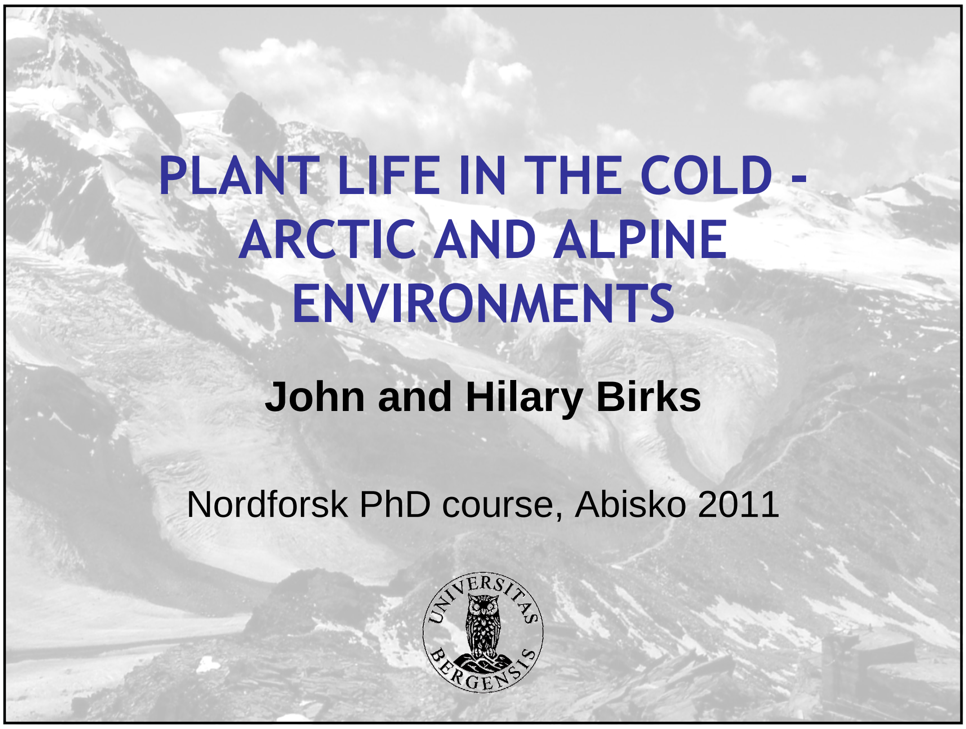


PLANT LIFE IN THE COLD - ARCTIC AND ALPINE ENVIRONMENTS

John and Hilary Birks

Nordforsk PhD course, Abisko 2011

UNIVERSITAS BERGENSIS

INTRODUCTION

Requirements for plant growth

- space, water, light, warmth, basic elements (Ca, Mg, Na, etc.), and essential nutrients (N, P, etc.)

Arctic and alpine environments

- extreme cold, much snow, extreme wind, some shortage of water, short growing season, low nutrients, high ultra-violet irradiance, low atmospheric pressure
- no shortage of light
- suitable space or habitat (e.g. crevices in cliffs) may be rare

General features

- absence of trees
- low-growing plants (vascular plants, bryophytes, lichens, fungi, algae)
- low annual mean temperatures
- low overall plant growth and production

Alpine - above altitudinal tree-line

Arctic - beyond the natural latitudinal tree-line, generally 65°-70° N

High arctic in northern Spitsbergen 79ºN

Jotunheimen Mountains, Norway

Swiss Alps

Dolomites, N Italy

Mt. Edith Cavell,
Canadian Rockies

Beartooth Mountains, Montana & Wyoming

Borah Peak, Idaho

White Clouds Peak, Idaho

Yukon-Alaska border

Mediterranean mountains, SE Turkey

Zagros Mountains, near Aligourdarz, Iran

Min-Shan, Sichuan, China

Jhomolhari (7,314 m), Bhutan

Makalu (8475 m), Tibet

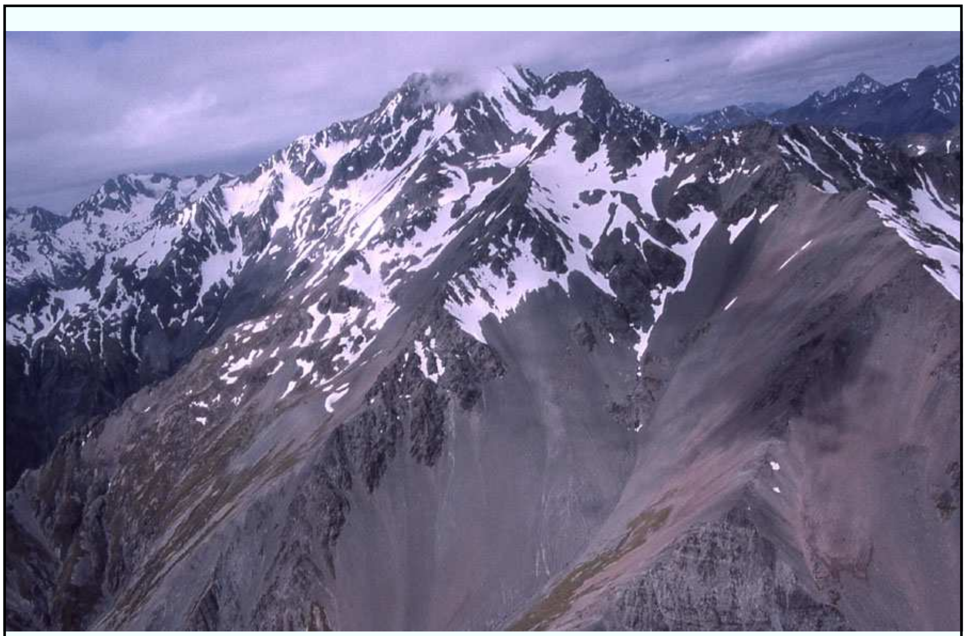
Photo: Harry Jans

Qomolangma (Everest 8848 m), Tibet

Photos: Harry Jans

Cho Oyu (8201 m), Tibet

Sani Pass, Drakensberg



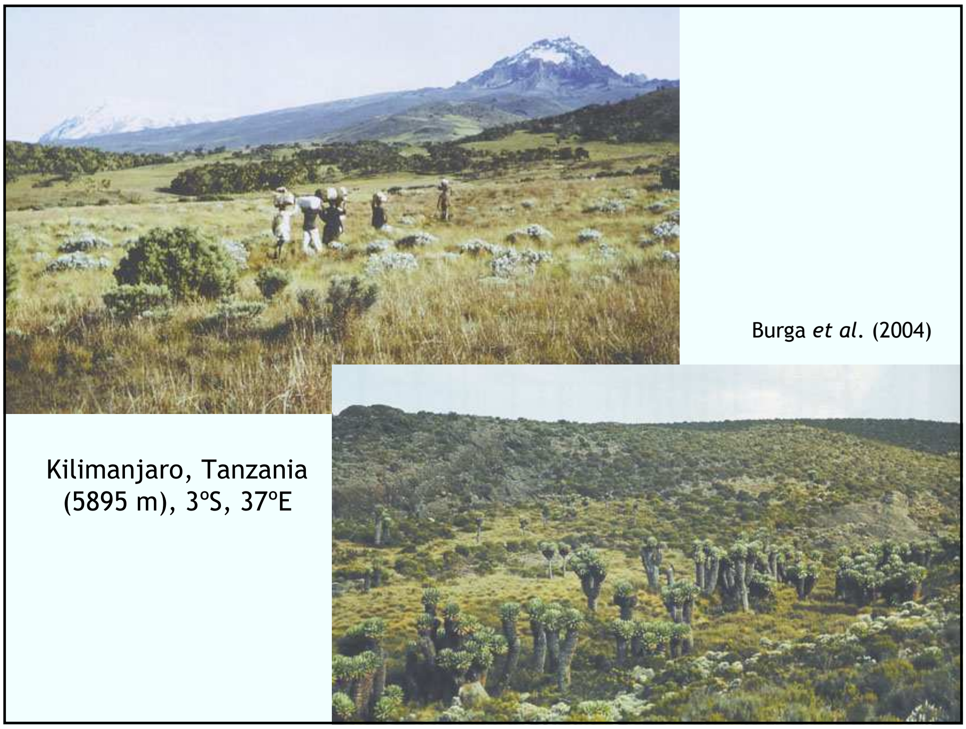
Southern Alps, New Zealand

Torres del Paine, Patagonia, Chile

Mount
Kinabalu,
Borneo
(4095 m)
6°N, 116°E

Burga *et al*.
(2004)

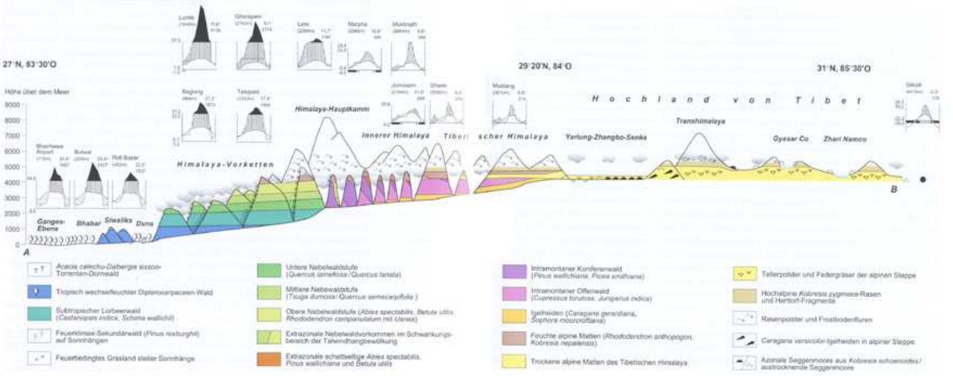
Mount Kenya,
Kenya (4400 m)



Burga *et al*. (2004)

Kilimanjaro, Tanzania
(5895 m), 3ºS, 37ºE

Afro-Alpine vegetation,
Mt Kenya



Cross-section across Himalaya from Nepal to Tibet

Burga *et al.* (2004)

High Tibet Plateau, 4700-5000 m

Burga *et al.* (2004)

MOUNTAINS IN WORLD BIOMES

Major world biomes

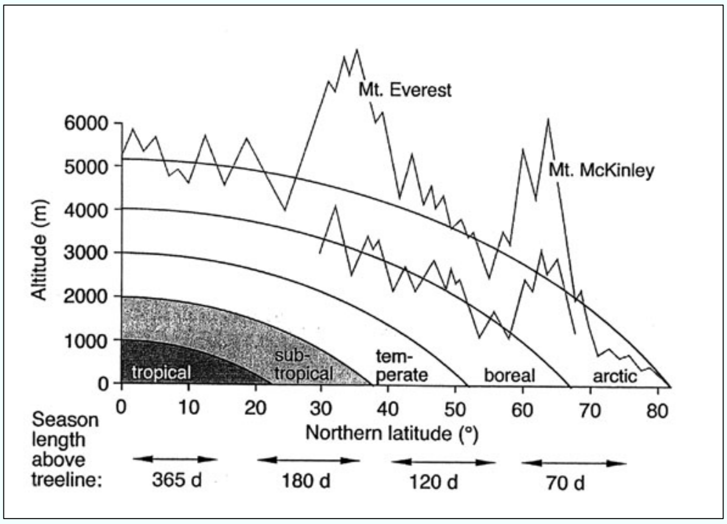
1. Tropical rain forest
2. Tropical dry forest
3. Tropical savannah
4. Desert
5. Temperate woodland and shrubland
6. Temperate grassland
7. Temperate forest
8. Boreal forest
9. Arctic tundra
10. Antarctic tundra

Mountains present in all these biomes. Common in 5, 6, 7, 8, and 9, less common in 1, 3, 4, and 10, very rare in 2.

'Azonal' ecosystem – not a function of latitude or longitude in contrast to 'zonal' biomes or ecosystems. Occurs within biomes.

Mountain ecosystems occur in all biomes of the world – only major ecosystem to occur in all biomes. 'Natural' experiment for ecologists interested in biodiversity and life in extreme conditions.

Unique in occurring world-wide at all latitudes but at different elevations – low elevations at high latitudes, high elevations at low latitudes.



Mountains in relation to latitude and main biomes

Bear eats berries in alpine heath during the day and sleeps in temperate forest 2 km downhill. In 24 hours the bear walks 2-4 km, equivalent climatically to 2000-3000 km range of climate latitudinally.

Compression of life zones and biomes explains why, at a 100 km square scale, no landscape has a HIGHER botanical richness than mountains.

Mountains are HOT SPOTS of biodiversity.

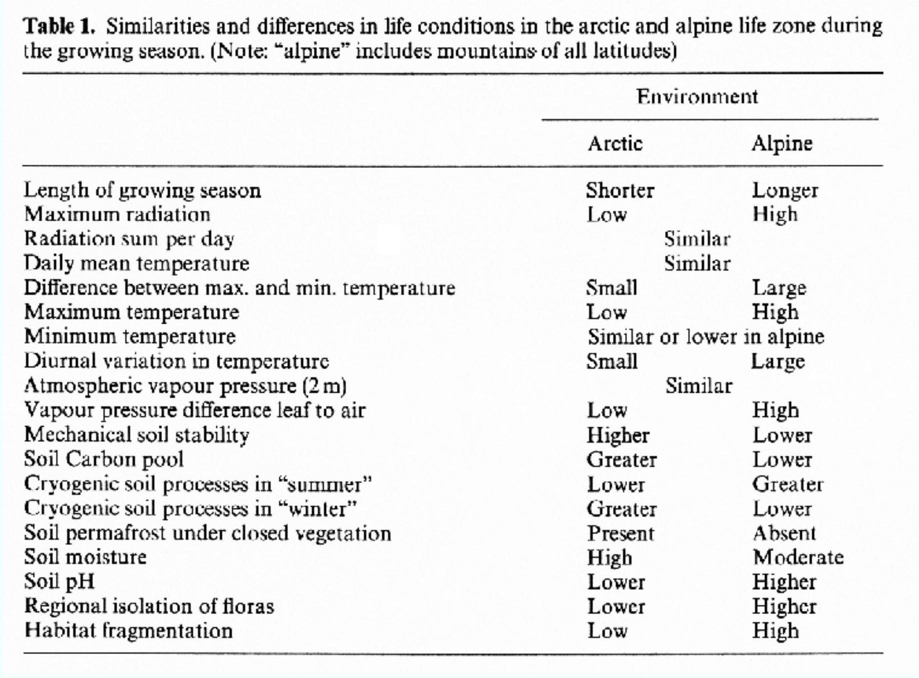
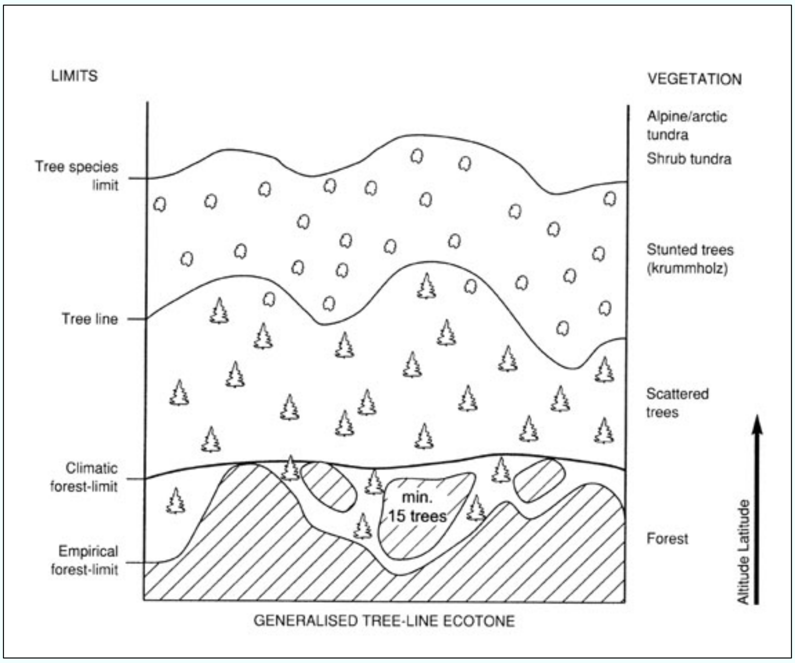


Table 1. Similarities and differences in life conditions in the arctic and alpine life zone during the growing season. (Note: "alpine" includes mountains of all latitudes)

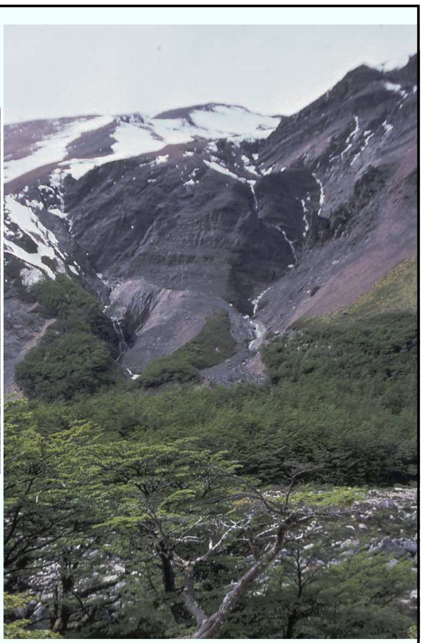
	Environment	
	Arctic	Alpine
Length of growing season	Shorter	Longer
Maximum radiation	Low	High
Radiation sum per day	Similar	
Daily mean temperature	Similar	
Difference between max. and min. temperature	Small	Large
Maximum temperature	Low	High
Minimum temperature	Similar or lower in alpine	
Diurnal variation in temperature	Small	Large
Atmospheric vapour pressure (2 m)	Similar	
Vapour pressure difference leaf to air	Low	High
Mechanical soil stability	Higher	Lower
Soil Carbon pool	Greater	Lower
Cryogenic soil processes in "summer"	Lower	Greater
Cryogenic soil processes in "winter"	Greater	Lower
Soil permafrost under closed vegetation	Present	Absent
Soil moisture	High	Moderate
Soil pH	Lower	Higher
Regional isolation of floras	Lower	Higher
Habitat fragmentation	Low	High

TREE-LINES

The alpine and arctic areas are defined as areas above the tree-line in the mountains of the world or beyond the tree-line in the arctic tundra of the far north.



Nothofagus pumilo, Chile (900 m)



Nothofagus pumilo
Argentina (1250 m)

Picea engelmannii,
Utah (3400 m)

Picea engelmannii,
Wyoming (3500 m)

Nothofagus solanderi,
New Zealand (1100 m)

Nothofagus menzieszii,
New Zealand (1250 m)

Betula utilis,
Bhutan (4000 m)

Cedrus libani,
Turkey (1750 m)

Betula pubescens,
Abisko, Sweden
(1200 m)

Betula pubescens, Finnmark (200 m)

What controls the tree-line?

Where moisture is not limiting (as it is in mountains in some arid areas of the world), the tree-line and upper forest limit are controlled primarily by low temperature.

Körner & Paulsen (2004) 46 data-loggers at tree-line between 68°N and 42°S measuring root-zone temperatures at 1 hourly intervals for 1-3 years between 1996 and 2003.

Mean soil temperature in rooting zone 6.7°C ± 0.8°C during the growing season irrespective of latitude. Range is only 2.2°C in means

- 7-8°C in temperate and Mediterranean tree-lines
- 6-7°C in arctic and boreal tree-lines
- 5-6°C in equatorial tree-lines

Suggests a common thermal threshold for forest growth at a global scale.

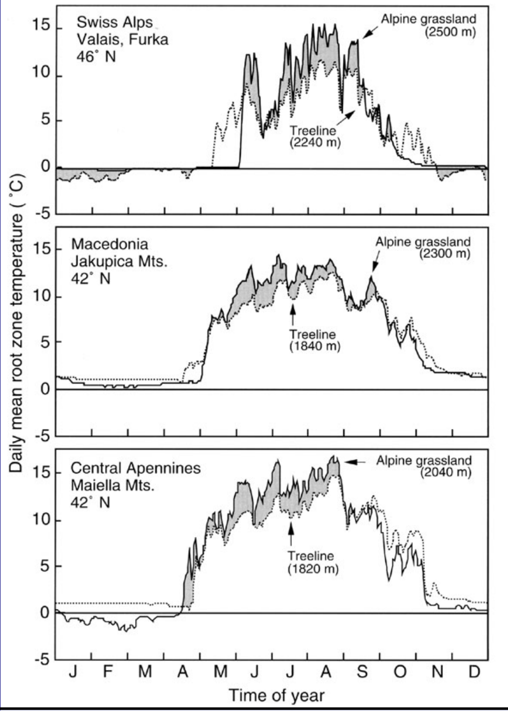
Thermal threshold for the formation of new tissue ('growth') at about 6.5-7ºC.

Trees cannot grow at higher altitudes simply because their upright growth couples them to the cold air.

In contrast, low-growing alpines can trap solar heat near the ground and permit solar heat to warm up soils.

Soils under trees are screened from the sun and do not capture radiative warming and are actually COLDER than soils under alpine grasslands at a higher elevation.

Temperature at 10 cm depth under trees at the tree-line and alpine vegetation 200-250 m higher.



Nagy *et al.* (2003)

Growth-limitation hypothesis for tree-line

Tree life-form is limited by the possibilities for INVESTMENT.

Protein synthesis limited by low temperatures.

Minimum quantity of warmth required for 'tree life activities'.

