



High-elevation limits and the ecology of high-elevation vascular plants: legacies from Alexander von Humboldt

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Abstract

Alexander von Humboldt and Aimé Bonpland in their 'Essay on the Geography of Plants' discuss what was known in 1807 about the elevational limits of vascular plants in the Andes, North America, and the European Alps and suggest what factors might influence these upper elevational limits. Here, in light of current knowledge and techniques, I consider which species are thought to be the highest vascular plants in twenty mountain areas and two polar regions on Earth. I review how one can try to compare elevational limits in different parts of Earth. I discuss recent advances in high-elevation plant ecology that would surely have fascinated von Humboldt such as the special snow-roots in some snow-bed plants and the coldest place on Earth where a vascular plant is growing. I briefly outline an ignored von Humboldt legacy, Mendelssohn's Humboldt Cantata. In conclusion I summarise the foundations and legacies that von Humboldt created for global high-elevation ecology and biogeography.

Highlights

- The known uppermost elevation limits of vascular plants in 22 regions from northernmost Greenland to Antarctica through the European Alps, North American Rockies, Andes, East and southern Africa, and South Island, New Zealand are collated to provide a global view of high-elevation limits.
- The relationships between potential climatic treeline, upper limit of closed vegetation in tropical (Andes, East Africa), subtropical (Andes, southern Africa, Himalaya), and temperate areas (North America, South America, Scandinavia, central Europe, Mediterranean Europe, Asia, New Zealand) and problems in defining the potential climatic treeline in the tropical and subtropical Andes and tropical East Africa are outlined.
- Recent advances in the ecology of high-elevation plants are reviewed, including the recent discovery of so-called snow roots in at least five families, the ecology of the coldest place on Earth where a vascular plant is known to grow, and the complex interactions between temperature, snow-cover, and soil disturbance in determining plant survival and colonisation at very high elevations in Ladakh.
- An ignored legacy from von Humboldt is discussed: the Humboldt cantata composed by Felix Mendelssohn and performed in 1828.

Keywords: alpine belt, cold, elevation, Humboldt cantata, mountains, nival belt, snow roots, survival, treeline

Introduction

Mountains have long fascinated people who have been awestruck by their beauty and majesty. To some, mountains are mythical, mysterious, frightening, or challenging as they can arouse powerful emotions of trepidation, wonder, curiosity, and adventure (Macfarlane 2003). Originally thought to house wild and dangerous monsters and other strange biota, it

was only in the late 18th and early 19th centuries that their biota and environment began to be studied in a systematic and scientific manner by people such as Louis-François de Ramond (1755–1827), Kaspar Maria von Sternberg (1761–1838), and Alexander von Humboldt (1769–1859) (von Humboldt et al. 2009, Körner and Spehn 2019). The maximum and minimum elevations at which different species occurred began

to be recorded in different mountain areas (see von Humboldt et al. 2009, Dentant 2017, 2018).

On 23 June 1802, von Humboldt, Bonpland, Montufar, and a local guide climbed the slopes of Chimborazo, the highest peak (6263 m asl) in Ecuador and the equatorial Andes north of Peru, and thought at that time to be the world's tallest mountain (Troll 1960). They climbed to about 5875 m, a new elevational record not matched until Jean Baptiste Boussingault and Hall climbed to 6006 m in 1831 (McCosh 1984). Von Humboldt's group stopped about 400 m below Chimborazo's summit as their route was blocked by a steep ravine and crevasse and they were suffering from altitude sickness (von Humboldt et al. 2009). They recorded phanerogams up to 4600 m such as *Eudema nubigena*, *Senecio canescens*, and *S. nivalis* (Morueta-Holme et al. 2015). There is active debate about which mountains von Humboldt and Bonpland collected and recorded plants above about 3625 m (e.g., Morueta-Holme et al. 2015, 2016, Sklenář 2016, Hestmark 2019, Moret et al. 2019a, b, Morueta-Holme et al. 2019). Despite this debate, von Humboldt and Bonpland's discoveries of vascular plants growing near to 4600 m in the Andes, and of Joseph Hooker and others finding vascular plants occurring up to 6000 m in the Himalaya, laid the foundations for documenting and comparing the high-elevational limits of vascular plants in different mountain areas globally: a topic keenly initiated by von Humboldt (1817, 1845-1862) and von Humboldt and Bonpland (1807).

