Reproductive strategies of alpine plants

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When environmental conditions are difficult or

peculiar, such as in high mountains, plants must adapt to ensure their reproduction. Two main strategies allow alpine plants to persist generation after generation: the maintenance of sexual reproduction or the use of vegetative reproduction. This diversity will be highlighted through several examples of alpine plants that have adapted to their environment.

"Alpine" environments are environments which are found above the natural limit of the forest, in the absence of human intervention, in any part of the world: Alps, Andes Cordillera, Himalayas, New Zealand… These cold environments are often characterized by a very short growing season, with few sites suitable for seed establishment, difficult pollination due to the rarity of insects and violent winds as well as high interannual variability of climatic conditions.

Two main strategies allow alpine plants to persist, generation after generation: maintaining sexual reproduction or the use of vegetative reproduction.

1. Sexual reproduction

Sexual reproduction is a source of genetic diversity that allows animal and plant populations to cope with fluctuations in their environment. In plants, it involves the production of flowers, their pollination, the maturation of seeds and their dissemination and germination, all of which are often hazardous stages in alpine areas. Several strategies can be used to overcome environmental constraints.

1.1. Long life

The Alpine flora has less than 2% of annual alpine plants{ind-text}Plants that complete their life cycle over a year.{end-tooltip} [1] (Figure 1) which depend exclusively on the success of sexual reproduction and therefore on the environment. Even if seeds are produced on time, they require new sites for germination, often limited due to the presence of bedrock (rocky areas, screes) and the presence of other species. On the contrary, perennial species can wait for favourable conditions to reproduce (Figure 2). In contrast, in arid and Mediterranean alpine biotopes{ind-text}Living places with relatively uniform determined physical and chemical characteristics. This environment is home to a set of life forms that make up biocenosis: flora, fauna, micro-organisms. The biotope and the biocenosis it supports form an ecosystem.{end-tooltip}, annual plants are more widespread [2]. The seeds then represent a form of resistance.

Figure 2. Androsace helvetica All., Primulaceae, is an example of a perennial alpine plant living in an environment without annual species, here at 2800 m altitude, in shale rocks of the Galibier Pass. [Photo © Joseph Fourier Alpine Station/Serge Aubert]

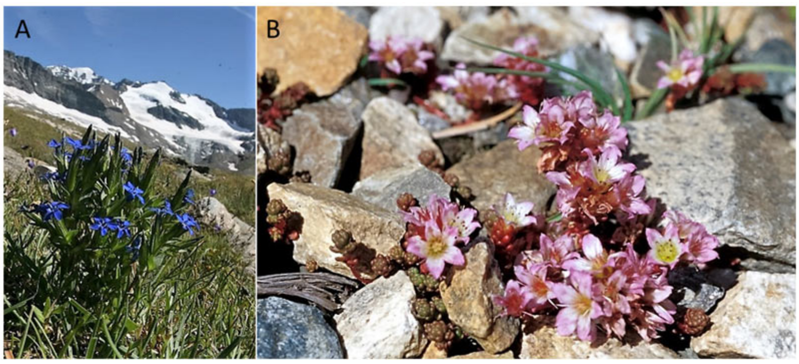

Figure 1. Two examples of annual alpine plants. On the left: the winter gentian (Gentiana nivalis L., Gentianaceae). Right: Mucizonia sedoides DC, a Crassulaceae growing in the snowy valleys of the Pyrenees. [Photos © Joseph Fourier Alpine Station/Serge Aubert]

1.2. Spread reproduction over several years

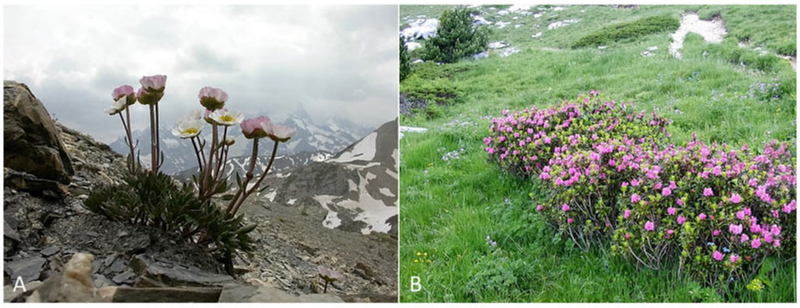

Figure 3. Examples of alpine plants pre-forming their flower buds in advance. Left: Glacier buttercup (Ranunculus glacialis L., Ranunculaceae. [Photo © Joseph Fourier Alpine Station/Serge Aubert); right: alpine rose (Rhododendron ferrugineum L., Ericaceae; Photo © Irène Till-Bottraud)]

Some species spread seed maturation over several years, or preform flowers in the year before flowering. This allows the flowers to bloom as soon as conditions are favourable. This is the case, for example, of the glacier buttercup (Figure 3), a species that breaks altitude records in the Alps (up to more than 4000 m in Switzerland) and the alpine rose (Figure 3), whose large autumn buds contain all the flowers, allowing it to flower as soon as the snow melts.