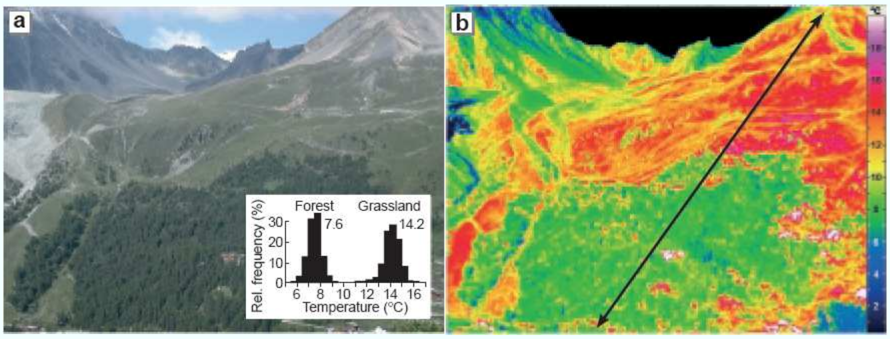
Trees with their own canopy can negatively influence their shoot and root temperatures.

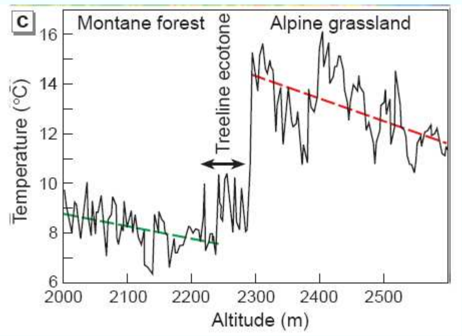
Determine their own limits at high altitudes or high latitudes.

Cold soil temperatures → no root growth → no or very little shoot growth → low rates of photosynthesis →poor growth, if any, of tree.

Feedback between soil temperature and tree growth.

Tree-line is a result of INTERACTIONS between plant growth-form and morphology AND CLIMATE.





Land-surface temperature across an elevational transect in Central Swiss Alps shown by modern thermal imagery. Forest has a mean of 7.6°C whereas the alpine grassland has a mean of 14.2°C. There is a sharp warming from forest into alpine grassland

Körner (2007)

Other factors important at more local scales

1. Long-lasting snow cover, avalanches, wind sheer on exposed ridges, and local freezing phenomena.
2. Non-climatic factors such as unstable soils or no rooting material.
3. Browsing by wild animals.
4. Human activities have lowered tree-line positions by clearance, burning, and alpine pastures.

No consistent evidence for reproductive limitations (no shortage of seedlings but very few young tress) or for carbon-balance hypothesis (no shortage of C uptake).

ALPINE ZONE

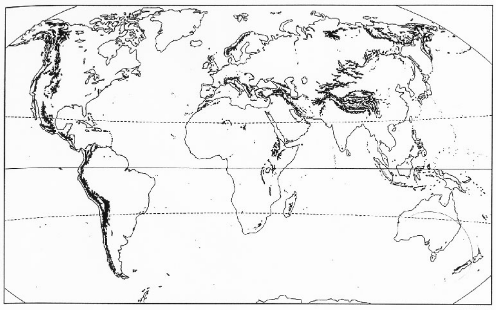


Fig. 2.2. The global distribution of the alpine life zone. Nearly 3% of the terrestrial land area is covered by true alpine vegetation, which includes approximately 10 000 species or 4% of all known higher plant species. (Körner 1995a)

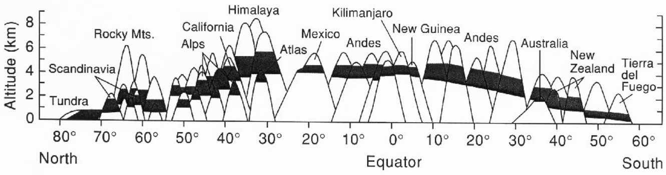


Fig. 2.1. A schematic presentation of the altitudinal position of the alpine life zone from arctic to antarctic latitudes

ALPINE ZONE EXTENT

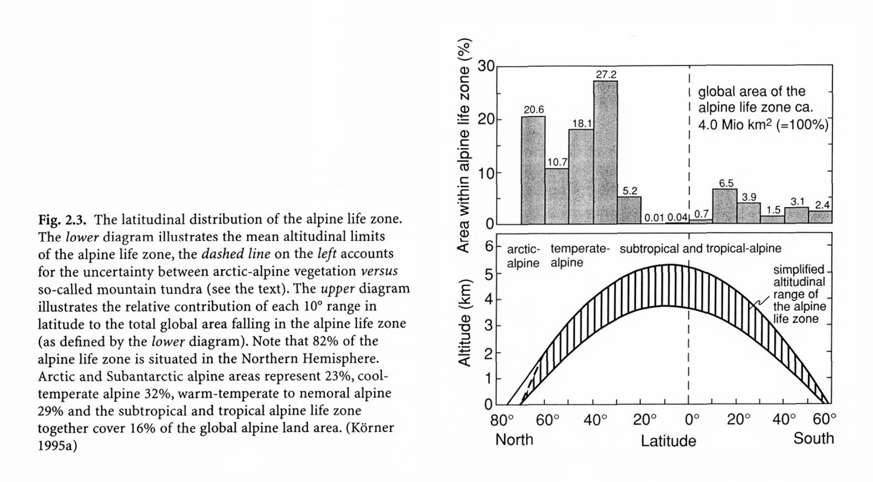


Fig. 2.3. The latitudinal distribution of the alpine life zone. The *lower* diagram illustrates the mean altitudinal limits of the alpine life zone, the *dashed line* on the *left* accounts for the uncertainty between arctic-alpine vegetation *versus* so-called mountain tundra (see the text). The *upper* diagram illustrates the relative contribution of each 10° range in latitude to the total global area falling in the alpine life zone (as defined by the *lower* diagram). Note that 82% of the alpine life zone is situated in the Northern Hemisphere. Arctic and Subantarctic alpine areas represent 23%, cool-temperate alpine 32%, warm-temperate to nemoral alpine 29% and the subtropical and tropical alpine life zone together cover 16% of the global alpine land area. (Körner 1995a)

EXTENT OF ALPINE AND ARCTIC ENVIRONMENTS

Alpine 4 million km²; 3% of earth’s land; only 18% in southern hemisphere

Arctic 7 million km²; 5% of earth’s land

Arctic + alpine 8% global land area

(Boreal forest 8.1%; total agricultural land 9.4%)

Global arctic + alpine carbon pool only 2% of global terrestrial biosphere carbon pool

Alpine and arctic areas hold about 66% of globe's freshwater in the form of snow and glaciers

Provide water for half of mankind, directly or indirectly. Key role in global hydrological cycle.

SUBDIVISIONS

Low alpine	- dwarf-shrub heath (= low-alpine in Norway)
Upper alpine	- open grasslands (= mid-alpine in Norway)
Subnival	- scattered plant growth (= high-alpine in Norway)
Nival	- permanent snow and ice

Low arctic	- dwarf-shrub ericaceous tundra
Middle arctic	- *Salix* and *Dryas* heath
High arctic	- sparse vegetation
Polar desert	- very sparse vegetation

ALTITUDE FOR LATITUDE SCALES

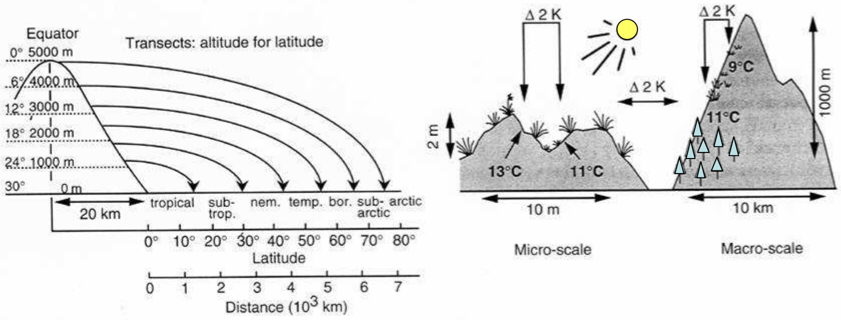


Fig. 1.4. Altitude for latitude: over short elevational distances thermal gradients represent the climate across vast latitudinal distances. Space for time: thermal contrasts across the relief "simulate" differences in temperature along elevational gradients. These are "natural" experiments, ideally suited for comparative functional ecology

100 m increase in elevation equivalent to 600 km distance north.

SPECIES DIVERSITY

Global scale

Alpine vascular plant flora 10,000-15,000 species, 2,000 genera, 100 ± 10 families. About 6% of world's flora (3% land is alpine)

Arctic flora 1,000-1,500 species, less than 1% world's flora (5% land is arctic)

General rule: arctic flora 1/10 alpine flora

Main families – better represented than on areal proportional representation

Asteraceae	Alpine	
Gentianaceae	Alpine	
Saxifragaceae	Alpine	
Poaceae	Alpine	Arctic
Brassicaceae	Alpine	Arctic
Caryophyllaceae	Alpine	Arctic
Rosaceae	Alpine	Arctic
Ranunculaceae	Alpine	Arctic
Ericaceae		Arctic
Cyperaceae		Arctic
Salicaceae		Arctic

(*Campanulaceae, Polygonaceae, Scrophulariaceae, Apiaceae, Hypericaceae, Primulaceae, Epacridaceae* – in some alpine areas)

Under represented:

Orchidaceae *Fabaceae* *Liliaceae*

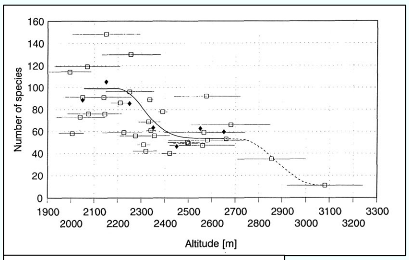
Regional scale

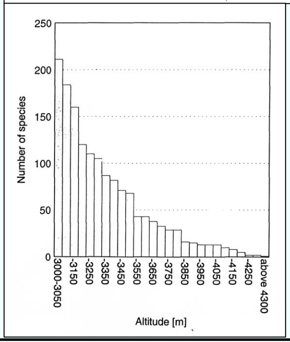
Alpine flora in 20-200 km^2 about 250-300 species in 40 families. About 20-25% of total regional flora (including lowlands)

Arctic flora in same area about 200-250 species. Fewer total arctic species (10%) than alpine species but much more widespread than alpines. Very few arctic endemics, very many alpine local endemics

Richness decreases with altitude and with latitude. On average, decreases by 15-45 species per 100 m altitude or by about 10-30 species per 1°C temperature drop in latitude.

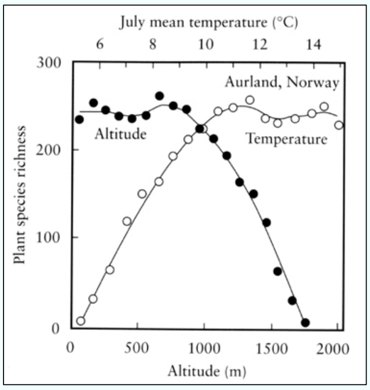
SPECIES RICHNESS DECREASE WITH ALTITUDE





Decreases on average, by 15-45 species per 100 m.

Grabherr *et al.* (1995)



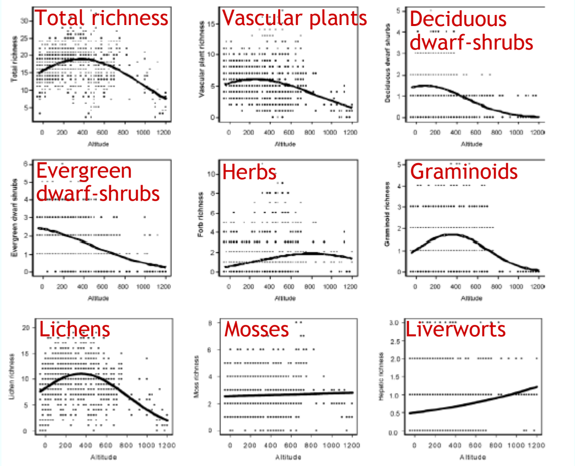
Species richness and temperature in relation to altitude (Odland & Birks 1999)

Körner (2002)

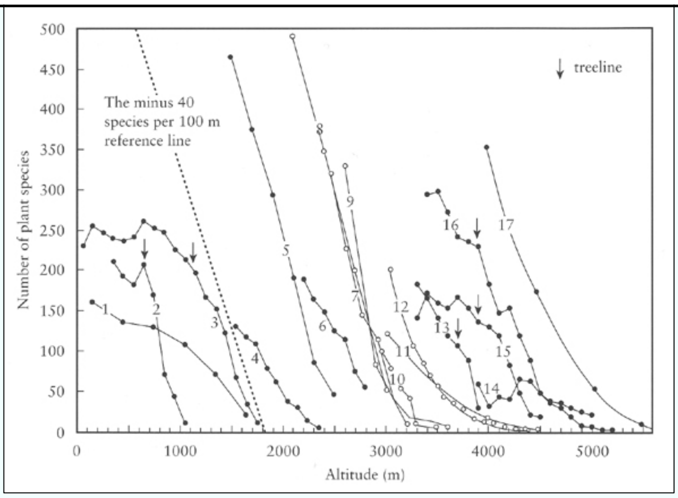
DOES RICHNESS OF ALL PLANT GROUPS DECREASE WITH ALTITUDE?

Bruun *et al*. 2006
J. Vegetation
Science 17: 37-46.

Six mountains in N. Norway and N. Finland



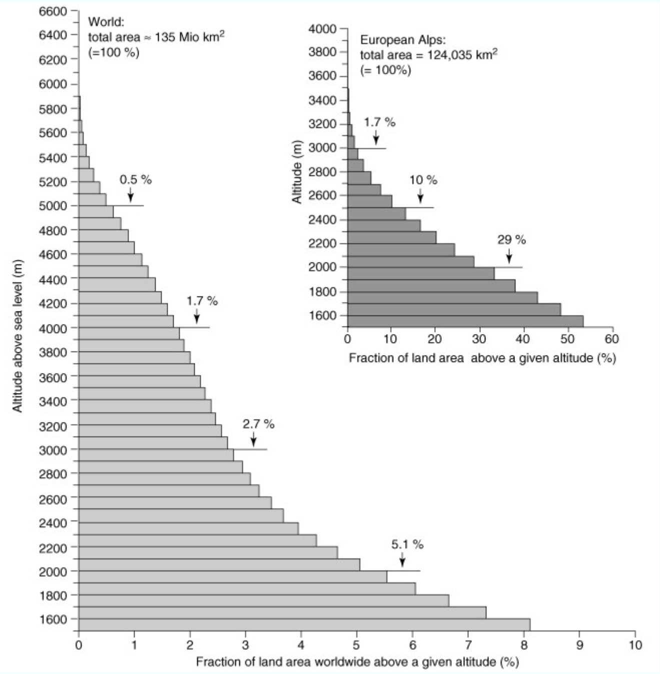
Not all plant groups show the same pattern. Liverwort richness increases with altitude, whereas mosses hardly change. Lichens have a unimodal peak and then decline, like graminoids and dwarf-shrubs.



Körner (2002)

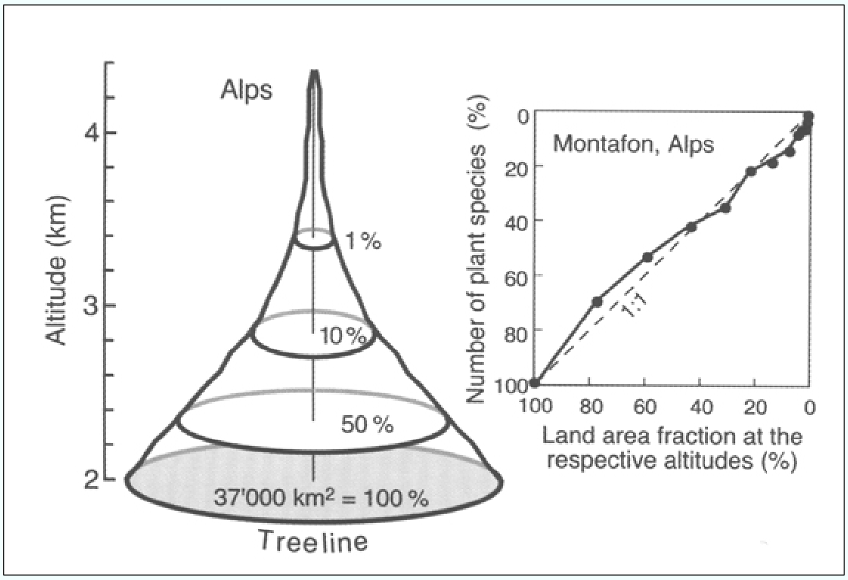
40 species decrease per 100 m ? general 'rule'

1. N.E. Greenland, 2. Scotland, 3. W. Norway, 4. Central Norway, 5. Polish Tatra, 6. Mount Olympus, Greece, 7-8 & 10. Swiss Alps, 9. French Alps, 11-12 Austrian Alps, 13-15. Himalaya, 16. Karakorum, 17. Hindu Kush



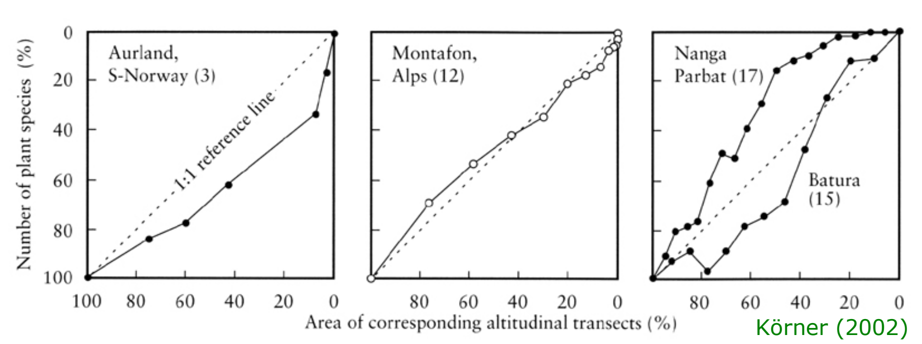
Global pattern of land area outside Antarctica in 100 m steps starting at 1500 m

Körner (2007)



Körner (2004)

Area changes with elevation. Species number decreases as available area decreases with increasing altitude. Habitat diversity also decreases with decreasing area.

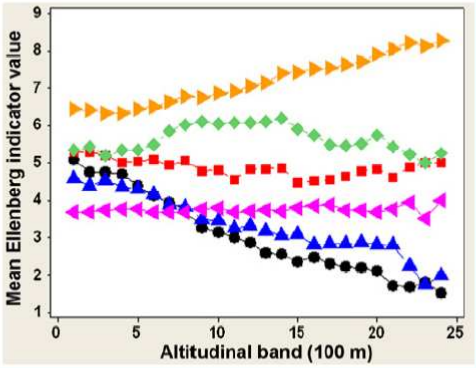


Körner (2002)

Above tree-limit, land area is halved, on average, for every 167 m increase in altitude (150 m in Alps, 178 m in Andes)

Besides changes in species richness with altitude, overall ecological conditions (e.g. soil nitrogen) also change.

Use ecological indicator values for species as an environmental 'measure'



Odland (2008)

Mean for every 100 m band from 0-2500 m, W Norway

Changes in light, nitrogen, and temperature

ALTITUDINAL LIMITS

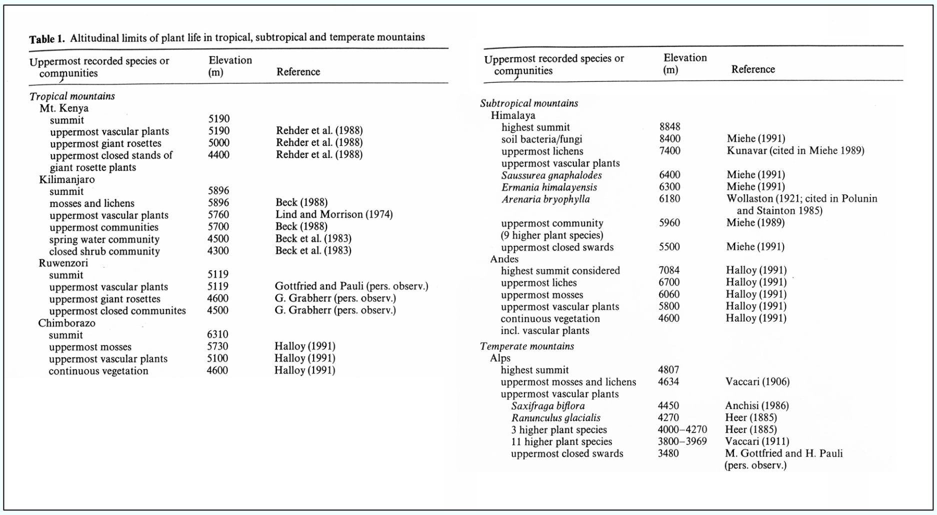


Table 1. Altitudinal limits of plant life in tropical, subtropical and temperate mountains

Uppermost recorded species or communities	Elevation (m)	Reference
Tropical mountains		
Mt. Kenya		
summit	5190	
uppermost vascular plants	5190	Rehder et al. (1988)
uppermost giant rosettes	5000	Rehder et al. (1988)
uppermost closed stands of giant rosette plants	4400	Rehder et al. (1988)
Kilimanjaro		
summit	5896	
mosses and lichens	5896	Beck (1988)
uppermost vascular plants	5760	Lind and Morrison (1974)
uppermost communities	5700	Beck (1988)
spring water community	4500	Beck et al. (1983)
closed shrub community	4300	Beck et al. (1983)
Ruwenzori		
summit	5119	
uppermost vascular plants	5119	Gottfried and Pauli (pers. observ.)
uppermost giant rosettes	4600	G. Grabherr (pers. observ.)
uppermost closed communites	4500	G. Grabherr (pers. observ.)
Chimborazo		
summit	6310	
uppermost mosses	5730	Halloy (1991)
uppermost vascular plants	5100	Halloy (1991)
continuous vegetation	4600	Halloy (1991)
Subtropical mountains		
Himalaya		
highest summit	8848	
soil bacteria/fungi	8400	Miehe (1991)
uppermost lichens	7400	Kunavar (cited in Miehe 1989)
uppermost vascular plants		
Saussurea gnaphalodes	6400	Miehe (1991)
Ermania himalayensis	6300	Miehe (1991)
Arenaria bryophylla	6180	Wollaston (1921; cited in Polunin and Stainton 1985)
uppermost community (9 higher plant species)	5960	Miehe (1989)
uppermost closed swards	5500	Miehe (1991)
Andes		
highest summit considered	7084	Halloy (1991)
uppermost liches	6700	Halloy (1991)
uppermost mosses	6060	Halloy (1991)
uppermost vascular plants	5800	Halloy (1991)
continuous vegetation incl. vascular plants	4600	Halloy (1991)
Temperate mountains		
Alps		
highest summit	4807	
uppermost mosses and lichens	4634	Vaccari (1906)
uppermost vascular plants		
Saxifraga biflora	4450	Anchisi (1986)
Ranunculus glacialis	4270	Heer (1885)
3 higher plant species	4000–4270	Heer (1885)
11 higher plant species	3800–3969	Vaccari (1911)
uppermost closed swards	3480	M. Gottfried and H. Pauli (pers. observ.)