Here I summarise current knowledge about which are the currently highest growing vascular plants on Earth and discuss how to compare upper elevational limits in different areas on Earth. I compare upper vascular-plant limits, treelines, and closed vegetation limits in major mountain areas. I review recent discoveries in high-alpine plant biology that would have stimulated von Humboldt's curiosity and I conclude with a brief discussion of a missing part of recent celebrations of von Humboldt's life, work, and legacy. My review is confined to mountain areas that I have personal field experience of and from which elevational data are available. It makes no attempt to be a comprehensive review: it is more a progress report adding to and updating Webster (1961), Grabherr et al. (1995), and Dentant (2018).

The use of the term 'elevation' follows the definitions and recommendations of McVicar and Körner (2013). Use of the terms 'treeline', 'alpine', and 'snowline' follows Körner (2021). The term 'tropical alpine' is used to refer to areas within the tropics between the upper limit of continuous closed-canopy forest and the upper limit of plant life (Troll 1959, 1968, Hedberg 1973, Smith 1994). It is used in preference to more local terms such as páramo, super-páramo, jalca, puna (Andes; e.g., Molina and Little 1981), Afroalpine, and moorland (Africa; e.g., Hedberg 1964, 1992, Grimshaw 2001). To avoid confusion, I use the nomenclature for species as given in the publications I cite except for generic names that may have changed in recent years according to The Plant

List (www.theplantlist.org). For plant families, I follow Mabberley (2017).

Elevational limits of vascular plants

Webster (1961) and Grabherr et al. (1995) summarise what was known at their time of publication about the elevational limits of vascular plants on Earth. Many new discoveries have been made in the last 25 years (e.g., Körner 2011, Dvorský et al. 2015, Morueta-Holme et al. 2015, Dentant 2018, Körner 2021). In this section I attempt to update the earlier compilations of Webster (1961) and Grabherr et al. (1995) for selected mountain regions.

Asia

Naturally, the highest vascular plants on Earth all grow in the Himalaya which contains the world's highest mountains. Current knowledge indicates that at least sixteen species grow above 6000 m, some in the central Himalaya but many in the dry north-western Himalayan area of Ladakh. The highest records at 6400 m are held by *Saussurea gnaphalodes* (Figure 1) along with the previously ignored but newly described *Lepidostemon everestianus* (Al-Shehbaz 2000, Dentant 2018). Both plants were found by the great mountaineer and explorer Eric Shipton on the 'big scree' bordering the north side of the East Rongbuk Glacier (28°67'N, 86°51'E) at Camp III close to the base of the North Col during the Everest reconnaissance expedition of 1935, described by Astill (2005) as "The Forgotten Adventure". Beside these plants, Shipton's party found and buried the body of the eccentric adventurer Maurice Wilson in a crevasse. They also found his rucksack and, most importantly, his diary. This diary forms the basis of Caesar's (2020) amazing account of Wilson's unbelievable adventures of 1933–34 flying single-handedly from northern England to Darjeeling, trekking through Sikkim and Tibet to the Rongbuk Monastery, and attempting to

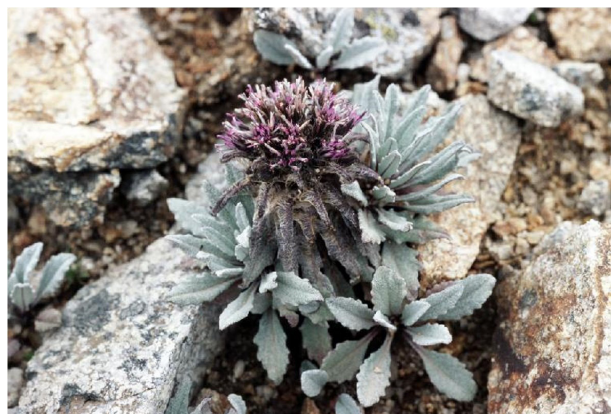


Figure 1. *Saussurea gnaphalodes* – one of two vascular plants (the other is *Lepidostemon everestianus*) that grow in the central Himalaya at a higher elevation (6400 m) than any other vascular plant on Earth. Photo: David Boufford (eFloras.org The Biodiversity of the Hengduan Mountains Project).

climb Everest alone. Wilson's body was found along the North Col at about 7000 m.

