing species on some lower mountains may run out of space. Populations of lowland species may migrate uphill and occupy ground left vacant by retreating glaciers.

This is an opportunity for botanists, specially in countries with mountains that are easily accessible to their summits and their open lower slopes. Here the montane flora of easily identified species such as purple saxifrage, alpine saxifrage, alpine gentian, also other rarer species, can be monitored in detail to inform conservation policies and methods.

Advance of tree-line and invasive species up-hill as alpine glaciers shrink.

Glacier des Bossons in the French Alps has lost ~ half is volume in last 100 years.

Mont Blanc

Glacier des Bossons

Herbs, shrubs and trees colonizing recently exposed moraines.

Where to live on a mountain in Scotland?

Summit at 1200 metres

850 metres

600 metres

Montane plants grow well on freshly fertile soils at base of cliffs, above the tree-line of ~550 metres.

Alpine saxifrage

Alpine gentian

Trailing azalea

Sibbaldia

Alpine forget-me-not

References:

Chapin, F.S., *et al*., 1994. Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. Ecological Monographs, 64: 149-175.

Coe, M.J., 1967. *The Ecology of the Alpine zone of Mount Kenya*. Dr. W.Junk, Den Haag. ISBN: 9789401178334. [Despite its age this facsimile edition has many important insights into how plants survive at high altitude.]

Crawford, R.M.M., 2008. *Plants at the Margin: ecological limits and climate change*. Cambridge University Press, England, ISBN: 9700521623094. [Most examples from Arctic regions, but most principles apply to montane flora.]

Grace, J., Berninger, F. & Nagy, L., 2002. Impacts of climate change on the tree line. Annals of Botany, 90: 537-544.

Körner, C., 2021. *Alpine Plant Life: functional plant ecology of high mountain ecosystems*. Springer, Berlin, ISBN: 9783030595371. [The single most useful source of information for this article, most examples from Europe.]

Lutz, C., 2012. *Plants in Alpine Regions: cell physiology of adaptation and survival strategies*. Springer, Vienna, ISBN: 9783709101353

Scott, M., 2016. *Mountain Flowers*. Bloomsbury Publishing, London, ISBN: 9781472929822.

Tsukaya, H., Fujikawa, K. & Wu, S.-G., 2002. Thermal insulation and accumulation of heat in the downy inflorescences of *Saussurea medusa* at high elevation in Yunnan, China. Journal of Plant Research, 115: 263-268.

Tusiime, F.M., *et al*., 2020. Afro-alpine flagships revisited: parallel adaptation, inter-mountain admixture and shallow genetic structuring in the giant senecios (*Dendrosenecio*). PLOS One (online: https://doi.org/10.1371/journal.pone.0228979)