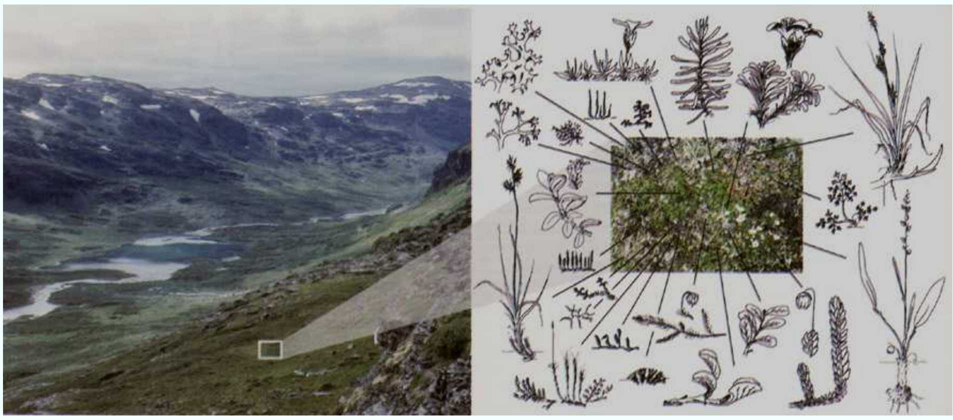
Micro scale

At global scale, alpine diversity is about or slightly above average

At regional scale, alpine diversity is high compared to other temperate areas

At micro scale (1m^2), highest diversity of anywhere – 50-60 species in 1m^2, nearby only 5 species in 1m^2

High micro-habitat differentiation (ridges, hollows, late-snow, cliffs, rock outcrops, hydrology, geology, etc.)



34 species in alpine area 25 x 35 cm, northern Sweden

EUROPEAN ALPINE FLORA

European alpine flora (species confined to or mainly above the tree-line) contains over 2,500 species and subspecies.

Equals 20% of the European native flora in contrast to world's alpine flora that is about 6% of the world's flora. European mountains very rich.

About 250 species (10%) are endemic to single mountain ranges or areas in Europe.

Very few introduced species grow in the European alpine zone (cf. New Zealand).

European alpine flora is more special than is often realised.

ALPINE ENVIRONMENTS

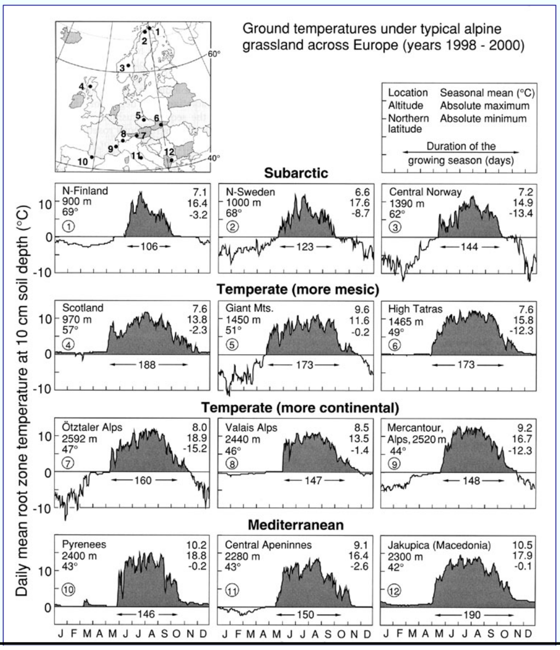
- Low temperatures, long-lasting or permanent snow, glaciers
- Steep rocky slopes. Screes, cliffs, exposed ridges and summits
- Temperature decreases, on average, 0.65°K 100 m^{-1} altitude because as air becomes thinner with altitude, there is less air to absorb solar energy and the air becomes colder. Snow and glaciers develop even on equatorial mountains
- Growing season decreases with altitude
- Atmospheric pressure decreases almost linearly with altitude. 2,600 m altitude total pressure is about 750 hPa (=mbar), about 75% of that at sea-level
- At 6,000 m in Himalaya, plants live at about 50% pressure compared to sea-level
- Partial pressures CO_2 and O_2 are reduced by the same proportion
- Reduction in pCO_2 at 2,600 m = difference in pCO_2 at sea-level between 1800 AD (pre-Industrial Revolution) and today

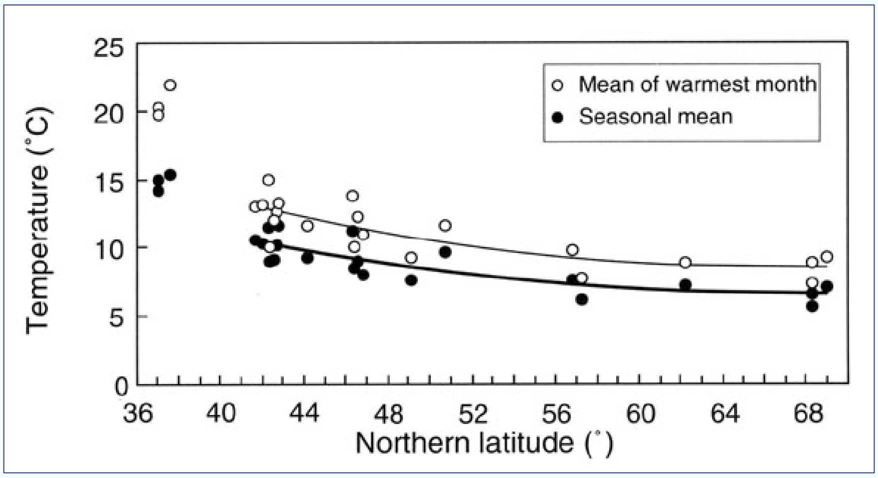
ALPINE ENVIRONMENTS (continued)

- By forcing moving air upwards, mountains cause it to lose its moisture as rain or snow. Most fall at lower altitudes
- At high altitudes air is often very dry
- Low moisture content and lack of dust and pollutant particles at high altitudes give very clear air, and hence high solar radiation including ultra-violet
- High reflectance from snow
- Large daily temperature changes with freezing conditions at night and high temperatures in day, especially at low latitudes
- High winds "Roaring Forties" and "Furious Fifties"
- Soils are thin, immature, unstable, suffer freeze-thaw and wind erosion. Much variation over very short distances from extremely dry and well-drained to wet and water-logged in hollows fed by snow-melt water

ALPINE ENVIRONMENTS (continued)

- Mean root-zone temperatures (10 cm depth) for growing season in low-alpine zone very consistent within Europe irrespective of latitude (42-68ºN). About 7-8ºC, except at low latitudes (36ºN).





Root-zone mean temperatures for growing season in 23 areas of Europe

ADAPTATIONS

Alpine and arctic plants show a high degree of specialisation. They are well adapted to these extremes.

Selected for small size and ability to cope with extremes.

Arctic and alpine plant life is an interplay of ADAPTATION and INCREASING CLIMATIC LIMITATION ON PLANT GROWTH

Alpine and arctic plants are not simply 'stressed' plants that tolerate extreme conditions. They are SPECIALISED to thrive where there is increasing CLIMATIC LIMITATION on plant growth; close to the physiological limits for plant growth.

Alpine and arctic plants are TRUE specialists of an extreme world.

ALPINE AND ARCTIC GROWTH FORMS

Growth-form – "plan" for life in a particular environment

Twelve major growth-forms, nine of which are shown by vascular plants.

Common growth-forms

1. Low-growing creeping prostrate woody shrubs or dwarf-shrubs (chamaephytes)

Betula nana, Norway

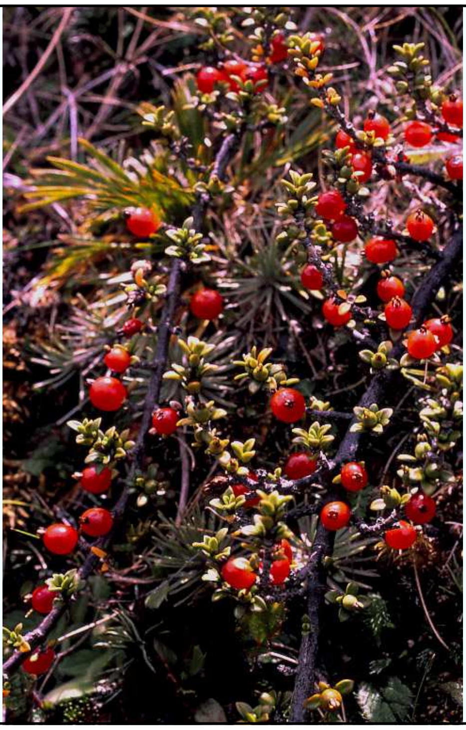
Rhododendron nivale, Sichuan

Salix herbacea, Norway
(male)

Salix herbacea, Scotland
(female)

Dryas octopetala, Austria

Cassiope hypnoides, Norway



Coprosma cheesemanii, New Zealand

Gaultheria pumila (= *Pernettya pumila*), Argentina

Common growth-forms

1. Low-growing creeping prostrate woody shrubs or dwarf-shrubs (chamaephytes)
2. Graminoids (grasses, sedges, etc.) forming tussocks or tufts

Chionochloa alpina, New Zealand

Carex firma, Austria

Common growth-forms

1. Low-growing creeping prostrate woody shrubs or dwarf-shrubs (chamaephytes)
2. Graminoids (grasses, sedges, etc.) forming tussocks or tufts
3. Herbaceous perennials, usually with basal rosettes of leaves

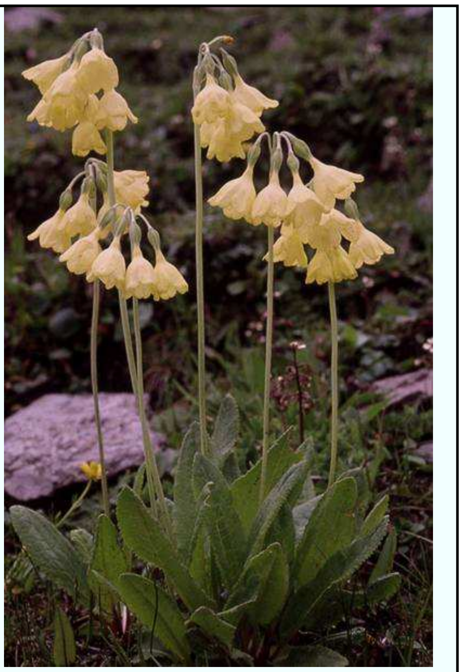
Draba aureola,
Oregon

Notothlaspi rosulatum, New Zealand

Valeriana moyanoi, Argentina

Papavar dahlianum,
Spitsbergen

Primula parryi, Wyoming



Primula sikkimensis, Sichuan

Meconopsis discigera, Bhutan

Meconopsis horridula ssp. *racemosa*, Sichuan

Meconopsis quintuplinervia, Sichuan

Meconopsis integrifolia, Sichuan

Meconopsis punicea, Sichuan

Meconopsis tibetica, Tibet

Hulsea nana, California

Xerophyllum tenax, Oregon

Ligularia holmii, Colorado

Polemonium confertum, Wyoming

Saxifraga cotyledon,
Norway

Common growth-forms

1. Low-growing creeping prostrate woody shrubs or dwarf-shrubs (chamaephytes)
2. Graminoids (grasses, sedges, etc.) forming tussocks or tufts
3. Herbaceous perennials, usually with rosettes
4. Cushion plants

Silene acaulis, Colorado

TEMPERATURES OF CUSHION PLANTS

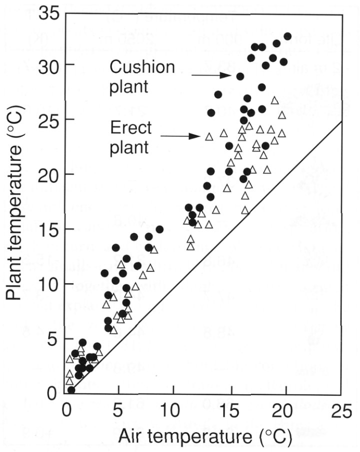


Fig. 4.9. Plant temperature as modified by plant life form at 3800 m altitude in the Rocky Mountains of Colorado. (Salisbury and Spomer 1964)

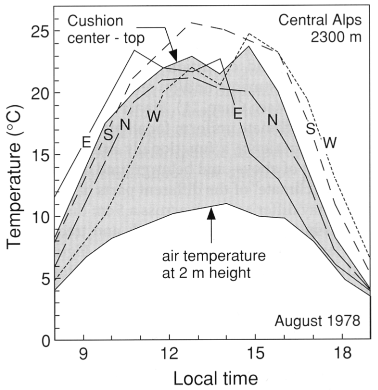
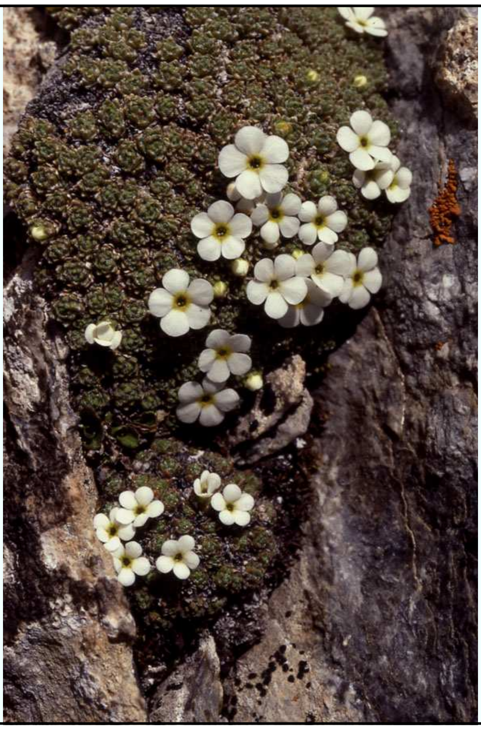


Fig. 4.10. The diurnal variation in surface temperature of a dome shaped specimen of the alpine cushion plant *Silene acaulis ssp. exscapa* (*above*), measured on a bright day at 2300 m altitude in the Alps. Letters mark the geographic orientation of measurement points. Note the large (*shaded*) differences between cushion (*center-top*) and air temperature. (Körner and DeMoraes 1979)



Androsace helvetica,
Switzerland

Androsace alpina, Switzerland

Eritrichium nanum, Switzerland

Draba oreades,
Bhutan

Draba incerta,
Wyoming

Saxifraga andersonii,
Bhutan

Saxifraga caveana,
Bhutan

Benthamiella patagonica, Argentina

Xerodraba patagonica, Argentina

Benthamiella nordenskjoldii, Argentina

Oreopolus glacialis, Argentina

Chionohebe myosotoides, New Zealand

Myosotis pulvinaris, New Zealand

Hectorella caespitosa, New Zealand

Phyllachne colensoi, New Zealand

Celmisia sessiliflora, New Zealand

Megacushions

Bolax gummifer, Argentina

Junellia mulinoides,
Argentina

Raoulia bryoides,
New Zealand

Raoulia eximia,
New Zealand

Haastia pulvinaris, New Zealand

Haastia pulvinaris, close up

Less common growth-forms

5. Spiny cushions (vegetable "hedgehogs") - thorns or spines, dwarf shrubs, hemispherical shape. Mainly Mediterranean-type climate.

Anarthrophyllum desideratum, Chile

Mulinum spinosum, Argentina

Erinacea anthyllis, Spain

Less common growth-forms

5. Spiny cushions (vegetable "hedgehogs")
6. Giant rosettes, mainly on tropical mountains

Dendrosenecio keniodendron, Kenya

Lobelia rhyncopetalum, Ethiopia

with coat

Lobelia keniensis, Mt Kenya

Lobelia telekii, Mt Kenya

Lobelia keniensis with anti-freeze

Carduus macranthus, Ethiopia

Cyathea dregei, Drakensberg

Echium wildpretii, Tenerife

Photos: Hermann Schmidt

Burga *et al.* (2004)

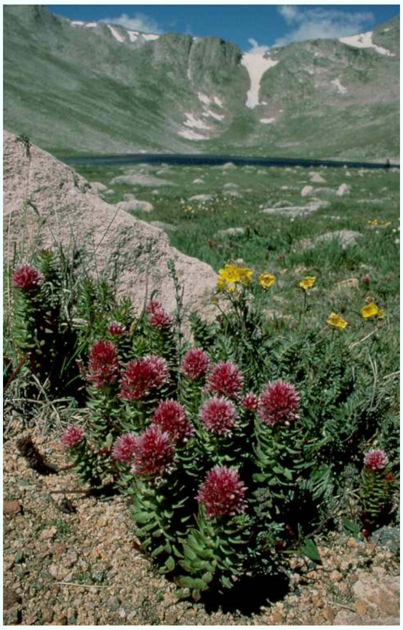
Espeletia Paramo, Ecuador-Columbian Andes 4000 m 0-3ºN, 77-78ºW

Dendrosenecio (=Senecio) brassica, Kenya, 4100 m

Less common growth-forms

5. Spiny cushions (vegetable "hedgehogs")
6. Giant rosettes, mainly on tropical mountains
7. Succulents

Sempervivum montanum, Austria



Clementsia (= *Rhodiola*)
rhodantha, Colorado

Sedum atratum, Slovenia

Sedum alpestre, Switzerland

Jovibarba arenaria, Austria

Rhodiola himalayensis, Bhutan

Mammillaria vivipara, N Dakota

Maihuenia patagonica,
Argentina

Less common growth-forms

5. Spiny cushions (vegetable "hedgehogs")
6. Giant rosettes, mainly on tropical mountains
7. Succulents
8. Geophytes (bulbs or tubers) mainly in strongly seasonal-climate areas, especially Mediterranean climate mountains (wet winters, dry summers)

Crocus biflorus, Turkey

Crocus corsicus,
Corsica

Narcissus bulbocodium, Portugal

Iris danfordiae, Turkey

Muscari azureum, Turkey

Colchicum szovitsii, Turkey

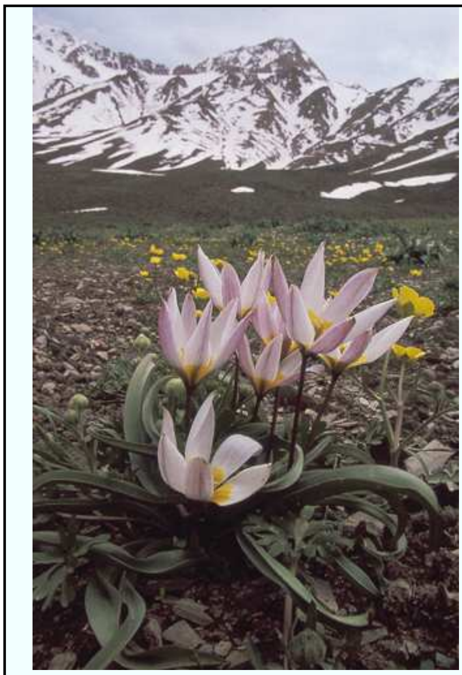
Fritillaria crassifolia, Turkey

Fritillaria lusitanica, Sierra Nevada

Photo:
Bill Baker

Fritillaria delavayi, Bhutan

Lilium nanum, Bhutan



Tulipa humilis, Iran

Tulipa stapfii, Iran

Tulipa bierbersteiniana,
Iran

Cypripedium himalaicum, Bhutan

Chloraea alpina, Argentina

Calochortus macrocarpus, Idaho

Calochortus gunnisonii, Colorado

Lewisia rediviva, Idaho

Alstroemeria patagonica, Argentina

Rhodophiala andicola, Argentina

Nerine bowdenii, Drakensberg

Brunsvigia racemosa, Drakensberg

Fritillaria imperialis, Iran

Less common growth-forms

5. Spiny cushions (vegetable "hedgehogs")
6. Giant rosettes, mainly on tropical mountains
7. Succulents
8. Geophytes (bulbs or tubers)
9. Annuals (therophytes)