Table 1 lists all the known vascular plants that have been recorded near, at, or above 5950 m elevation in the Himalaya including Ladakh in the Indian Trans-Himalaya (Jammu and Kashmir state; Dvorský et al. 2015, Dvorský et al. 2018). The dominant family is Brassicaceae (9 taxa) followed by Asteraceae (4) and Caryophyllaceae (4). A reviewer (personal communication) points out that members of these families are rarely associated with mycorrhizal fungi. Many large Himalayan families are very poorly represented (e.g., Poaceae, Primulaceae, Saxifragaceae) or are not present at these high elevations (e.g., Apiaceae, Boraginaceae, Crassulaceae, Cyperaceae, Ericaceae, Gentianaceae, Orobanchaceae, Ranunculaceae, Rosaceae, Scrophulariaceae).

The uppermost closed swards of vegetation occur at about 5300–5500 m depending on aspect and slope (Miehe 1987, 1989, 1991, H.J.B. Birks personal observations), whereas the uppermost assemblages or 'communities' defined by Miehe (1989, 1991) as stands consisting of at least nine vascular plants occur at about 5900–5960 m. There is often a sharp transition at about 5500 m between short but relatively closed turf and open, rather barren ground with scattered

herbs (H.J.B. Birks personal observations). There is thus at least 900 m available for occupation between this marked transition at 5500 m and the known upper limit of plant growth at 6400 m. The factors that might limit colonisation and survival at these high elevations are discussed below in the section on Ecological studies at high elevations.

Elsewhere in Asia high mountains above 7000 m occur in the Tian Shan where the highest peak (Pik Pobedy; 42°02'N, 80°07'E) reaches an elevation of 7439 m. The highest occurring vascular plant in the Tian Shan is *Thalycospermum caespitosum* (6000 m), followed by *Saussurea gnaphalodes* (5800 m), with *Biebersteinia odora*, *Rhodiola kirilowii*, *Saxifraga oppositifolia*, and *Trisetum spicatum* all growing up to 5600 m (Holubec and Horák 2018). Further west, the Caucasus only reach 5642 m on Mt Elbrus (43°21'N, 42°26'E). The highest occurring vascular plants there are *Veronica minuta* (4500 m), *V. telephiifolia* (4200 m), and *Draba araratica* (4095 m). Ten species reach 4000 m elevation including the elegant *Campanula biebersteiniana*, *Plantago saxatilis*, *Primula bayerni*, *Senecio sosnovskyi*, and *Tripleurospermum caucasicum* (Holubec and Křivka 2006).

The families of the ten species that have their highest elevational occurrences in the four Asian

Table 1. Known vascular plants that have been recorded near or above 6000 m in the Himalaya including Ladakh. The family, relevant reference, and highest elevation (m) are given. E = Everest region.