1.3. Increase flowering time

Figure 4. Chaetanthera pusilla (Asteraceae) an annual plant growing between 2200 and 3500 m above sea level in the Andes. [Photo © Irène Till-Bottraud]

In mountains species, flowering period and blooming duration increases with altitude, which compensates for the relative rarity of pollinators. For example, the annual plant *Chaetanthera pusilla* (Figure 4), which grows between 2200 and 3500 m above sea level in the Andes, produces many inflorescences{ind-text}Grouping flowers on the same base.{end-tooltip} that open one after the other. In addition, each flower head is receptive{ind-text}Characterizes the state of a flower or inflorescence likely to be fertilized by pollen from outside. {end-tooltip} almost twice longer at high altitude than at low altitude: from 7.7 days at 2700 m to 13.4 days at 3500 m [2].

1.4. Playing with colour?

Flowers are said to be more colourful at higher elevations to attract pollinators more effectively (Figure 5). In fact, there is no significant increase in colour, size or other characteristics associated with insect attraction [3]. The mountains of New Zealand are a remarkable example: the vast majority of species have white flowers (Figure 6).

Figure 6. In the New Zealand mountains, white is the dominant colour. From left to right, Raoulia grandiflora Hook. (Asteraceae), Ourisia macrophylla Hook. (Scrophulariaceae), Myosotis pulvinaris Hook. (Boraginaceae). [Photos © Joseph Fourier Alpine Station/Serge Aubert]

Figure 5. The multicoloured blooms of plants originating from the Caucasus (here at the Lautaret Alpine Botanical Garden) should not suggest that alpine plants are more colourful than those living in lowlands. [Photo © Joseph Fourier Alpine Station/Serge Aubert]

2. Conquering the territory: vegetative reproduction

To avoid the hazards of sexual reproduction, many alpine plants use vegetative reproduction{ind-text}Mode of multiplication allowing plant organisms to multiply without sexual reproduction. It generates new individuals with the same genome and which are therefore clones, we also speak of clonal reproduction.{end-tooltip}. This is not a specificity of mountain plants; however, the proportion of alpine plants using this reproductive strategy increases with altitude [1]. All vegetative reproduction modes are present in alpine plants: production of rhizomes{ind-text}An underground stem that carries leaf and root buds. A rhizome can be horizontal and more or less close to the surface, such as the iris, or much deeper, such as the bindweed.{end-tooltip} or stolons{end-text}A creeping stem from the base of the main stem of a plant with leaf and root buds that will become a new plant. This is the case with strawberries formed by the development of an underground bud, the drageon allows a natural propagation of the plant which will thus be reproduced in the same way.{end-tooltip}, formation of dense tufts, stuckers, reproduction by layering{ind-text}Roots development on a buried branch that allows the production of a new individual.{end-tooltip} but also viviparity{ind-text}Mode of reproduction where seed germination occurs while they are still in the fruit attached to the mother plant.{end-tooltip} and apomixis{ind-text}Production of seeds identical to the mother plant without fertilization. Apomixis transmits somatic mutations (mutations occurring in a non-germinal cell), thus allowing the creation of diversity.{end-tooltip}.

2.1. Rhizomes and stolons

Figure 7. Sexual and clonal reproduction in the creeping avens (Geum reptans L., Rosaceae). The plant has many flowers, which allows sexual reproduction. Clonal reproduction is ensured by aerial runners (stolons, S) which allow the plant to colonize shale scree (here in Galibier, at an altitude of 2800 m). A ramet (1) is developing at the end of the stolon produced by the initial individual (i). [Photos © Joseph Fourier Alpine Station/Serge Aubert]

They allow to explore the surroundings, for example to settle between the stones of the screes. Figure 7 presents the example of the creeping avens which uses clonal reproduction by aerial runners, which will explore shale screes and produce ramets{ind-text}Natural or artificial clones of a plant multiplied by cuttings.{end-tooltip} (see Figure 7) that settle between the stones and individualize from the mother plant once the runner is destroyed.