Koenigia islandica, Norway

Gentiana nivalis, Norway

Gentianella nana, Austria

Cryptogamic growth-forms

10. Bryophytes and some pteridophytes; erect tufts, cushions, mats

Polytrichum sexangulare, Scotland

Bartramia ithyphylla, Sweden

Racomitrium lanuginosum, Scotland

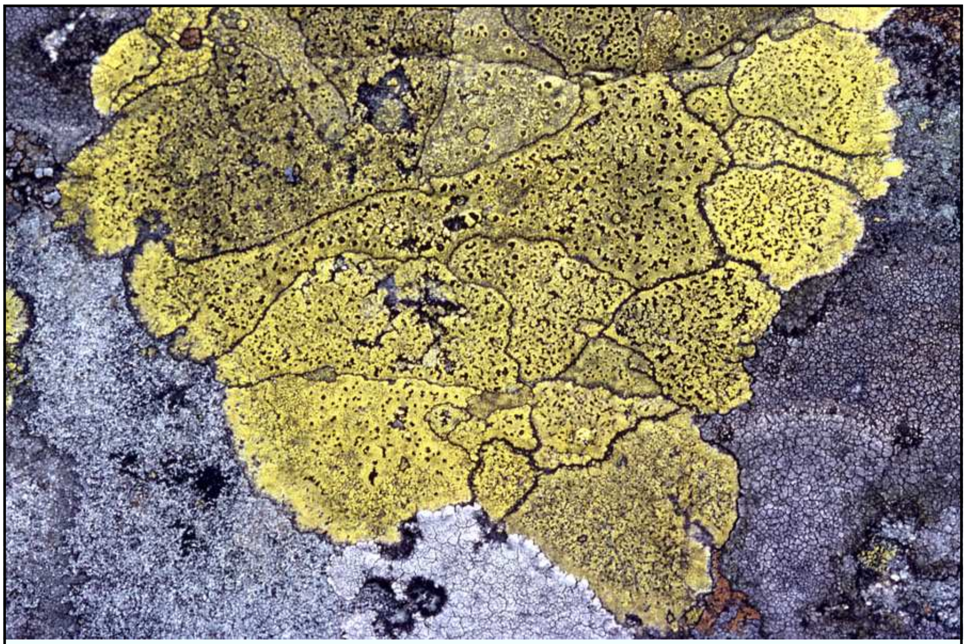
Selaginella densa, Alberta (club-moss, a fern ally)

Cheilanthes gracillima, Oregon

Cryptogamic growth-forms

10. Bryophytes and some pteridophytes; erect tufts, cushions, mats
11. Lichens – fruticose, thalloid, crustose

Thamnolia vermicularis, Yukon

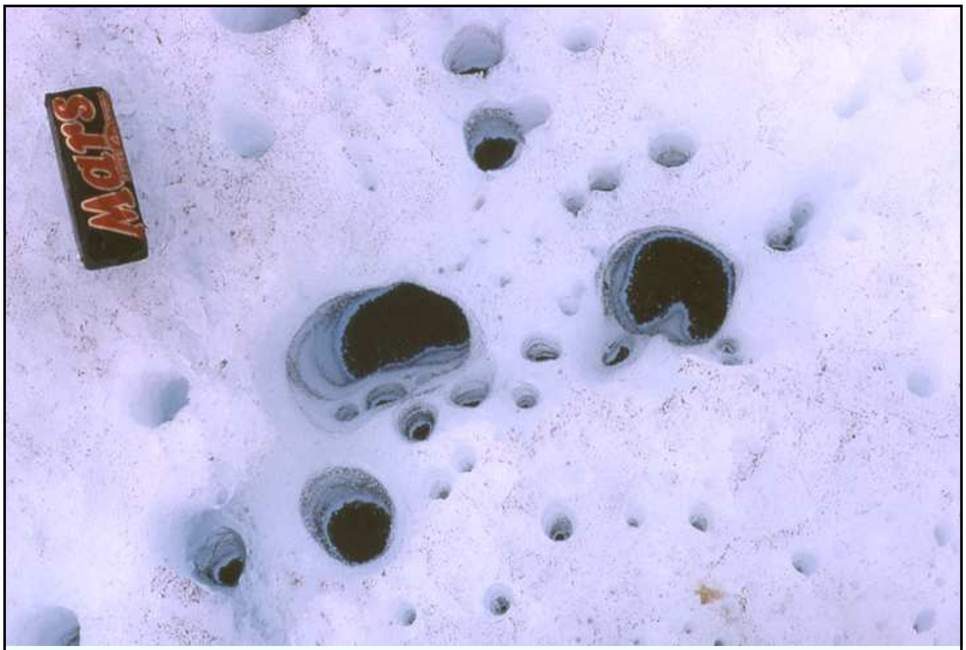


Rhizocarpon geographicum, Wales

Cryptogamic growth-forms

10. Bryophytes and some pteridophytes; erect tufts, cushions, mats
11. Lichens – fruticose, thalloid, crustose
12. Microscopic algae and bacteria

Klutan Glacier, Yukon



Snow algae, Yukon

COLD AND WIND IN THE ALPINE WORLD

Low temperatures are very characteristic of Alpine World.

Growing leaves will tolerate freezing down to -7ºC (*Ranunculus glacialis*), -12ºC (*Saussurea pamirica*), and -20ºC (*Viola chrysantha*).

Highest flowering plant in the world is *Saussurea gnaphalodes*, 6400 m on Mount Everest in 1938. Nine species above 6000 m.

Mosses and liverworts to 7000 m, lichens to 7400 m, snow algae to 7700 m, bacteria and micro-fungi to 8400 m on Everest.

Northernmost flowering plant in the world is *Saxifraga oppositifolia* (84ºN).

Highest in the Alps are *Saxifraga oppositifolia* (4510 m) and *S. biflora* (4400 m) closely followed by *Androsace alpina* and *Ranunculus glacialis*. Twelve species above 4000 m.

Saxifraga oppositifolia, Norway – the world's northernmost plant (84ºN)

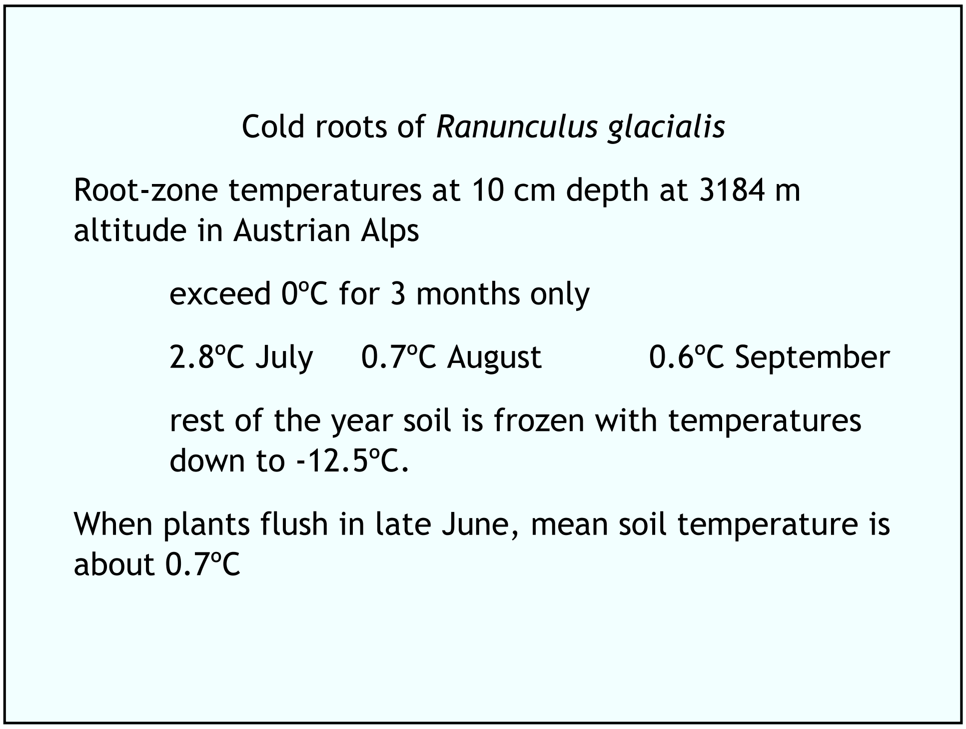
Colobanthus lycopodiodes, Argentina – one of the world's southernmost plants (65ºS)

Saxifraga biflora, Switzerland – one of the Alps' highest plant (4400 m) along with *S. oppositifolia* (4510 m)

Saussurea gnaphalodes, N Pakistan – the world's highest plant (6400 m)

Photo: Toshio Yoshido

Ranunculus glacialis, Switzerland – very cold roots! Up to 4275 m in Alps and 80°N in Greenland



Cold roots of *Ranunculus glacialis*

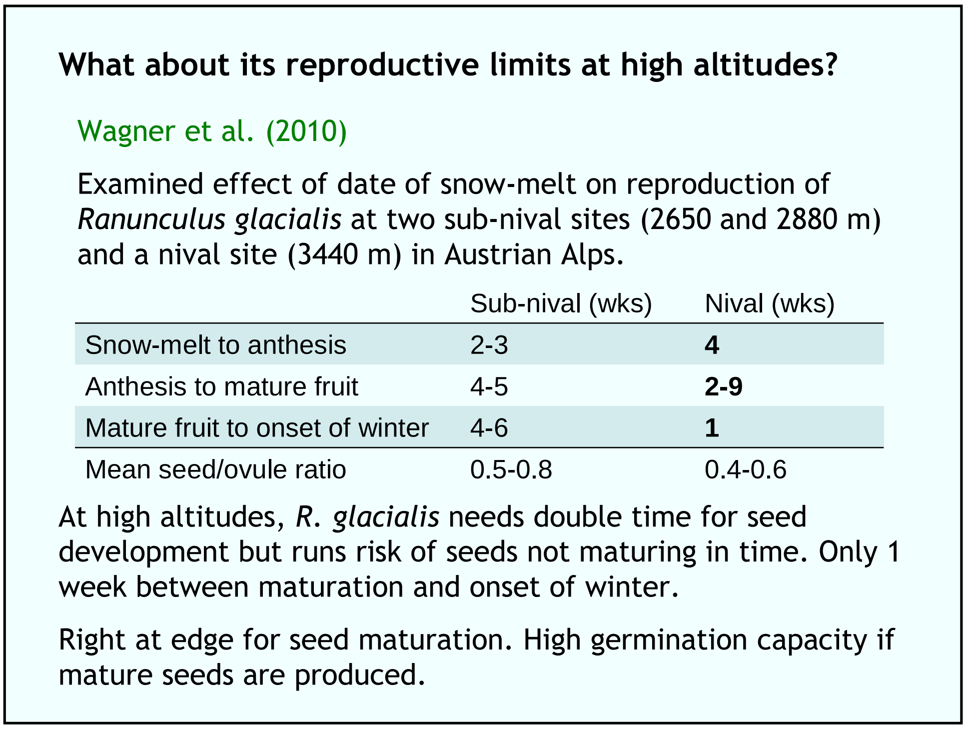
Root-zone temperatures at 10 cm depth at 3184 m altitude in Austrian Alps

exceed 0°C for 3 months only

2.8°C July   0.7°C August   0.6°C September

rest of the year soil is frozen with temperatures down to -12.5°C.

When plants flush in late June, mean soil temperature is about 0.7°C



What about its reproductive limits at high altitudes?

Wagner et al. (2010)

Examined effect of date of snow-melt on reproduction of *Ranunculus glacialis* at two sub-nival sites (2650 and 2880 m) and a nival site (3440 m) in Austrian Alps.

	Sub-nival (wks)	Nival (wks)
Snow-melt to anthesis	2-3	**4**
Anthesis to mature fruit	4-5	**2-9**
Mature fruit to onset of winter	4-6	**1**
Mean seed/ovule ratio	0.5-0.8	0.4-0.6

At high altitudes, *R. glacialis* needs double time for seed development but runs risk of seeds not maturing in time. Only 1 week between maturation and onset of winter.

Right at edge for seed maturation. High germination capacity if mature seeds are produced.

Climatic tolerances of alpine and nival ('high alpine') plants

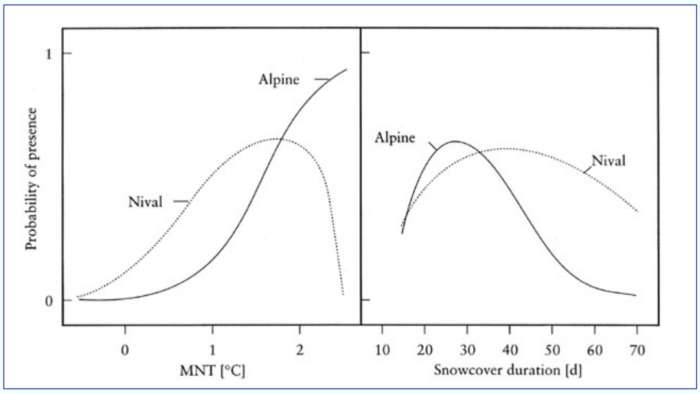
Gottfried *et al*. 2002

Austrian Alps 2900-3500 m 32 temperature recorders

Mean night-time temperature (MNT) and snow-cover duration at 32 localities recorded at every 1.5 hours between 1 May 1998 and 31 July 1998

6 Alpine species, 8 nival zone species

Fitted statistical model for probability of occurrence in relation to MNT and snow-cover duration



Gottfried *et al.* (2002)

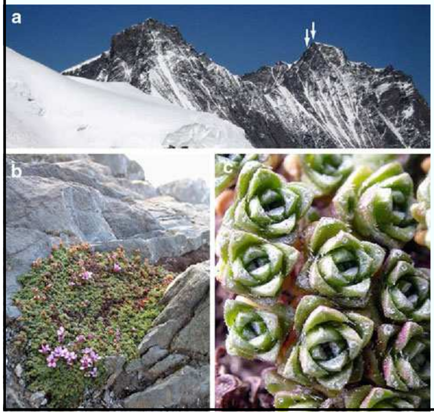
Alpines – higher mean night-time temperatures (>2°C) and early snow melt (ca. 25 days after 1 May)

Nival species – lower mean night-time temperature (1.5°C) and late snow melt (40-50 days after 1 May)

Where is the coldest place on Earth with angiosperm life?

Körner (2011)

4505-4543 m near the summit of the Dom, the highest mountain in Switzerland (4545 m) near the Matterhorn (4478 m), and third highest in the Alps.



Cushions of *Saxifraga oppositifolia* 4505-4507 m, >30 yrs old. Also lush moss flora (3 spp.), lichens (>3 spp.), fungi (7 spp.), and arthropods (Collembola and mites)

Thermal conditions assessed with a data logger.

2008-09 growing season had 66 days with a daily mean rooting (2-3 cm below ground) temperature > 0°C

Degree hours >0°C sum to 4277 °hours = 178 °days

Absolute winter minimum = -20.9°C

Absolute summer maximum = 18.1°C

Mean temperature for growing season = 2.6°C

All plant parts including roots experience temperatures <0°C every night

Colder than in the Himalaya or Svalbard in growing season

	Dom (4543 m)	Himalaya (5960 m)	Svalbard (450 m)
Absolute minimum (°C)	**-21**	**-20**	-13
Absolute maximum (°C)	18.1	**11.8**	**12.0**
Seasonal mean (°C)	**2.6**	4.0	4.8
Mean of warmest month (°C)	**2.8**	-	4.7
Duration of growing season			
Degree days	**178**	290	210
Hours >3°C	**585**	1085	893
Hours >0°C	**1053**	1684	1189

Likely limit for vascular plant growth to persist may be 60-70 day growing season with at least 1 hour >3°C or a daily mean >0°C in the uppermost rooting zone) and a seasonal mean top soil temperature *ca*. 2.6°C at roughly 180 degree days >0°C over entire growing season.

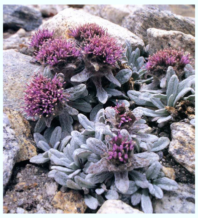
Do not know about absolute limits for sexual reproduction.

Dom’s *Saxifraga* may be a result of natural ‘transplant’ in one or few favourable seasons in recent past.

Once established, can persist even beyond species’ reproductive range. Critical role of plant establishment and possible role of chance events in extreme habitats.

What about plant life at the highest places vascular plants can grow on Earth?

In Himalaya, highest known vascular plants are



Saussurea gnaphalodes at 6400 m

Arenaria bryophylla at 6180 m

Ermania himalayensis at 6300 m

Highest stand of vegetation (9 species) at 5960 m

Highest closed sward of vegetation at 5500 m

Often sharp transition at 5500 m, plants become much more sparse. Potentially 900 m available for occupation today (assuming no climate change), about 6°C. Limiting factors may include available habitat, presence of soil, nutrients, etc. Very barren landscape.

What is known about control of upper elevational limit of vascular plants in Himalaya?

Kliměs & Doležal (2010) experimental transplants in E Ladakh from 5800 m to 5960 m, 6030 m, and 6160 m.

Ten years later, *Waldhemia* survived at 6030 m but not at 6160 m.

Suggests physiological constraints as well as lack of suitable habitat.

AQUATIC PLANTS AND EXTREME COLD

Recently recorded at 4760 m in lakes on the southern slope of Cho Oyo, east of Mt. Everest. Possibly a recent invasion in response to longer ice-free season as a result of global warming.

Ranunculus trichophyllus

Cho Oyo (8153 m)
Photo: Harry Jans

High winds characteristic of Alpine World

Winds up to 100-200 km per hour can occur on ridges and summit tops, resulting in bare open gravel areas with very sparse vegetation and a few species adapted to extreme winds.

How do plants survive?

Grow under stones – shelter

Low transpiration rate

Cushion or mat form – conserve heat and moisture

Thin flexible leaves – e.g. grasses

Hunt Mountain, Big Horns, Wyoming

Aquilegia jonesii, Wyoming

Douglasia montana, Montana

Artemisia norvegica, Norway

Luzula confusa, Norway

Mountains of southern Andes are some of the windiest mountains in the world.

Cushion growth-form is more frequent there than anywhere else.

Tight cushions reduce water and heat loss, and their aerodynamic form reduces wind and ice abrasion.

Of world's cushions;

- 50% are in the Andes
- 16% in Asia (including Himalaya)
- 14% in New Zealand
- 12% in the European Alps
- only 3% in the arctic
- and 2% in North America

Cerro Moyano, Argentina – 1100 m

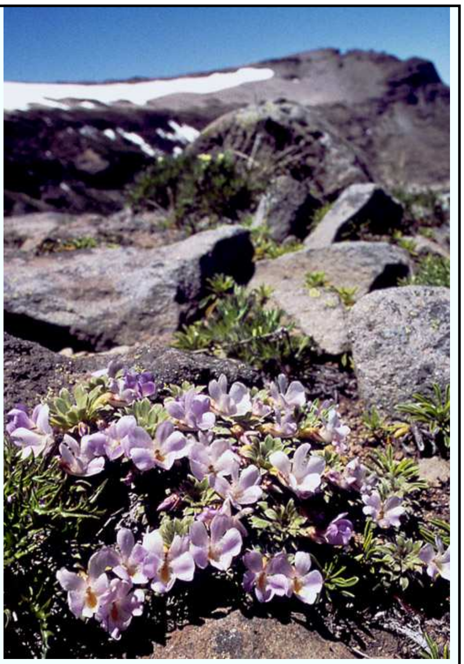
La Hoya, Argentina – 1850 m

Benthamiella longifolia, Argentina


Viola sacculus, Argentina


Viola dasyphylla,
Argentina

Viola auricolor, Argentina



Viola cotyledon, Argentina

Viola coronifera, Argentina

Viola petraea, Argentina

ADDITIONAL ADAPTATIONS FOR GROWTH TO THE ALPINE AND ARCTIC WORLD

Other adaptive growth-form features

1. Small above-ground biomass (50-80% less), large below-ground biomass (25-60% more). Leaf mass ratio (% green leaf dry matter within total plant dry matter) of alpine and arctic communities 20-25% worldwide but individual plants 8-48%

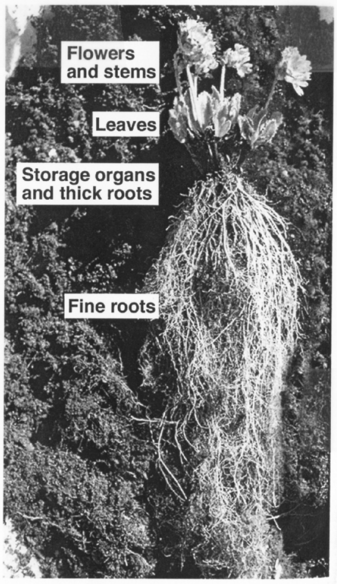


Fig. 12.13. Dry matter fractionation in alpine plants into flowers and stems, leaves, special storage organs and fine roots can influence whole plant carbon gain. Here, an excavated individual of *Primula glutinosa* at 3000 m elevation in the Ötztal Alps, Tirol

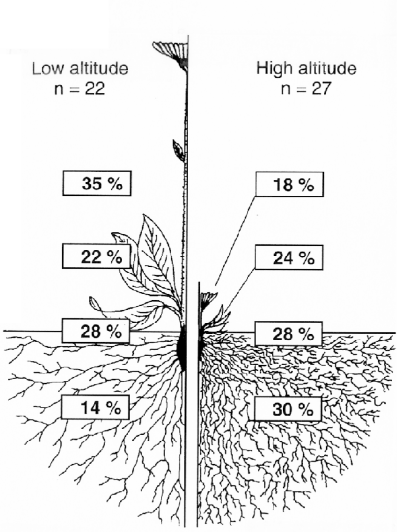


Fig. 12.14. Dry matter allocation in perennial herbaceous plant species from low and high altitudes in the Alps (stem plus flower, leaves, special storage organs plus thick roots, fine roots). (Körner and Renhardt 1987)

ROOT BIOMASS

ROOT BIOMASS

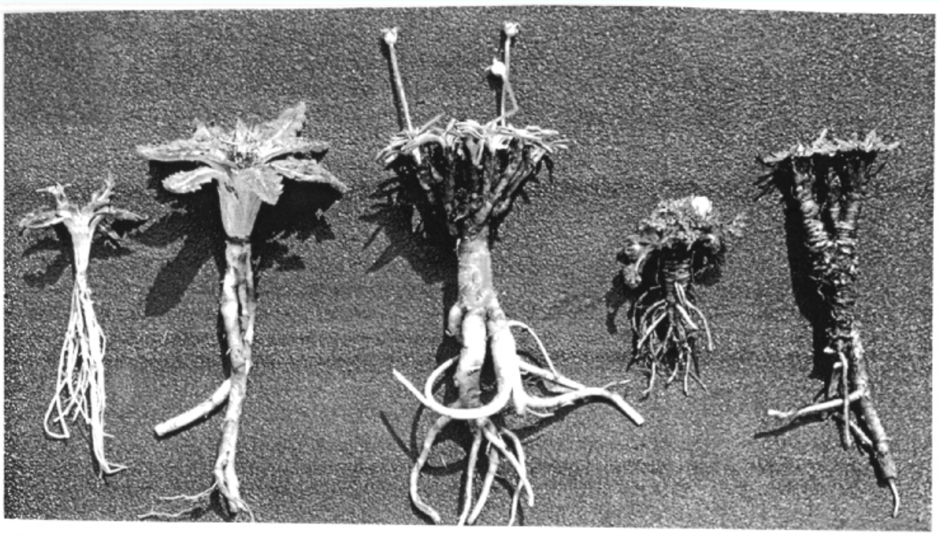


Fig. 12.16. While alpine plants commonly do not allocate more biomass to special belowground storage organs (tubers, rhizomes, thick roots) than comparable low altitude plants, these specimens from 4250 m elevation in northwest Argentina show massive investments in tap roots (more than 50% of total plant mass).