Species		Elevation (m)	Family	Reference
<i>Saussurea gnaphalodes</i>	E	6400	Asteraceae	Miehe (1991), Dentant (2018)
<i>Lepidostemon everestianus</i>	E	6400	Brassicaceae	Al-Shehbaz (2000), Dentant (2018)
<i>Androsace khumbuensis</i>	E	6350	Primulaceae	Dentant (2018)
<i>Saxifraga lychnitis</i> var. <i>everestianus</i>	E	6350	Saxifragaceae	Dentant (2018)
<i>Arenaria bryophylla</i>	E	6335	Caryophyllaceae	Dentant (2018)
<i>Desideria himalayensis</i>	E	6300	Brassicaceae	Miehe (1991)
<i>Saussurea glacialis</i>		6150	Asteraceae	Dvorský et al. (2015)
<i>Saussurea inversa</i>		6150	Asteraceae	Dvorský et al. (2015)
<i>Waldheimia tridactylites</i>		6150	Asteraceae	Dvorský et al. (2015)
<i>Draba alsehbazii</i>		6150	Brassicaceae	Klimeš and German (2009), Dvorský et al. (2015)
<i>Draba altaica</i>		6150	Brassicaceae	Dvorský et al. (2015)
<i>Ladakiella klimesii</i>		6150	Brassicaceae	Dvorský et al. (2015)
<i>Poa attenuata</i>		6150	Poaceae	Dvorský et al. (2015), Angel et al. (2016)
<i>Stelleria decumbens</i>		6130	Caryophyllaceae	Dvorský et al. (2015)
<i>Draba oreades</i>		6100	Brassicaceae	Dvorský et al. (2015)
<i>Aphragmus oxycarpus</i>		6000	Brassicaceae	Dvorský et al. (2015)
<i>Saxifraga nancellae</i>		5995	Saxifragaceae	Dvorský et al. (2015)
<i>Desidera pumila</i>		5990	Brassicaceae	Dvorský et al. (2015)
<i>Eritricium hemisphaericum</i>		5990	Boraginaceae	Dvorský et al. (2015)
<i>Draba himachalensis</i>		5960	Brassicaceae	Dvorský et al. (2015)
<i>Thalycospermum caespitosum</i>		5960	Caryophyllaceae	Dvorský et al. (2015)
<i>Stellaria depressa</i>		5950	Caryophyllaceae	Dvorský et al. (2015)

mountains ranges considered (Table 2) are Asteraceae, Brassicaceae, and Caryophyllaceae, followed by Plantaginaceae, Primulaceae, and Saxifragaceae. Species-diverse families in Asia such as Boraginaceae, Cyperaceae, Ericaceae, Gentianaceae, Lamiaceae, Poaceae, Ranunculaceae, and Rosaceae are very poorly represented or are absent in the high-elevation Asian flora.

Cryptogams and fungi attain higher elevations than vascular plants. In the Everest range, bryophytes (primarily mosses) reach 6500 m, lichens (mainly microcrustose taxa) are recorded up to 7400 m (Makalu, Miehe 1989, Körner 2003, 2021), snow algae reach 7700 m, and bacteria and micro-fungi have been found up to 8400 m, only 448 m below Everest's summit in the so-called 'aeolian biome' (Swan 1961, 1992, Körner 2021).

Europe and North America

The colony of *Saxifraga oppositifolia* (Figure 2) growing at 4505–4507 m near the summit of Dom de Mischabel (the highest mountain in Switzerland (4545 m; 46°05'N, 30°51'E) and the third highest in the European Alps) is currently the highest known vascular plant in Europe (Körner 2011, 2021). The previous record was held by *S. biflora* (4450 m) and *Ranunculus glacialis* at 4275 m (Wagner et al. 2010) followed by a small number of taxa (e.g., *Androsace alpina*, *S. bryoides*) at 4270 m (Grabherr et al. 1995, Körner 2003, Wagner et al. 2010, Körner 2011). At present, only twelve species are known to occur above 4000 m in Europe (Heer 1885, Anchisi 1985, Ozenda 1988, Wagner et al. 2010). The cushions of *S. oppositifolia* on the Dom are more than 30 years old and are associated with at least three species of moss, several lichens, nine species of mycorrhizal and non-mycorrhizal fungi, and several arthropods (Collembola, Mites) (Körner 2011, Oehl and Körner 2014). In the Alps, bryophytes are known up to 4559 m (Körner 2011).

The highest known vascular plant in Norway is *Ranunculus glacialis* growing at 2370 m (61°38'N, 8°18'E), closely followed by *Saxifraga oppositifolia* at 2350 m.

A further five species are known at or above 2300 m elevation (*Draba fladnizensis*, *Festuca vivipara*, *Poa flexuosa*, *Saxifraga cernua*, *S. rivularis*) (Gjærevoll 1990, Lid and Lid 2005, Holten and Aune 2011). *Saxifraga oppositifolia* is one of the two northernmost vascular plants in the world, growing with *Papaver radicum* agg. on Kaffeklubben Island in northern Greenland at 83°N, 40°W (Sagax 2007). *Saxifraga oppositifolia* is also the highest vascular plant in the North American Rockies growing at 4265 m on Mt Elbert, Colorado (4401 m; 39°07'N, 106°26'W) (Loraine Yeatts, personal communication).