2.2. Stuckers, tufts and layering

Figure 8. Tufted plants. On the left,ciliate bellflower of Mont Cenis, (Campanula cenesia L., Campanulaceae), a rare alpine plant growing in the schists and gypsums of the Col du Galibier (altitude: 2600 m). Right: Alpine sedge (Carex curvula All., Cyperaceae), it dominates in many lawns in the mountains of temperate Europe. [Source: Photo © Joseph Fourier Alpine Station/Serge Aubert]

These types of vegetative reproduction allow a dense space occupancy which has two important consequences on alpine ecosystems: the stabilization of steep soils and the creation of a favourable microclimate in terms of both temperature and humidity. For example, the ciliate bellflower, which forms a compact, slow-growing tuft, is an example of a plant that reproduces by suckering (Figure 8).

Figure 9. Example of layering in thyme-leaved willow (Salix serpyllifolia Scop., Salicaceae). [Source: Photo © Joseph Fourier Alpine Station/Serge Aubert]

The Alpine sedge (Figure 8) is an example of a tussock plant. It dominates in many lawns in the mountains of temperate Europe. Recent studies using genotyping methods{ind-text}Laboratory techniques, such as whole genome sequencing, that classify and compare sequences.{end-tooltip} (see "DNA Barcode") have confirmed the genetic similarity of ramets present within the same tuft. Based on an average annual increase of 0.4 mm per year, the age of a clone with 7000 ramets has been estimated at about 2000 years [4]!

In the case of layering, rooting occurs when branches come in contact with the soil as shown in Figure 9 in the thyme-leaved willow. Short bushes of alpine rose (rhododendron moors) or willows can shelter several genets (genetic individuals), each made up of dozens of ramets, all forming a somewhat impenetrable canopy. Only a genetic analysis can allow to distinguish the different genets.

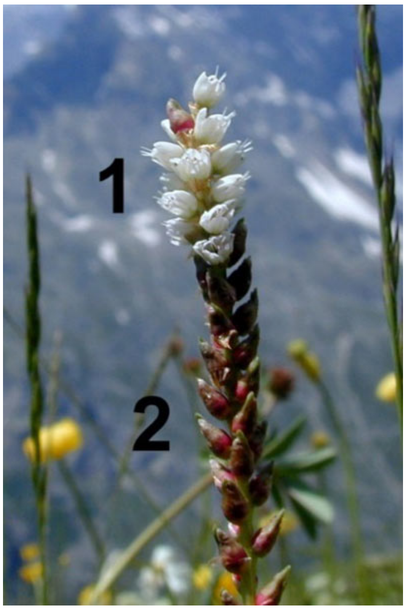

Figure 10. Inflorescence of the the alpine bistort (Polygonum viviparum L., Polygonaceae) showing sexually reproducing flowers (upper part, 1) and bulbils produced by asexual reproduction (lower part, 2). [Source: Photo © Joseph Fourier Alpine Station/Serge Aubert]

2.3. Viviparity

Viviparity, for example through the production of bulbils that begin to develop on the mother plant, and apomixis ensure dispersion over greater distances. Figure 10 shows the inflorescence of the alpine bistort (*Polygonum viviparum* L., Polygonaceae), illustrating the combination on the same floral stem of sexually reproducing flowers and bulbils produced by asexual reproduction. Since the stem length available for flowers and bulbils is constant, the proportion of bulbils increases with altitude and latitude. In other words, clonal reproduction is more important when living conditions become more difficult [1].

3. How do plants deal with environmental change?

With their multiple modes of reproduction, alpine plants are adapted to their environment. These modes of reproduction are very effective both for the stability of the environment and for the maintenance of genetic diversity. This genetic diversity may be an opportunity for the alpine flora, which is currently facing major climate change, with a temperature increase expected during this century ranging from 2 to 8°C. This warming, which is very rapid compared to temperature fluctuations during the alternating series of glacial and interglacial periods, will lead to an upslope displacement of vegetation belts and will reduce the sites favourable to alpine flora.

References and notes

Cover image. The Meige massif seen from the Lautaret Alpine Garden [Source: © Photo Joseph Fourier Alpine Station/Serge Aubert]

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