Claytonia megarhiza, Colorado - deep roots

CONSTANT LEAF MASS RATIO

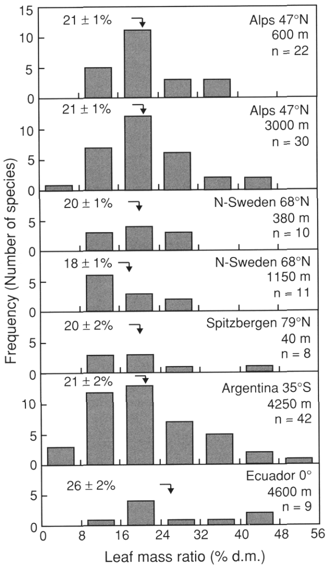
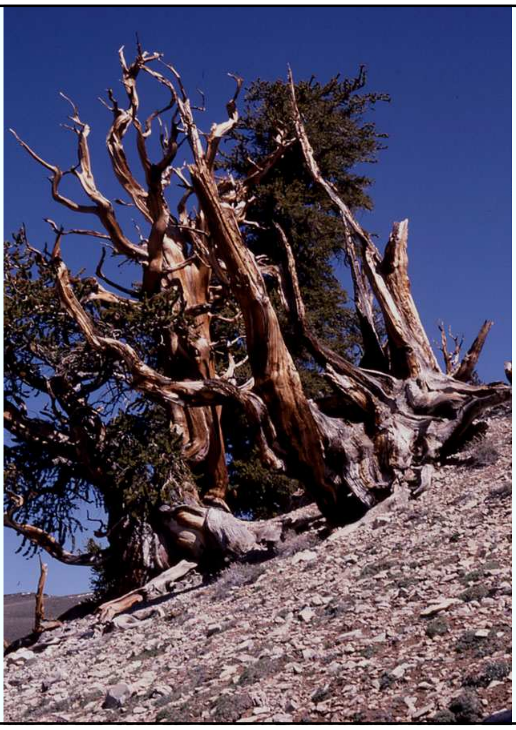


Fig. 12.15. Frequency distribution of leaf mass ratios in perennial herbaceous plant species excavated at various high and low altitude sites. Data for the Alps are from the Ötztal-Alps in Tirol and from low altitude meadows near Innsbruck (47°N lat). Data for Sweden are from Mount Slåttatjåkka near Abisko and Abisko itself (68°N lat) and those from Spitzbergen from fellfields near Ny Ålesund (79°N lat). Argentinean samples were collected in the Cumbres Calchaquies Mts. near Tucuman (26°S lat) and those from Ecuador near the upper limit of plant growth on Mt. Cayambe (0°). *Arrows* indicate means ± SD. (Körner and Renhardt 1987; Körner 1994; Prock and Körner 1996)

Other adaptive growth-form features

1. Small above-ground biomass (50-80% less), large below-ground biomass (25-60% more).
2. Average leaf life-span 2-3 times longer than in lowlands
3. Very slow growth rate, great age, often poor competitors

Pinus longaeva,
California - great age



Dendrosenecio keniodendron,
Kenya – great age

Junellia patagonica, Argentina - great age

Other adaptive growth-form features

1. Small above-ground biomass (50-80% less), large below-ground biomass (25-60% more).
2. Average leaf life-span 2-3 times longer than in lowlands
3. Very slow growth rate, great age, often poor competitors
4. Alpine plants are generally more HAIRY than their lowland relatives.

   Hair cover creates a local micro-environment by trapping a layer of still air thus reducing water and heat loss. Also heats flower and increases seed ripening = "micro-greenhouse" effect.

   Silver hairs reflect damaging radiation away from leaves. They prevent liquid water reaching the leaf surface but they maintain a humid atmosphere, thus reducing water loss.

Greenland

Norway

Eriophorum scheuchzeri, - hairy heads
Hairs also used as parachutes for seed dispersal

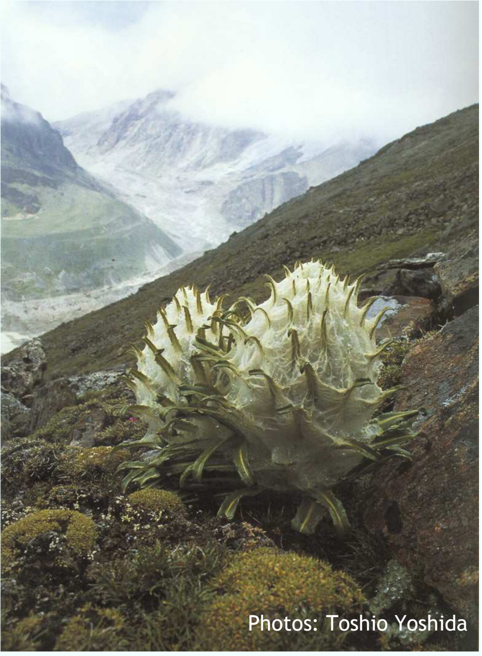
Hamadryas kingii,
Argentina – hairy
leaves

Pedicularis kanei,
Alaska – hairs

3-5ºC warmer inside than outside

Cirsium scopulorum,
Colorado - hairs

Saussurea medusa,
China - hairs

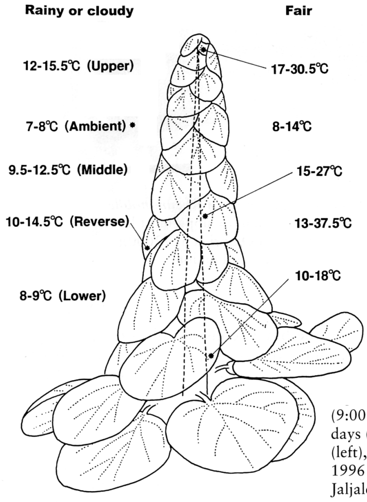

Photos: Toshio Yoshida

Saussurea gossipiphora, Nepal – hairs

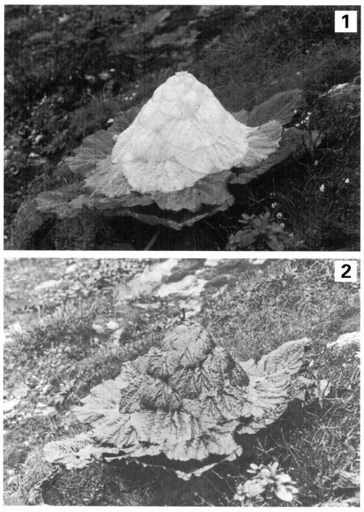
Saussurea tridactyla, Nepal – hairs

Other ways of protecting and warming flowers

Rheum nobile, Bhutan - 'greenhouse'



Rheum nobile and daytime (9:00 to 15:00) temperatures on fair days (right) and rainy or cloudy days (left), measured from 3 to 14 August 1996 at Banduke, 4250 m, in the Jaljale Himal, eastern Nepal.



Figures 1, 2. Flowering shoot and rosette of *Rheum nobile*. Fig. 1. Photo through a UV absorbing filter. The translucent bracts are reflected in white and the rosulate leaves are in black. Fig. 2. Photo through a UV transmitting filter. The bracts and leaves are both reflected in black.

Silene uralensis,
Spitsbergen -
'greenhouse'

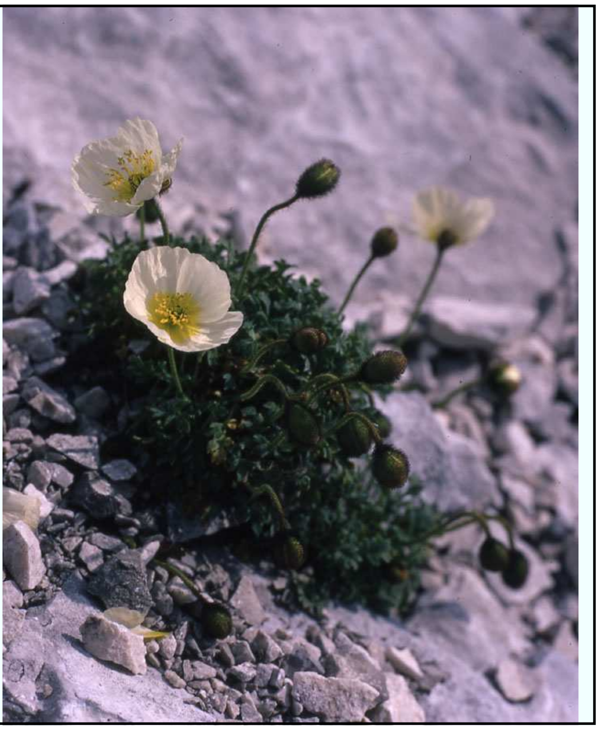
Other adaptive growth-form features

1. Small above-ground biomass (50-80% less), large below-ground biomass (25-60% more)
2. Average leaf life-span 2-3 times longer than in lowlands
3. Very slow growth rate, great age, often poor competitors
4. Hairy – traps a layer of still air, reduces water and heat loss and heats flowers and increases seed ripening ("Greenhouse" effect)
5. Parabolic flower shape concentrates heat in the middle of the flower and flowers track the sun (heliotropism) as it circles overhead. Reflects the warmth from the sun's rays towards the flower centre. Helps to attract pollinating insects and to speed seed development

Ranunculus glacialis, Switzerland - parabolic flowers and heliotropism
flowers close & turn deep pink, making a small greenhouse

Papaver kerneri, Austria - parabolic flowers and heliotropism

Papaver rhaeticum,
Italy - parabolic flowers and heliotropism



Papaver ernesti-mayeri,
Slovenia - parabolic flowers and heliotropism

Hymenoxis grandiflora, Colorado - huge flowers all facing same direction

Other adaptive growth-form features

1. Small above-ground biomass (50-80% less), large below-ground biomass (25-60% more).
2. Average leaf life-span 2-3 times longer than in lowlands
3. Very slow growth rate, great age, often poor competitors
4. Hairy – traps a layer of still air, reduces water and heat loss and heats flowers and increases seed ripening ("Greenhouse" effect)
5. Parabolic flower shape concentrates heat in the middle of the flower and flowers track the sun (heliotropism) as it circles overhead
6. Grey or silver leaves – reflect damaging UV radiation. May also be able to absorb heat in near infrared range. Prevents water from reaching the leaf-surface. Silver hairs may achieve the same purpose. Protection from 'sun-burn'

Celmisia semicordata, New Zealand - UV radiation

Raoulia grandiflora, New Zealand

Haastia recurva, New Zealand

Leucogenes grandiceps, New Zealand

Leucogenes neglecta, New Zealand

Raillardia argentea, Oregon

Leontopodium alpinum, Slovenia

Other adaptive growth-form features

7. Resistance, in snow-bed plants, to fungi and other microbes that live in snow

   Prolonged snow-lie is part of the Alpine World.

   Snow can persist for up to 330 days a year and yet vascular plants can still grow.

   Snow is good. It prevents exposure to low temperatures, winter desiccation, and high solar radiation.

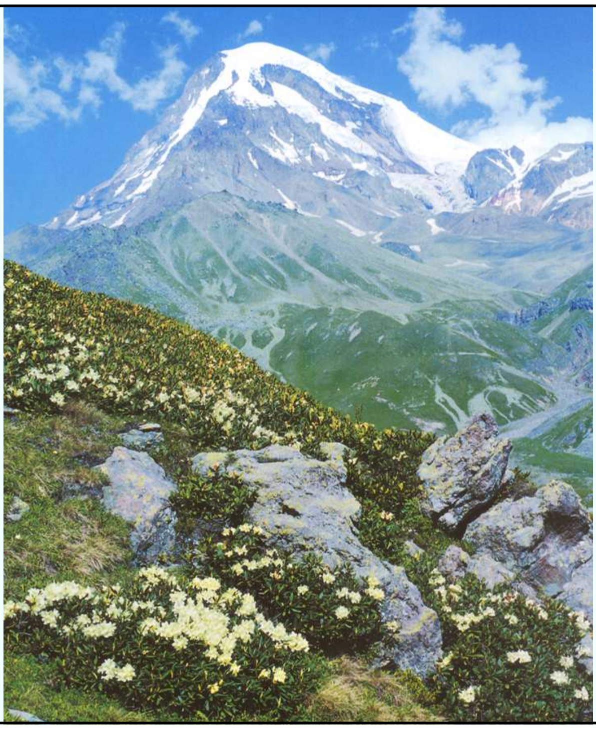
   Snow is bad. Its adverse effects are a very short growing season, water-logged soils, attacks from snow-living fungi and other microbes that live in the snow, and intensive below-snow rodent activity (lemmings, pikas).

   Many alpines are confined to snow-beds, known as CHIONOPHILES. Presumably immune to snow-mould fungi and bacteria and have growth rhythms or detection sensors to match closely the timing of snow-melt.

Soldanella alpina, Switzerland - snow-bed 6 days later

Ranunculus adoneus,
Colorado

Erythronium grandiflorum,
Wyoming - snow-bed



Caucasus
Mountains,
Russia

Corydalis conorhiza, Caucasus, snow-bed

Has a recently-discovered ‘extra’ root system, so-called snow-roots

Onipchenko et al. (2009)

As snow melted, a layer of matted snow-roots emerged from the snow. An addition to normal roots that anchor the plant in the soil and absorb nutrients.

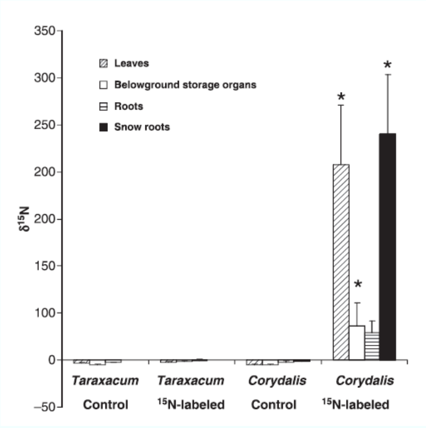

Onipchenko et al. (2009)

In alpine areas plant growth limited by N and P.

Corydalis gets P from fungal partners, but what about N?

Are snow-roots important?

Watered snow with ^{15}N and compared *Corydalis* with *Taraxacum* (no snow-roots), plus controls with no ^{15}N.



Can see ^{15}N taken up by snow-roots and in leaves of *Corydalis*

Onipchenko et al. (2009)

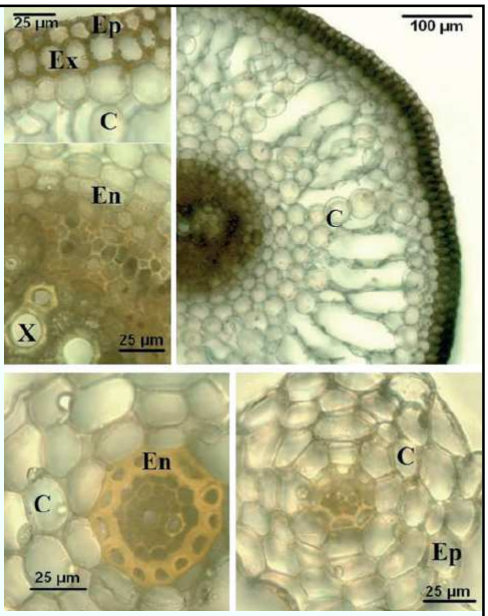
Snow-roots different anatomically from soil roots

- very fine (0.1 mm diameter)

- dense network covering a vast area under the snow, like a filamentous alga

- disappear when snow melts, hence never noticed until recently!

What about other snow-bed plants – do they have snow-roots?



Onipchenko et al. (2009)

Just as snow melts, flush of flowers (e.g. *Primula*)

Primula minima, Austria

Primula angustifolia, Colorado

Primula cusickiana, Idaho

Snow melt-water provides specialised conditions for many alpines

Saxifraga aizoides, Norway

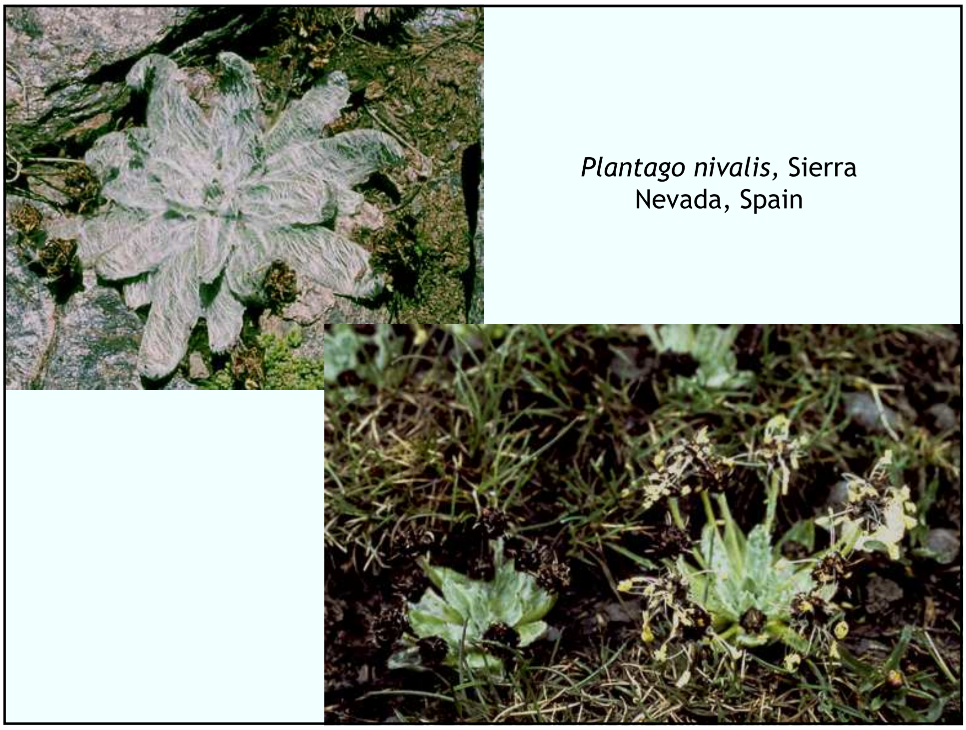
Primula parryi, Colorado

Trollius laxus, Wyoming

Caltha leptosepala, Colorado

Crocus chrysanthus, Turkey

Eranthis hyemalis, Turkey



Plantago nivalis, Sierra Nevada, Spain

Ranunculus acetosellifolius, Sierra Nevada, Spain

Mimulus cupreus,
Argentina

Other adaptive growth-form features

7. Resistance, in snow-bed plants, to fungi and other microbes that live in snow
8. Clonal vegetative growth – stolons, rhizomes, mats

Saxifraga flagellaris, Colorado - runners

Other adaptive growth-form features

7. Resistance, in snow-bed plants, to fungi and other microbes that live in snow
8. Clonal vegetative growth – stolons, rhizomes, mats
9. Asexual reproduction – bulbils, vivipary

Saxifraga cernua,
Norway - bulbils

Bistorta vivipara,
Norway - bulbils

Other adaptive growth-form features

7. Resistance, in snow-bed plants, to fungi and other microbes that live in snow
8. Clonal vegetative growth – stolons, rhizomes, mats
9. Asexual reproduction – bulbils, vivipary
10. Spread plant development over several seasons