The highest plant growing on Svalbard is *Papaver dahlianum*, recorded at the surprisingly high elevation of 940 m on Nordenskoldfjellet (78°13'N, 15°38'E) by Longyearbyen (Sunding 1962). *Saxifraga oppositifolia* also occurs there, up to 915 m (Sunding 1962).

The highest mountain in Sweden is Kebnekaise (2096 m; 67°54'N, 18°31'E) and seven other mountains above 2000 m all lie in Swedish Lapland. There is



Figure 2. *Saxifraga oppositifolia* – the world's northernmost plant (83°N) and the highest vascular plant in Europe (4506 m; 46°N) and in North America (4265 m; 39°N). It is considered by Körner (2011) to be growing in the "coldest place for angiosperm plant life on earth". Photo: HJB Birks, Finse, Norway.

Table 2. The families that contain the ten highest occurring species in four areas of Asia along with the number of species in the families in these four areas.

Family	Caucasus	Tian Shan	Ladakh	Himalaya	Total
Asteraceae	2	1	3	3	9
Brassicaceae	1	2	4	2	9
Caryophyllaceae		2	2	2	6
Plantaginaceae	3				3
Primulaceae	1			2	3
Saxifragaceae		2		1	3
Poaceae		1	1		2
Apiaceae	1				1
Biebersteiniaceae		1			1
Campanulaceae	1				1
Crassulaceae		1			1
Juncaceae	1				1

only one species in these mountains that reaches 1800 m – *Ranunculus glacialis*. Four species occur above 1700 m (*Huperzia selago*, *Luzula confusa*, *Phippsia algida*, *Salix herbacea*) (du Rietz 1925). Although *Saxifraga oppositifolia* is relatively common in the area, it only reaches 1500 m (H.J.B. Birks personal observations). Further south in south-west Jämtland in central Sweden (highest point 1796 m; 63°02'N, 12°30'E), Kilander (1955) records that six species occur at or above 1700 m, with *Poa flexuosa* being the highest (1792 m), followed by *Ranunculus glacialis* (1782 m), *Huperzia selago* (1750 m), *Salix herbacea* (1739 m), *P. x jemtlandica* (1701 m), and *Luzula arcuata* (1700 m). *Saxifraga oppositifolia* only reaches a maximum of 1426 m elevation.

In Britain, where the highest mountain (Ben Nevis; 56°47'N, 5°0'W) only reaches 1345 m, the highest vascular plants growing at or above 1300m are *Huperzia selago*, *Juncus trifidus*, *Luzula spicata*, *Salix herbacea*, *Sibbaldia procumbens* (all at 1310 m); *Carex bigelowii*, *Gnaphalium supinum*, *Festuca ovina*, *Silene acaulis* (all at 1305 m); and *Vaccinium myrtillus* at 1300 m (Pearman and Corner 2004). *Saxifraga oppositifolia* reaches 1211 m on the botanically rich schistose Ben Lawers in the central Scottish Highlands.

Moving further to the mountains of the Mediterranean basin, Mt Olympus (Olimbos; 2917 m; 40°05'N, 22°21'E) is the second highest mountain in the Balkans and it has one of the highest treelines (2750 m) in Europe. It supports a very rich flora with many endemic taxa (Strid 1980, 1986, Strid and Tan 1991). The highest occurring vascular plant is *Festuca olympica* that grows on the summit at 2917 m. There are thirty species from sixteen families that occur at or above 2900 m. These include the ferns *Asplenium viride*, *Dryopteris villarii* ssp. *villarii*, and *Polystichum lonchitis* (ferns are generally very rare at high elevations). Other plants at or above 2900 m include *Alyssum handelii*, *Arabis bryoides*, *Arenaria cretica*, *Campanula oredum*, *Carex kitaibeliana* ssp. *kitaibeliana*, *Cerastium theophrasti*, *Doronicum columnae*, *Erigeron alpinus*, *Paronychia rechingeri*, *Saxifraga glabella*, *S. exerata*, *S. scardica*, *S. spruneri*, *Sesleria tenerrima*, *Thymus boissieri*, *Veronica thessalica*, and *Viola thriis-notata* (Strid 1986, Strid and Tan 1991). Although the summit areas appear to be extremely dry and barren, at least 55 species have been recorded above 2800 m (Strid 1980).