Ranunculus nivalis,
Sweden - hairs and
pre-formed buds

Other adaptive growth-form features

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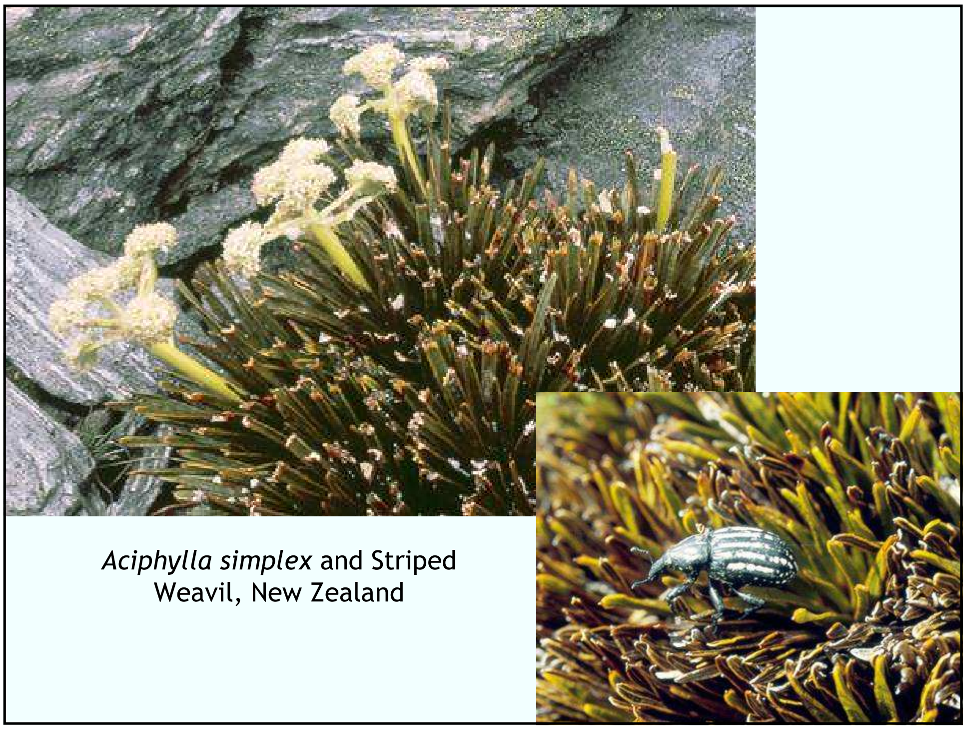
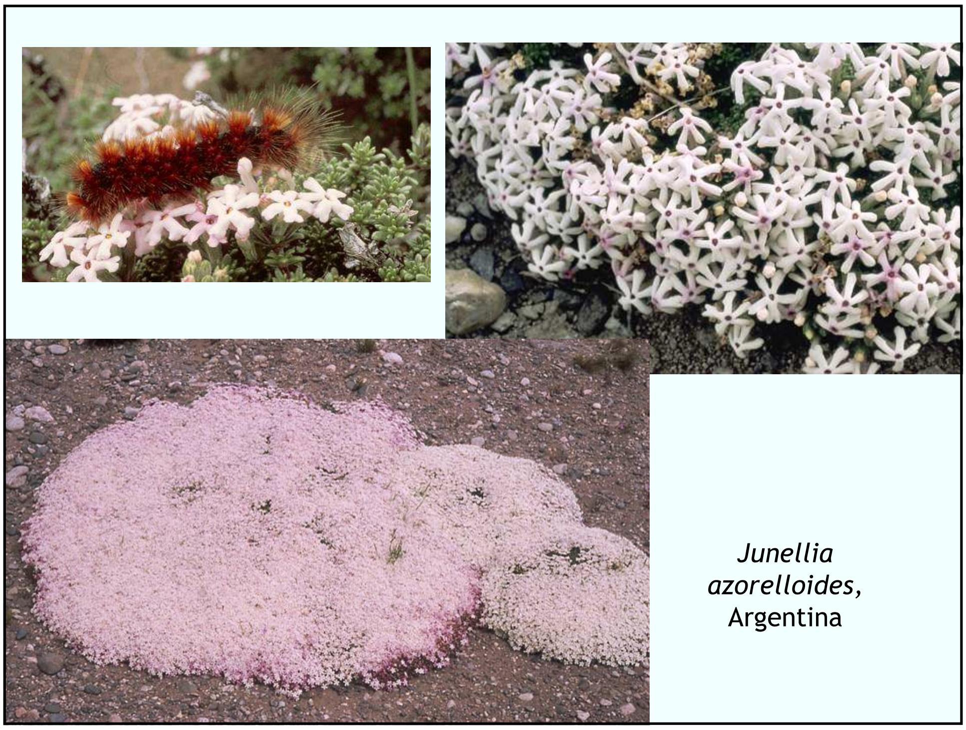
8. Clonal vegetative growth – stolons, rhizomes, mats
9. Asexual reproduction – bulbils, vivipary
10. Spread plant development over several seasons
11. Defence against natural vertebrate and invertebrate herbivores

Marmot, Colorado



Aciphylla simplex and Striped Weavil, New Zealand



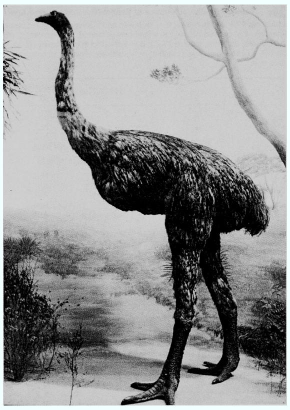
Junellia azorelloides, Argentina

Abundance of spiny 'vegetable hedgehogs' in arid mountains may be a defence to minimise damage by grazing

Vella spinosa, Spain - spines

Astragalus balearicus,
Mallorca

Scree plants and plants of very open habitats may have leaves almost the same colour as the rocks or soil, possibly providing camouflage and protection from herbivores, including the extinct moa (13 species).



Ranunculus haastii, New Zealand - camouflage

Ranunculus crithmifolius, New Zealand - camouflage

Leptinella atrata, New Zealand - camouflage

Myosotis elderi, New Zealand - camouflage

Lignocarpa carnulosa,
New Zealand -
camouflage

In grassland

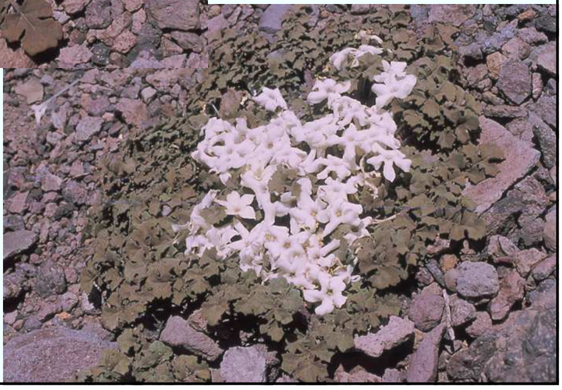
On scree

Geranium sessiliflorum, New Zealand

Notothlaspi rosulatum, New Zealand - camouflage

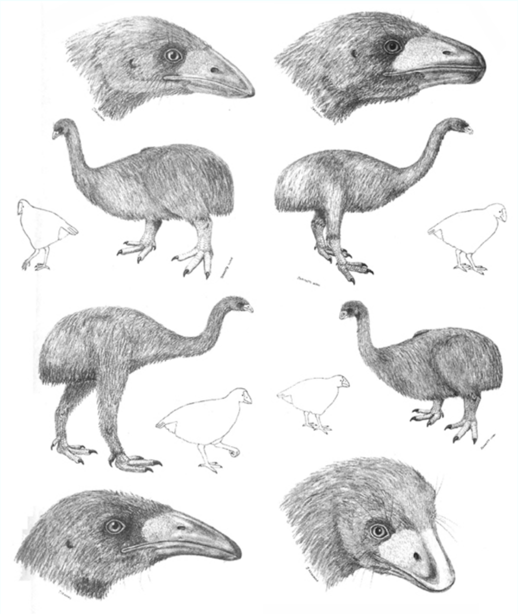
Viola vulcanica, Argentina - camouflage

Viola columnaris,
Argentina -
camouflage



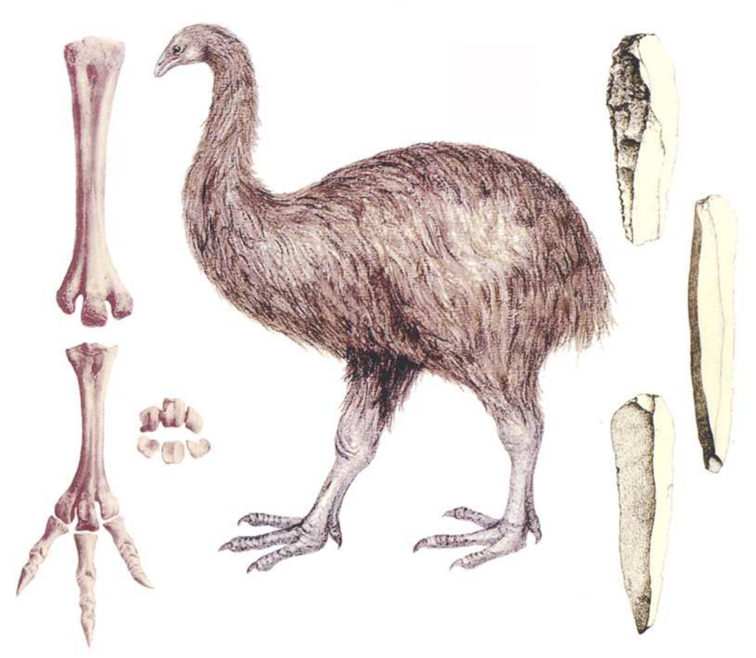
Jaborosa volkmannii,
Argentina - camouflage

Several extinct species of moa in New Zealand



Two were 'alpine' species, two were 'subalpine' species

(Scale is large chicken, 40 cm high)



Moas had acute vision, small eyes, and a poor sense of smell.

Colour and form were significant in food choice.

Colours at the indigo-violet end of the spectrum not perceived well. Would make plants less obvious. Plants purplish-black, brown, or dark bronze difficult for moas to see.

Selection pressure against predators greatest at low population density, e.g. in extreme habitats such as steep (45°) screes.

Other adaptive growth-form features

7. Resistance, in snow-bed plants, to fungi and other microbes that live in snow
8. Clonal vegetative growth – stolons, rhizomes, mats
9. Asexual reproduction – bulbils, vivipary
10. Spread plant development over several seasons
11. Defence against natural vertebrate and invertebrate herbivores
12. Nitrogen fixation by symbiotic root-nodules and by cyanobacteria on soil crusts, in lichens, and in mosses, or obtaining nitrogen by trapping insects (insectivorous plants)

Dryas drummondii, Yukon - nitrogen fixation

Hedysarum mackenzii, Yukon – nitrogen fixation

Lupinus aridus var. *ashlandensis*, Oregon – nitrogen fixation

Oxytropis nana, Wyoming – nitrogen fixation

Pinguicula alpina, Norway - insectivorous

Darlingtonia californica, California - insectivorous

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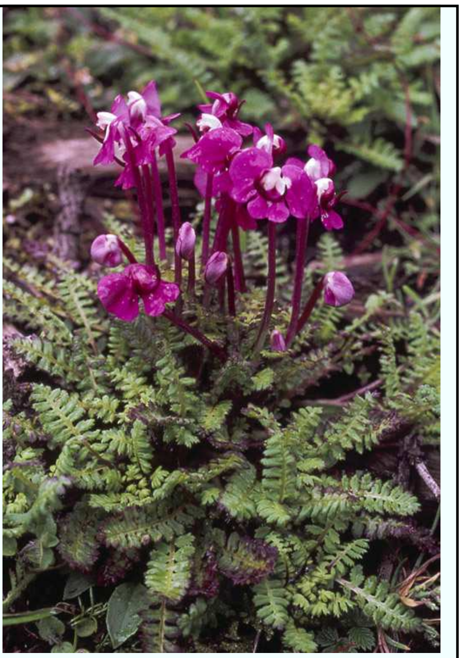
13. Abundant root mycorrhiza or semi-parasitic nutrition

Rhododendron macrophyllum, Oregon – root mycorrhiza

Pedicularis oederi, Norway - hemi-parasite

Pedicularis tricolor, Sichuan - hemi-parasite

Pedicularis przewalskii, Qinghai - hemi-parasite



Pedicularis siphonantha, Bhutan – hemi-parasite

Pedicularis bella, Bhutan – hemi-parasite

Pedicularis decorissima, Sichuan – hemi-parasite

Bartsia alpina, England – hemi-parasite

Castilleja applegatei, Oregon – hemi-parasite

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14. Tolerance of heavy metals in soils

Mountains usually contain mineral-rich veins that have commonly been mined. The mine waste is rich in heavy metals (e.g. lead, copper, zinc) and supports specialised alpines that are able to avoid being poisoned.

Mine, Mosquito Pass, Colorado with *Physaria alpina*

Physaria alpina, Colorado

Lychnis alpina,
Norway

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14. Tolerance of heavy metals in soils
15. Deep but very narrow roots to allow growth in rock crevices

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Some habitats (e.g. crevices in vertical cliffs, screes, boulder fields, wind-exposed ridges) appear to have NO SOIL, but alpines still manage to grow. Have deep but narrow roots and somehow manage to get a root-hold.

Cliff plants – chasmophytes; many are local endemic plants, restricted to a small geographic area.

Campanula zoysii, Slovenia

Saxifraga kotschyii, Turkey

Telesonix jamesii, Colorado

Gladiolus flanaganii, Drakensberg

Viola cazorlensis, Spain

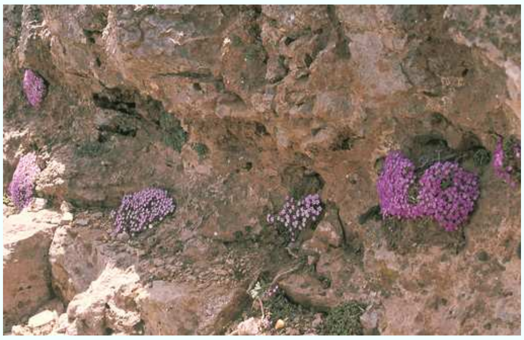
Ourisia fragans, Argentina

Kelseya uniflora, Idaho

Paraquilegia anemonoides, Sichuan

Physoplexis comosa, Dolomites

Dionysia (Primulaceae) – the ultimate cliff-crevice cushion plant. Confined to Iran, Afghanistan, and Iraq, also one species in Oman and one in Pamirs



Habitat of *Dionysia bryoides*, Iran

Habitat of *Dionysia haussknechtii*, Iran

Dionysia bryoides, Iran

Dionysia haussknechtii, Iran

Dionysia lamingtonii, Iran

Dionysia mozzafarrianii,
Iran

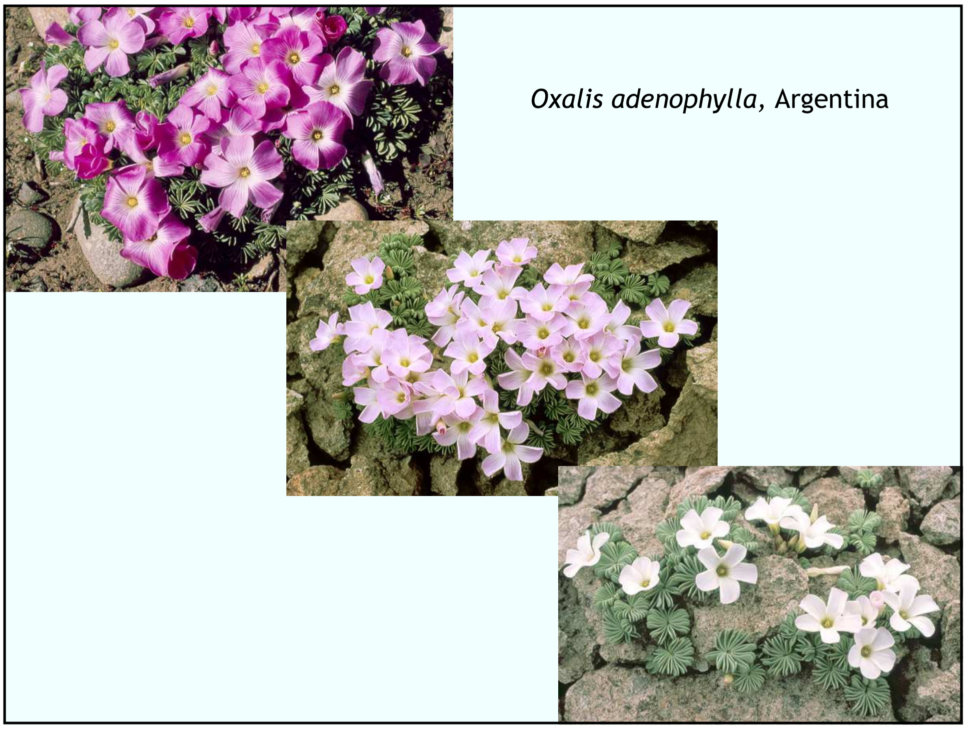
Screes and blockfields

Thlaspi rotundifolia,
Dolomites

Eriophyton wallichii, Bhutan

Corydalis melanochlora, Sichuan

Collomia debilis, Utah



Oxalis adenophylla, Argentina

Oxalis erythrorhiza, Argentina

Ranunculus buchananii,
New Zealand

Ranunculus semiverticillatus, Argentina

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15. Deep but very narrow roots to allow growth in rock crevices
16. Large, attractive flowers

Why do so many alpine plants (to our eyes!) have such beautiful flowers, often very large in proportion to the plant?

They need to attract POLLINATORS (not only photographers!)

Sexual reproduction as a result of pollination is vital to diversify the gene pool.

Attractive flowers can be:

1. Single large flowers

Campanula lasiocarpa, Yukon

Campanula shetleri, California

Pulsatilla patens,
Wyoming

2. Massed inflorescences

Polemonium viscosum, Wyoming

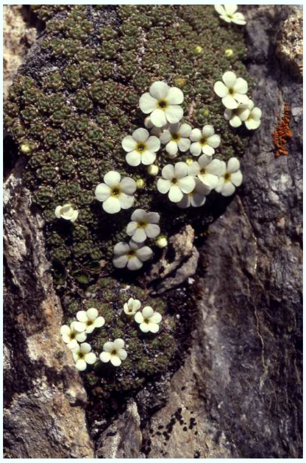
Hymenoxis grandiflora, Colorado

3. Massed on cushions

Townsendia leptotes, Wyoming

Phlox diffusa, Oregon

4. Scented


Androsace helvetica


Androsace alpina


Eritrichium nanum

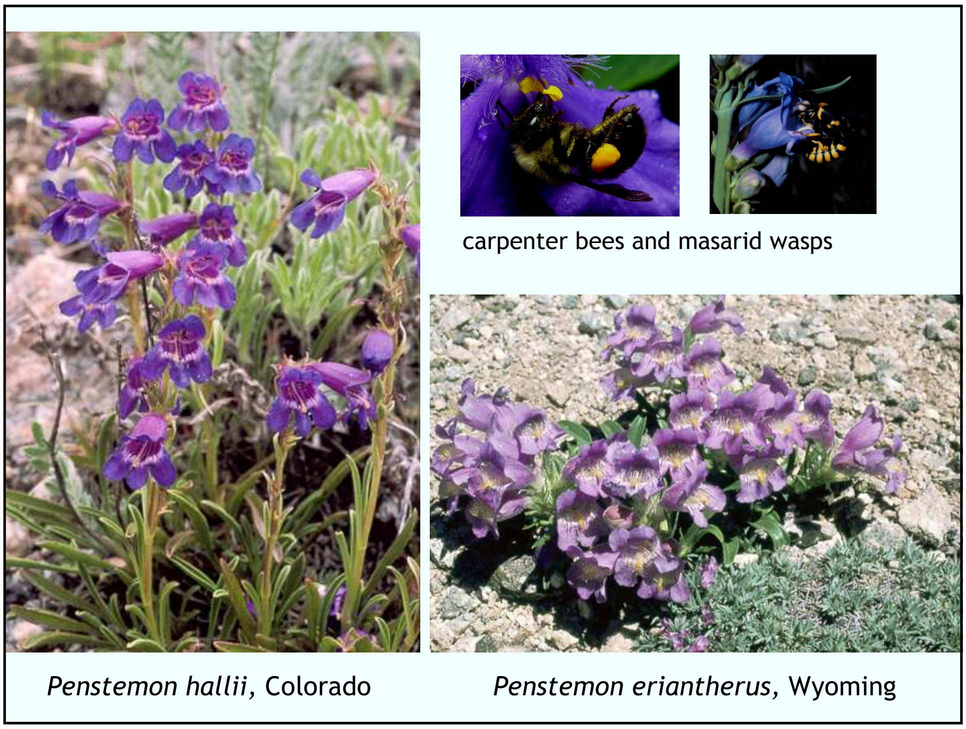

Viola sacculus, Argentina (giant!)

Viola columnaris, Argentina

5. Specialised for specific pollinators

Calceolaria uniflora, Argentina – least sandpiper

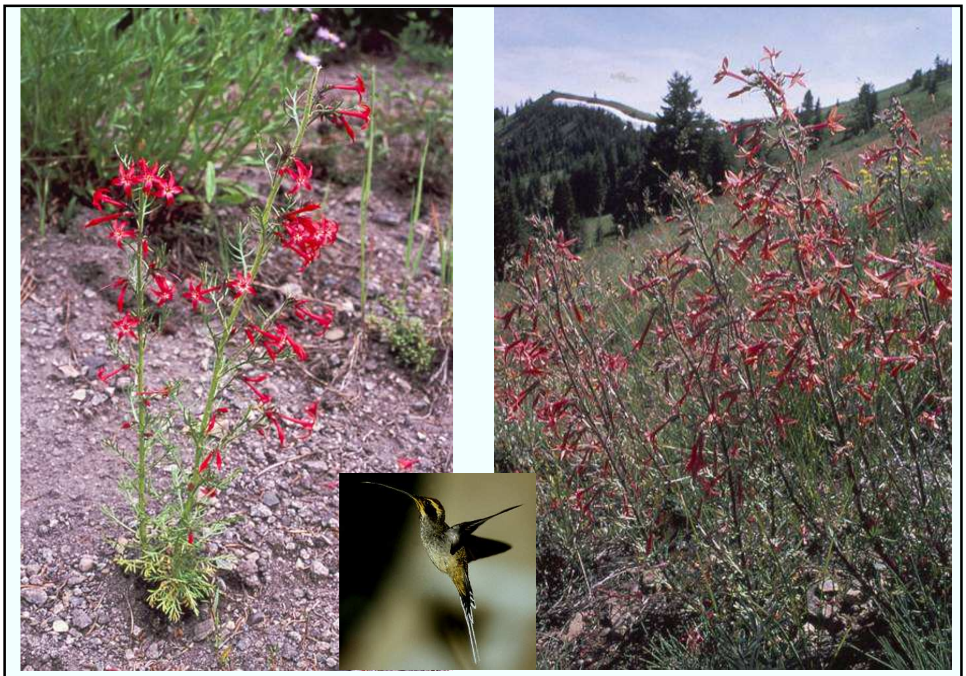
Incarvillea compacta, Sichuan - bumblebees



carpenter bees and masarid wasps

Penstemon hallii, Colorado

Penstemon eriantherus, Wyoming



Gilia aggregata, Colorado – humming birds

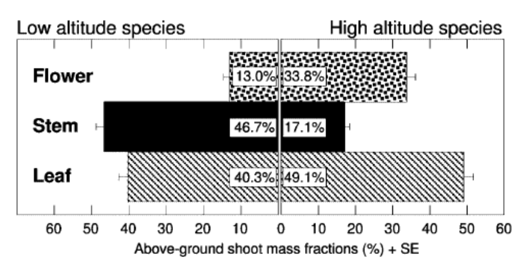
Penstemon eatonii, Utah - hummingbird

Kniphofia caulescens, Drakensberg – sun birds

Zaluzianskya microsiphon, Drakensberg – tangle-veined fly

Is there a relationship between altitude and its decreasing pollinator sources and the allocation of plant growth to flowers?

Fabbro & Körner (2004) compared 20 spp. at 600 m altitude with 30 spp. at 2700 m altitude



No difference in leaf mass

Three times smaller fraction allocated to stems in alpines

Nearly three times greater allocation to flowers in alpines

At high altitude, smaller allocation to stems, associated with a change in function from **leaf support** for photosynthesis at low altitudes to **flower support** at high altitudes. Plants generally smaller.

Display area and biomass of individual flowers **similar**.

All flowers together attracted pollinators with about the same total display area relative to overall plant size.

Alpine flowers **maintain flowers longer** than lowland species, presumably to attract pollinators over a longer period.

Small size and large flowers can result in **self-shading**, suggesting that carbon gain is not a priority.

As alpine stems are short, flowers may be warmer, which may increase seed-set and attractiveness for pollinators.

Alpines invest more biomass in structure for sexual reproduction than maximising vegetative growth in alpine plants.

Other adaptive growth-form features

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14. Tolerance of heavy metals in soils
15. Deep but very narrow roots to allow growth in rock crevices
16. Large, attractive flowers
17. Seed production

Many alpines produce seeds regularly. Some germinate immediately (e.g. *Primula, Celmisia, Pulsatilla*).

Most need cold dormancy and germinate next spring.

Some can survive several winters or even decades in 'seed bank'.

A few need extreme conditions for germination.

Diapensia lapponica, Swedish Lapland
Needs run of 5-10 yrs of cold summers for seedling establishment

RECENT CHANGES AND THE FUTURE FOR ALPINE PLANTS AND ARCTIC PLANTS

Last 100 years

Decline of traditional grazing practices has resulted in regrowth of scrub and forest. Tree-lines have risen in the last 50 years - ? land-use changes or climate changes or both.

Hydroelectric development, flooding of valleys, and river regulation.

Tourism, trampling, ski centres, use of artificial snow, mining - generally rather localised.

In northern areas, lichen- and bryophyte-rich vegetation has declined because of trampling and too much or too little grazing. Perhaps also because of changes in atmospheric inputs as a result of 'global change'.

Reports on seedling establishment and shift of tree-line in last 50-100 years

Area	Since	Shift (m)	Genus
Chile	1850	10	*Nothofagus*
NW Canada	1850	10-20	*Picea*
N Urals	1920	100-500	*Larix*
New Zealand (South Island)	1950	10	*Nothofagus*
Sweden	1960	120-375	*Betula, Picea, Pinus*
Spain	1955	70	*Fagus*
Australia	1967	15	*Eucalyptus*
Bulgaria	1950	130	*Pinus*
Oregon, USA	1980	10	*Abies*
Montana, USA	1973	10-15	*Abies, Picea, Pinus, Larix*

GLOBAL CHANGE

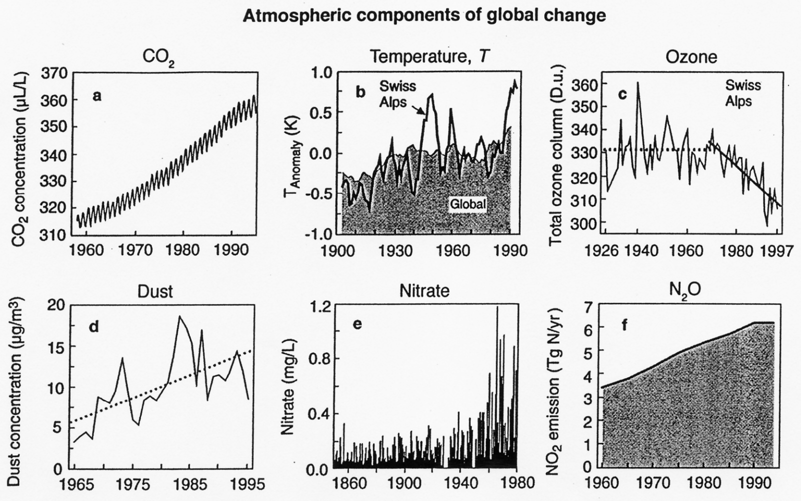
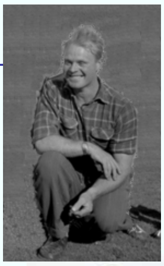


FIG. 1. Major components of global atmospheric change: (a) CO_2 enrichment (Keeling 1993: Fig. 2); (b) global warming with strong regional deviations as illustrated for the Alps (Beniston et al. 1997: Fig. 1); (c) the ozone column above 1900 m elevation in central Europe (Staehelin et al. 1998: Fig. 1) (D.u., a Dobson unit = 100 hPa·cm); (d) the mineral dust surface concentration (Moulin et al. 1997: Fig. 4); (e) wet nitrogen deposition as documented in glacier ice (Döscher et al. 1995: Fig. 1); (f) trends in N_2O emission (Mosier and Kroeze 1998: Fig.2). All panels have been redrawn, after originals.

In last 150 years, atmospheric CO_2 concentrations and global temperatures have increased, as have atmospheric nitrogen levels.

Are alpine plants responding to these changes?



Jotunheimen mountains of central Norway

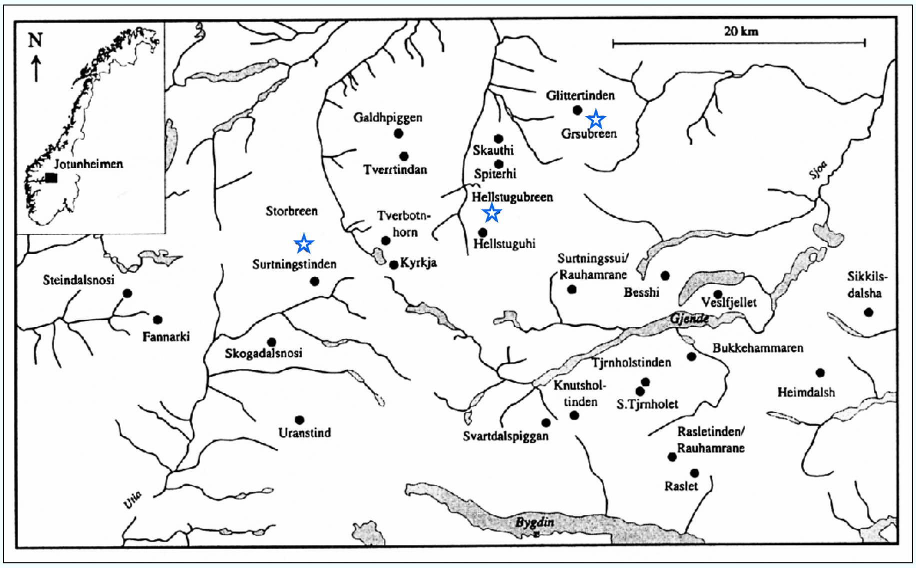
24 mountains surveyed by Reidar Jørgensen in 1930-1931

Re-located over 400 of his localities in 1998

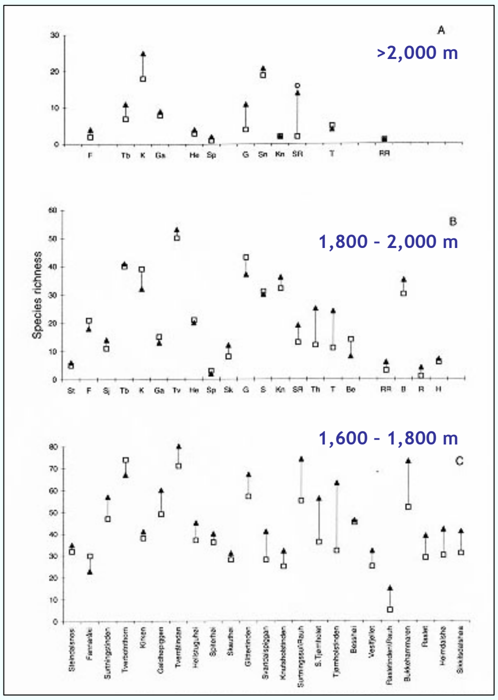
Could see how flora had changed in 68 years

Kari Klanderud and John Birks

Galdhoppigen, Norway



Map of Jotunheimen, central south Norway, showing the 25 mountains studied by Jørgensen (1933) and this study. Three local glaciers are indicated by stars.



Little change

Some increase

Big increase

Changes in species numbers

❑ 1930-31

▲ 1998

Some plants have extended their altitudinal limits in last 70 years by 200-300 m.

1. Dwarf-shrubs –
   - *Phyllodoce caerulea*
   - *Empetrum nigrum*
   - *Salix lapponum*
   - *Vaccinium myrtillus*
   - *Vaccinium vitis-idaea*

2. Grasses –
   - *Festuca vivipara*
   - *Deschampsia flexuosa*

Phyllodoce caerulea, Norway

Vaccinium myrtillus, Norway

Vaccinium vitis-idaea,
Swedish Lapland

Empetrum nigrum,
Norway

Salix lapponum,
Scotland

Some summit plants have **declined** in frequency in last 70 years (e.g. *Saxifraga cespitosa, Cerastium alpinum, Erigeron uniflorus, Ranunculus glacialis*).

Decline because of **direct warming** or, more likely, **increased competition** from faster-growing species expanding from lower altitudes.

Erigeron uniflorus
Norway

Cerastium alpinum
Norway

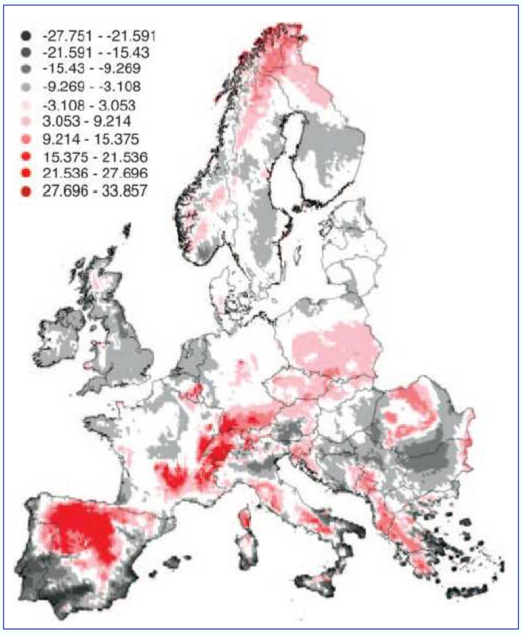
Saxifraga cespitosa
Norway

Similar floristic changes reported from Swiss and Austrian Alps, the Swedish mountains, north-east Greenland, and Glacier National Park, Montana.

Long-term future for high alpines is not good if they continue to decline, even on the highest mountains in the Alps or Scandinavia.

If global change and global warming continue to the extent predicted by climatologists, the Alpine World will be a very different place in a hundred years time compared to today.

Many species may have gone extinct or be committed to extinction because of climate warming, loss of specialised habitats (e.g. snow-beds), the absence of anywhere higher or cooler to spread to, and competition from larger, faster growing dwarf-shrubs and grasses that are rapidly moving upwards in response to climate warming.



Thuiller *et al.* (2005)

Attempt to assess species status by 2080 under various future climate scenarios. Main drivers are temperature and moisture changes.

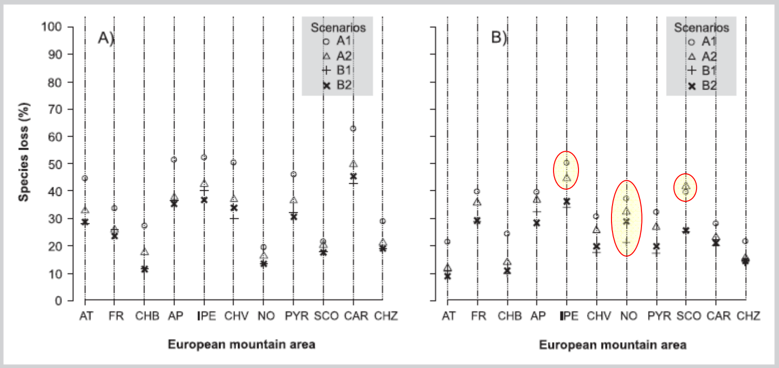
Excess species loss (red) in Alps, Pyrenees, central Spain, Balkans, Scandinavia, Carpathians, and Corsica.

Alpine flora ≈60% loss

Four different climate scenarios

EU scale extinction

Local scale extinction

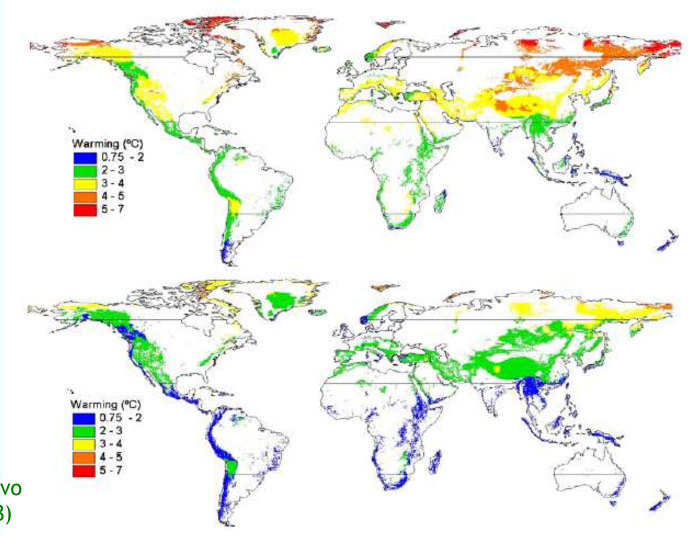


MRI (2007)

AT=Austrian Alps, FR=French Alps, CHB=Swiss Central Alps[1], AP=Apennines, IPE=Pyrenees[1], CHV=Swiss Western Alps, NO=Norway, P=Pyrenees[2], SCO=Scotland, CAR=Carpathians, CHZ=Swiss Central Alps[2]

Extinction rates generally >10%. At local scale, highest extinctions are predicted to be Pyrenees[1] and Scotland, followed by Norway

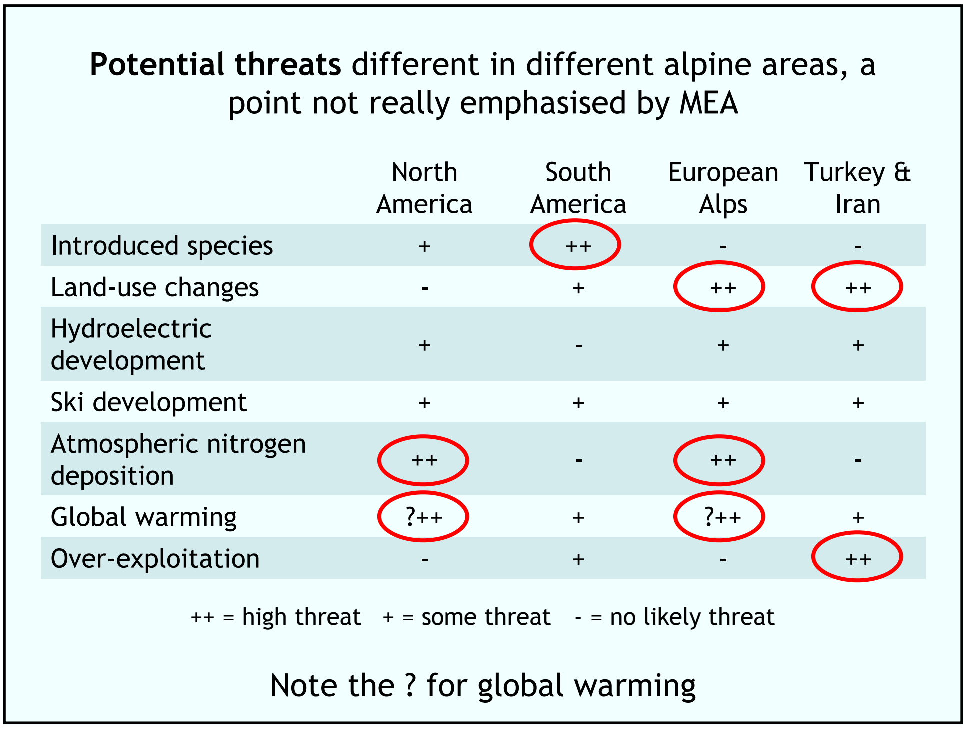
Projected warming by 2055 in alpine and arctic areas according to IPCC Fourth Assessment Report. Average of five climate predictions under two different future scenarios



Nogués-Bravo *et al.* (2008)

Order of temperature change (1=high, 13=low)

	2055	2085	
Northern Asia	1	1	←
N American Arctic	2	2	←
European Arctic	3	4	←
Central Asia (Himalaya, etc)	4	3	←
N Africa	5	6	←
N American Rockies	6	5	←
European Alps	7	7	
N and Central Andes	8	9	
Equatorial Africa	9	8	
South Africa	10	10	
Low Asia (e.g. Borneo)	11	11	
Southern Andes	12	12	
Australia/New Zealand	13	13	

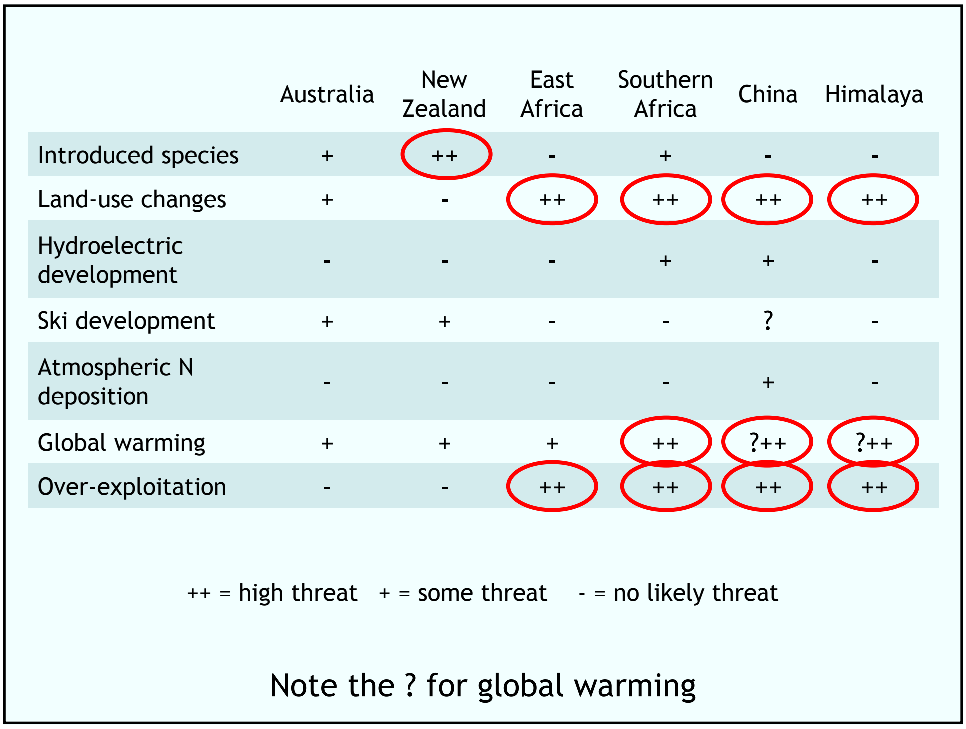


Potential threats different in different alpine areas, a point not really emphasised by MEA

	North America	South America	European Alps	Turkey & Iran
Introduced species	+	++	-	-
Land-use changes	-	+	++	++
Hydroelectric development	+	-	+	+
Ski development	+	+	+	+
Atmospheric nitrogen deposition	++	-	++	-
Global warming	?++	+	?++	+
Over-exploitation	-	+	-	++

++ = high threat   + = some threat   - = no likely threat

Note the ? for global warming



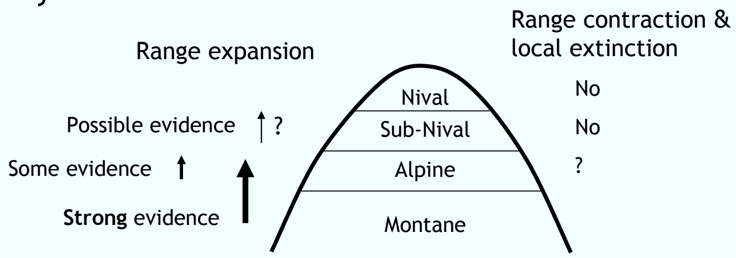
	Australia	New Zealand	East Africa	Southern Africa	China	Himalaya
Introduced species	+	++	-	+	-	-
Land-use changes	+	-	++	++	++	++
Hydroelectric development	-	-	-	+	+	-
Ski development	+	+	-	-	?	-
Atmospheric N deposition	-	-	-	-	+	-
Global warming	+	+	+	++	?++	?++
Over-exploitation	-	-	++	++	++	++

++ = high threat   + = some threat   - = no likely threat

Note the ? for global warming

Very good evidence from many re-surveys of floristic analyses made in the 1900s-1950s and recently in Europe and N America that

1. Summit floras are becoming **more species-rich** as Montane species (e.g. dwarf-shrubs, grasses) move up mountains, presumably in response to climate warming
2. But evidence for **local extinction** of high-altitude alpine or sub-nival species is almost **non-existent.** Why?