In northern and central Europe, high-elevation species are mainly confined to a small number of families (8), predominantly Saxifragaceae (5 species) and Poaceae (3 species). In contrast, in Mediterranean Europe, high-elevation species occur in twelve families, but like further north, the predominant families are Saxifragaceae (5 species) and Poaceae (4 species). This contrasts with the Asian mountains (Table 2) where Brassicaceae and Asteraceae followed by Caryophyllaceae provide the bulk of the high-elevation flora.

Africa

The tropical mountains of East Africa such as Kilimanjaro (5895 m; 3°4'S, 37°21'E), Mt Kenya

(5199 m; 0°9'S, 37°18'E), and Ruwenzori (5109 m; 0°23'S, 29°52'E) are famous for their rich and varied alpine floras (e.g., Hedberg 1957, 1965, Grimshaw 2001, Assefa et al. 2007, Gehrke and Linder 2014) and their spectacular endemic giant rosette plants (e.g., *Carduus keniensis*, *Dendrosenecio* spp., *Lobelia* spp.) (Hedberg 1964). The high-elevation flora on Ruwenzori is poor with only one species listed above 4900 m (*Poa ruwenzoriensis*) by Hedberg (1964). In contrast, Kilimanjaro and Mt Kenya have eleven and fourteen species, respectively, found above 4900 m elevation and five and six species, respectively, recorded at or above 4950 m. There are six species found at or above 5000 m on Kilimanjaro (all in the Asteraceae except for the endemic *Festuca kilimanjarica*) (Hedberg 1957). Three species (*Helichrysum newii*, *Senecio meyeri-johannis*, *S. telekii* – all Asteraceae) have been found at 5700 m (Beck 1988). Of the five species recorded at or above 4950 m of Mt Kenya (Hedberg 1957, 1968), all are in the Asteraceae except for *Arabis alpina* that inhabits shaded crevices in the summit cliffs with *H. brownei* at 4970 m. The highest moss recorded on Mt Kenya is *Grimmia ovata* at 5000 m (Hedberg 1968).

The highest mountains in Africa south of Kilimanjaro are in the Khahlamba-Drakensberg range and in Lesotho with Thabana Ntlenyana (3482 m; 29°28'S, 29°16'E) being the highest point in southern Africa (Pooley 2003). They support a very diverse flora with about 2200 species, 200 of which are endemic. The summit basalt plateau with an average elevation of about 3000 m supports at least 181 species (Pooley 2003). There are forty species growing at or above 3300 m from twelve families, dominated by the Asteraceae (16 species) followed by the Scrophulariaceae (6 species). On the very highest ground at or above 3400 m, only five species have been recorded (4 Asteraceae, 1 Brassicaceae). These are *Euryops decumbens*, *Helichrysum milfordiae*, *H. pagophilum*, *Senecio barbatus*, (all Asteraceae), and the diminutive crucifer *Heliophila alpina* (Pooley 2003).

South America and Antarctica

The Andes are the longest mountain range in the world, forming a continuous highland along the western edge of South America. They are 7000 km in length, 200–700 km wide, and have an average elevation of about 4000 m. They are the highest extensive mountain range outside the Himalaya. Within the Andes, Aconcagua (6962 m; 32°39'S, 70°0'W) in Argentina is the highest mountain outside Asia and the highest peak in both the Southern and Western Hemispheres. Chimborazo (6263 m; 1°28'S, 78°49'W) in the Ecuadorian Andes is further from the Earth's centre than any other location on Earth due to the equatorial bulge resulting from the Earth's rotation (Krulwich 2007). Halloy (1989) divides Andean alpine areas into tropical (north of the Tropic of Capricorn at 23°26'S), subtropical (south of the Tropic of Capricorn to about 30°S), and temperate areas.

In the tropical part of the Andes, the uppermost elevational limit of vascular plants on Chimborazo (Morueta-Holme et al. 2015, 2016, Moret et al.