Range expansion

Range contraction & local extinction

Possible evidence ↑ ? — Nival — No

Sub-Nival — No

Some evidence ↑ — Alpine — ?

Strong evidence ↑ — Montane

Why is there little or no evidence for local extinction of high-altitude species?

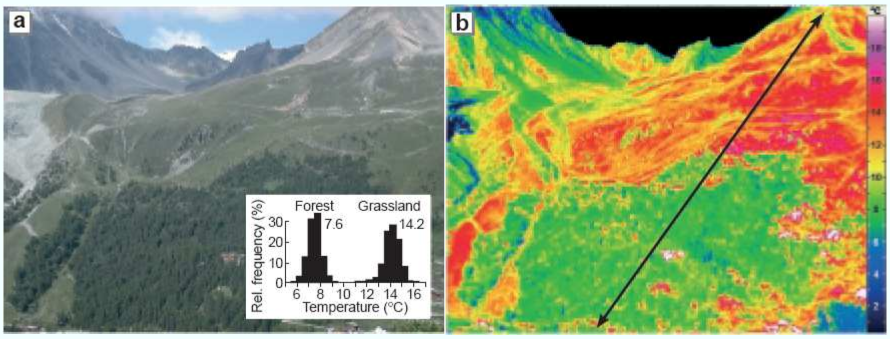
Need to assess an alpine landscape not at a climate-model scale or even at the 2 m height of a climate station, but at the plant level.

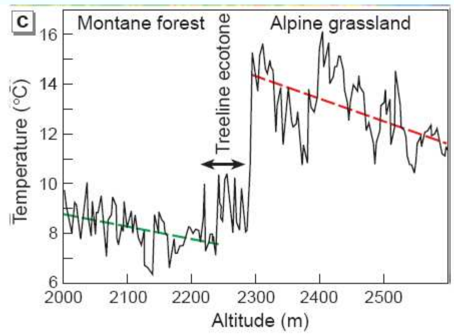
Use thermal imagery technology to measure **land surface temperature**.

Körner 2007 *Erdkunde*

Scherrer & Körner 2010 *Global Change Biology*

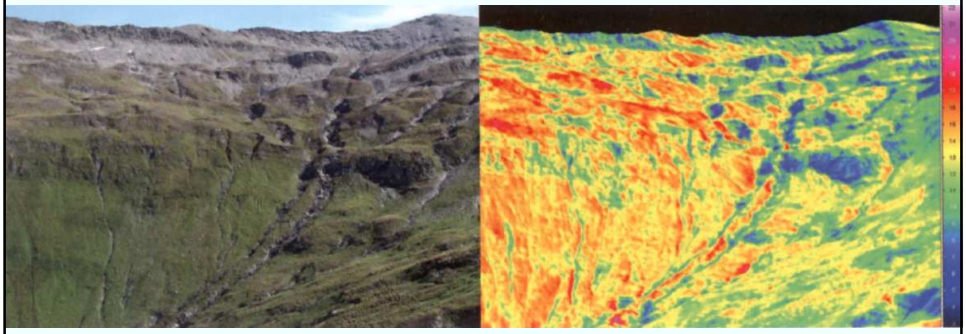
Scherrer & Körner 2011 *Journal of Biogeography*





Land-surface temperature across an elevational transect in Central Swiss Alps shown by modern thermal imagery. Forest has a mean of 7.6°C whereas the alpine grassland has a mean of 14.2°C. There is a sharp warming from forest into alpine grassland

Körner (2007)



Furka Pass, Switzerland

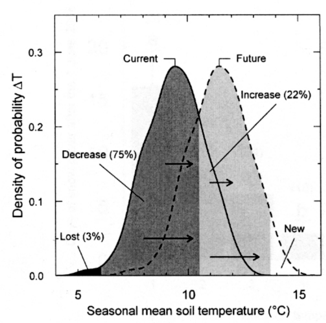
One slope, huge thermal imagery variation showing varied network of micro-habitats

In two alpine areas in Switzerland (2200-2800 m), used infrared thermometry and data-loggers to assess variation in plant-surface and ground temperature for 889 plots.

Found growing season mean soil temperature range of 7.2°C, surface temperature range of 10.5°C, and season length range of >32 days. Greatly exceed IPCC predictions for future, just on one summit.

IPCC 2°C warming will lead to the loss of the coldest habitats (3% of current area). 75% of current thermal habitats will be reduced in abundance (competition), 22% will become more abundant.

Scherrer & Körner (2011)



Warn against projections of alpine plant species responses to climate warming based on a broad-scale (10’ x 10’) grid-scale modelling approach.

Alpine terrain is, for very many species, a much ‘safer’ place to live under conditions of climate change than flat terrain which offers no short distance escapes from the new thermal regime.

Landscape local heterogeneity leads to local climatic heterogeneity which confers biological resilience to change.

ALTITUDINAL GRADIENTS OF SPECIES RICHNESS IN THE HIMALAYA

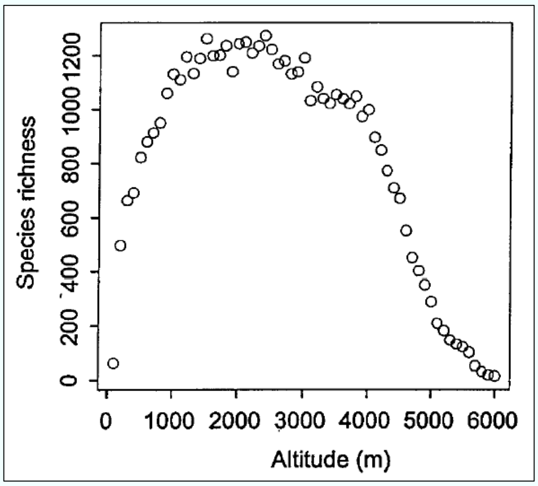
Jhomolhari (7,314 m)
Bhutan

Cho Oyu (8201 m) Tibet

Makalu (8475 m)
Tibet

Photos: Harry Jans

Nepal – longest altitudinal gradient in world



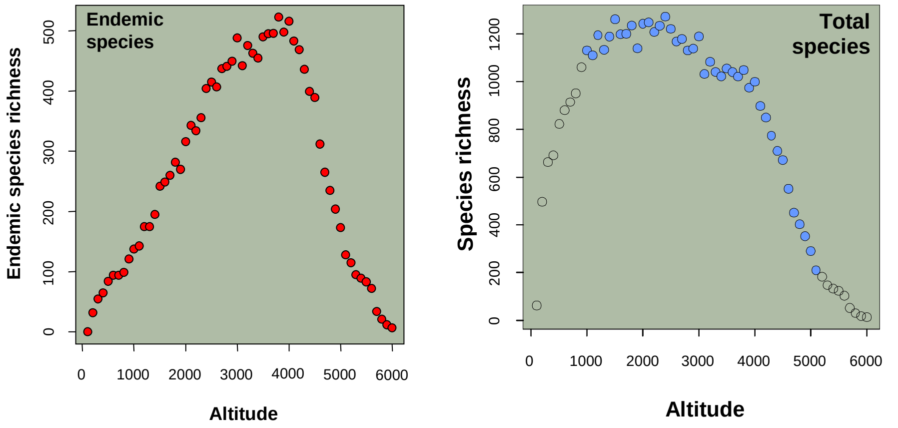
Species richness of flowering plants (4928 taxa) and altitude (0-6000 m) in Nepal

Ole Reidar Vetaas

John-Arvid Grytnes

Vetaas & Grytnes (2002)

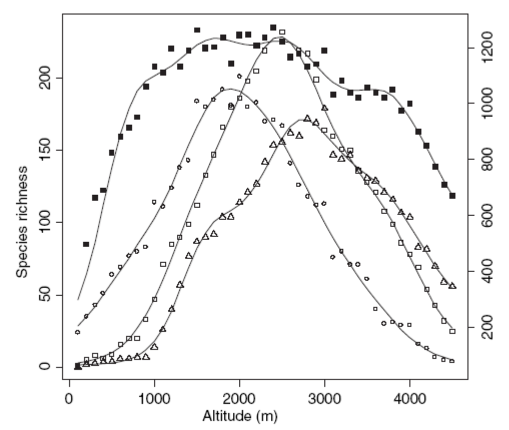
Species endemic to Himalaya



Patterns very different – **endemics** have peak at 4000 m, whereas **total species richness** peaks between 1500 and 2500 m.

Vetaas & Grytnes (2002)

Other groups of plants in Nepal



Khem Bhattarai

Oriol Grau

■=Vascular plants – peak 1500-2500 m

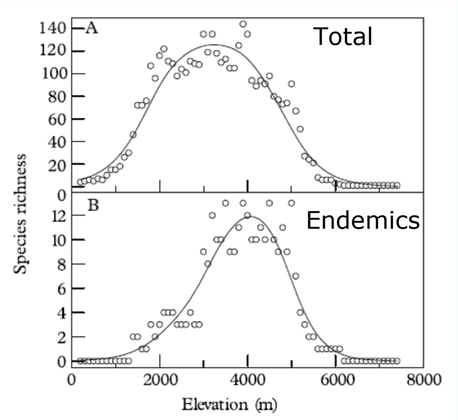
○=Ferns – peak 1900 m

□=Mosses – peak 2500 m

△=Liverworts – peak 2800 m

Bhattarai *et al.* (2004)
Grau *et al.* (2007)

Lichens in Nepal

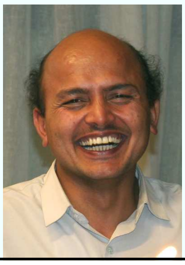


Baniya *et al.* (2010)

Total lichen richness peaks at 3100-3400 m

Higher than for other plant groups (1500-2800 m)

Endemic peak at 4000-4100 m, same as for vascular plants



Chitra Baniya

Why do all Nepalese species-richness patterns show a unimodal pattern?

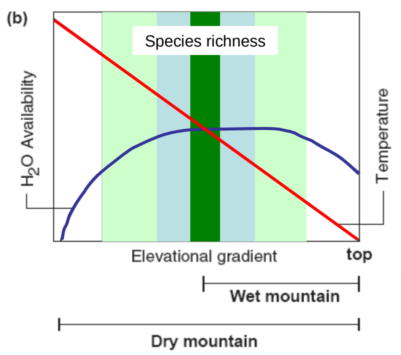
Various **technical problems** in compiling data for such studies due to interpolation. Also problems of ‘hard boundaries’.

Grytnes & Vetaas (2002) did numerical simulations to investigate the effects of these problems on the observed patterns. When allowed for, there is a **strong decrease** of richness with altitude and the unimodal pattern is not an artefact.

Why is there a unimodal pattern in species richness in the Himalaya?

Unimodal pattern may be more widespread than previously thought, especially over long **ecological** gradients (not always equivalent to long altitudinal gradients).

Energy-water model ideas of O'Brien (1993, 1998, 2006), whereas richness is a function of water + energy.



Temperature (α energy) decreasing with altitude

Water availability often has a unimodal pattern in some mountain areas

Species richness shaded

Grytnes & McCain (2007)

Appears that globally, unimodal relationships are most frequent on dry, continental mountains where there is a mid-altitude peak in water availability.

Monotonically decreasing patterns are most frequent on wet, oceanic mountains (e.g. western Norway, Mt Kenya, Ruwenzori).

In general, dry continental mountains are the most species-rich mountains. Alpines are intolerant of oceanic conditions – need cold winters and a sharp transition to summer growing season.

How does precipitation change with altitude?

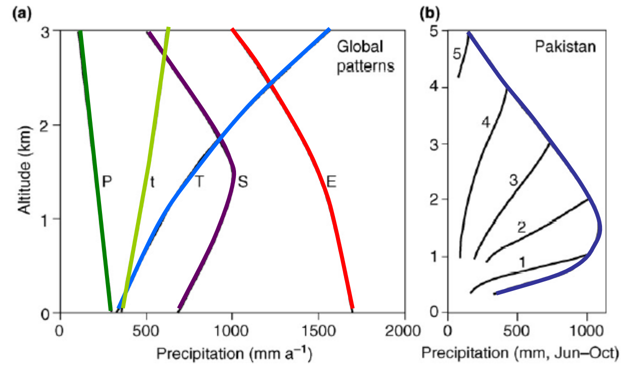
Polar mountains (Greenland)

Temperate mountains (40°-60°) (e.g. W USA)

transition (30°-40°) (e.g. Turkey, Iran)

Subtropical (10°-30°) (e.g. Drakensberg, Himalaya)

Equatorial (0°-10°) (e.g. Mt Kenya, Kilimanjaro)



Pakistan – rise then fall in precipitation in monsoon season (1-5 are different mountain ranges)

Körner (2007)

Examples of mountains with very different precipitation-altitude patterns

Polar – decreases with altitude (Svalbard)

Temperate – increases with altitude (Patagonia)

Sub-tropical – peak at mid altitude (Turkey)

Equatorial – decreases with altitude (Kenya)

Species richness patterns and precipitation – altitude patterns globally based on personal observations

	Species pattern	Pptn pattern		Species pattern	Pptn pattern
Svalbard	M	D	Central Turkey	U	P
W Norway	M	I	SW Iran	U	P
E Norway	U	D	Tien Shan	U	P
Alps	U	D	NW India	U	P
Pyrenees	U	D	Sichuan	U	P
Bulgaria	U	P	Qinghai	U	P
Greece	U	P	Tibet	U	P
Kenya	M	D	Bhutan	M	I
Ethiopia	M	D	Yunnan	U	P
Drakensberg	U	P	Rockies	U	P
Tasmania	M	I	Patagonia	U	P
S Is., New Zealand	M	I	Tierra del Fuego	M	I
SE Australia	U	P			
NE Turkey	U	P			

U=Unimodal; M=Monotonic
I=Increasing; D=Decreasing;
P=Peak at mid-altitude

To summarise

Rainfall:	I	D	P
Species:			
Unimodal	-	3	**15**
Monotonic	**5**	**3**	-

(1) Most **unimodal** species patterns are seen on mountains with a **precipitation peak** at mid-altitudes (i.e. the sub-tropical type including Himalaya)

(2) All **monotonic** species patterns are seen on mountains with **precipitation increasing or decreasing** with altitude (e.g. Mt Kenya, Tierra del Fuego, western Norway)

SOME CONCLUSIONS

1. The world of high alpines is a specialised and extreme environment with low temperatures, much snow, high winds, and low atmospheric pressure.
2. Alpine plants show an extraordinary diversity of adaptations to the demands of the Alpine World. They are true alpine "specialists".
3. Alpine plants have a range of growth-forms or "plans for life".
4. Alpine plants often have high below-ground biomass, have average leaf life-spans 2-3 times longer than in lowland plants, grow very slowly, live to a great age, and are poor competitors.

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5. Alpine plants show remarkable adaptations to extreme cold, extreme winds, infertile soils, and prolonged snow-lie, to reproducing asexually or sexually, and to protecting themselves against herbivores.
6. Despite this great diversity of adaptation, many alpine plants may not be adapted to warmer temperatures that are occurring as a result of global warming. The long-term future for high alpines is not good, given the predictions of a global increase in temperature of 5-8°C in the next hundred years.

WHY ARE ALPINE SYSTEMS SO DIVERSE?

1. Climate zones are compressed
2. Slopes cause exposure and micro-climate to vary over small distances
3. Gravity-induced erosion fragments the continuous vegetation into 'micro-islands'
4. Mountain summits are themselves isolated 'islands' in the sky or in the lowland 'sea'
5. Topography - climate – geography interactions thus create a multitude of microhabitats, each with its own specific set of organisms, and hence high local and regional diversity

WHY IS ALPINE BIODIVERSITY SO IMPORTANT?

1. Catchment slopes depend on soil stability
2. Soil stability depends on near continuous plant cover
3. Plant species diversity ensures a sustained plant cover and hence soil stability
4. Biodiversity therefore provides insurance – intact systems provide insurance against system failure
5. Ecosystem functioning (plants, animals, micro-organisms co-existing and functioning together) important for full ecosystem services
6. Ethical aspects (the right of all species to exist)
7. Aesthetic values (the beauty of alpine plants)
8. Alpine areas are the living place of many human populations

9. The world's water-supply

Alpine terrain (alpine + montane) covers 24% of the global land area

All mountains have **slopes**, sometimes very steep slopes

Slopes (and the peaks behind them) not only capture water but channel it to the foothills and, via large river systems, feed the lowland plains

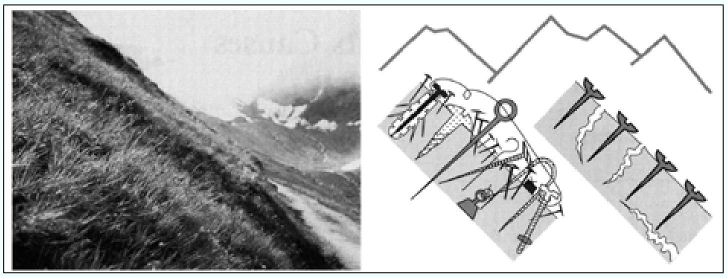
Mountains therefore **provide water for half of mankind**, directly or indirectly. Hold about **66%** of world's freshwater as **snow or ice**

Runoff and associated sediment load are **beneficial** (water supply, mineral nutrients) and also **non-beneficial** (floods, mud-flows, etc.)

Unless made of solid rock, the only way loose substrates are secured to slopes is through **VEGETATION**.

Alpine vegetation provides the '**screws**' and '**nails**' that maintain slopes and prevent slope dangers and disasters.

Slopes are only as stable and safe as the integrity and **stability** of their **vegetation**.

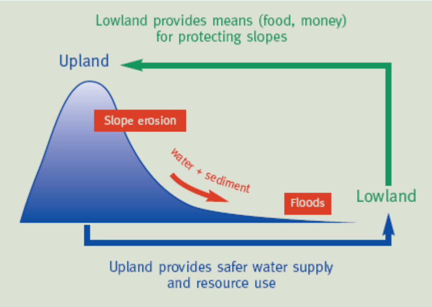


Körner (2002)

Much lowland productivity is required to support the needs of up-slope society and to maintain sustainable management in the uplands.

Down-slope ⇆ Up-slope interdependencies

"Lowland – Upland Contract of Society" (Körner 2002)



Needs the effectiveness of alpine vegetation, natural or cultural, to **control slope and soil erosion**.

Must avoid this happening

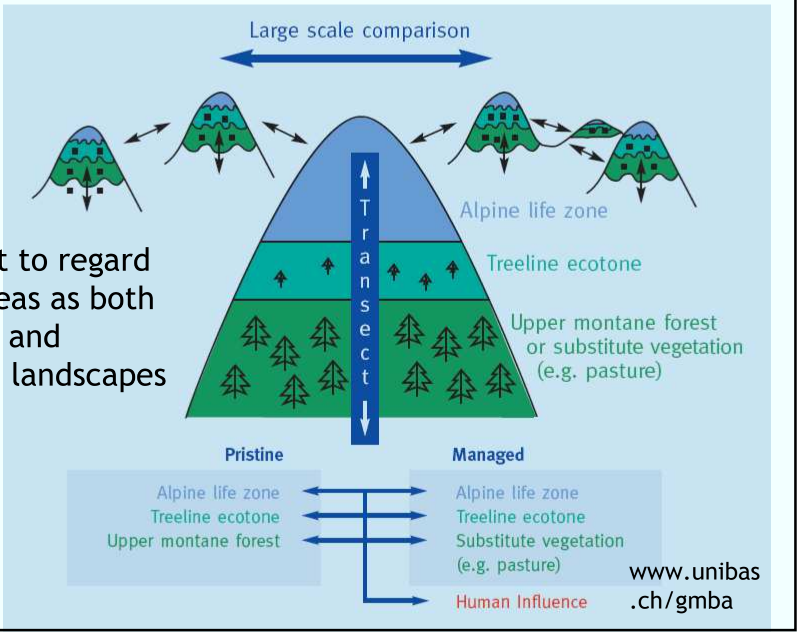
Mountain desert, Andes, S America

Grabherr (1997)

Central Tibet, 4520 m

Miehe *et al*. (2008)

Global Mountain Biodiversity Assessment



Important to regard alpine areas as both 'pristine' and 'cultural' landscapes

www.unibas.ch/gmba