2019a) and the volcanic Mt Antisana, Ecuador (5753 m; 0°28'S, 78°08'W) (Hestmark 2019, Grubb et al. 2020) appear to be between 5200 m (*Pentocalia chimborazensis* = *Senecio hallii*) (Diels 1937) and 5185 m (*Draba aretioides*). Sklenář (2016) argues that there are no reliable records for this taxon from Chimborazo, whereas Morueta-Holme et al. (2015, 2016) collected sterile specimens and note that León-Yáñez and Pitman (2003) list *D. aretioides* from Chimborazo. *Pentocalia chimborazensis* and *D. aretioides* are the only taxa that Morueta-Holme et al. (2015) found above 5000 m on Chimborazo. Six species were found at about 4600 m, the upper elevation that von Humboldt and Bonpland recorded vascular plants in 1802 (von Humboldt et al. 2009). These six species are *Baccharis caespitosa*, *Chuquiraga jussieui*, *Hypochaeris sessiliflora*, *Lasiocephalus ovatus*, *Senecio canescens*, and *Xenophyllum humile*. The uppermost limit on Chimborazo of mosses is about 5730 m (Dixon 1924, Halloy 1991) and of continuous vegetation about 4600 m (Halloy 1991).

Further south on Cachi, north-west Argentina (24°55'S, 66°22'W), Halloy (1991) reports the upper limit of vascular plants to be 5500–5800 m but he does not list what species are concerned. On Socompa Volcano, north-west Argentina (24°25'S, 68°15'W), Halloy (1991) notes lichens, liverworts, and mosses all reaching 6060 m, vascular plants to 4600 m, and continuous cryptogam-dominated vegetation as high as 6060 m. To the south, Halloy (1991) reports vascular plants and mosses growing up to 5100 m on Anconguija, north-west Argentina (27°05'S, 66°05'W) but he does not list what species were found. I have examined many publications (e.g., Reiche 1934, Correa 1969–1984, Villagrán et al. 1981, Brako and Zarucchi 1993, Hoffmann et al. 1998, Montesinos-Tubée 2013, Cuesta et al. 2017) for elevational data for the southern tropical and subtropical Andes. Based on these publications, unpublished information from Daniel Montesinos-Tubée (personal communication), and my own field observations, high-elevation plants in these areas include *Pernettya prostrata* (5100 m; 28°30'S, 77°50'W), *Nototriche caesia* (5050 m; 9°40'S, 70°45'W), and *Azorella compacta*, *A. corymbosa*, *Oxalis exigua*, *Pycnophyllum bryoides*, *P. molle*, and *Senecio rosamarinus* var. *ascotatensis* (all 5000 m), all in southern Peru, Chile, or north-west Argentina. New alpine species are continually being found and described (e.g., Montesinos-Tubée 2014, Montesinos-Tubée et al. 2018, Pringle 2019, Montesinos-Tubée et al. 2020), so these lists will no doubt change as botanical explorations and studies in remote alpine areas of Peru, Bolivia, Chile, and Argentina continue (e.g., Cuesta et al. 2017, Cuesta et al. 2020, Tovar et al. 2020, Testolin et al. 2021).

In the far temperate south, the highest summit in Tierra del Fuego, Chile is currently considered to be Mt Shipton (2488 m; 54°39'S, 69°35'W). The treeline lies between 500 and 600 m and twenty-two species reach 1100 m elevation (Moore 1983). Asteraceae is the family most represented at this elevation with three species of *Nassauvia* (*N. lagascae*, *N. magellanica*, *N.*

pygmaea) and three species of *Senecio* (*S. alloephyllus*, *S. humifusus*, *S. magellanicus*). Other species include *Cardamine glacialis*, *Cerastium arvense*, *Colobanthus subulatus*, *Hamadryas magellanica*, and *Moschopsis rosulata*.

The world's southernmost vascular plants (*Colobanthus quitensis*, *Deschampsia antarctica*) are in Antarctica on Alamode Island in the Terra Firma Islands (68°43'S, 67°32'W) growing at up to 80 m elevation (Komárková et al. 1990, Peat et al. 2007, Buma et al. 2021).

New Zealand

New Zealand (Aotearoa), particularly the Southern Alps on South Island, has a relatively rich (c. 600 species) alpine vascular-plant flora. The highest point is Mt Cook (Aoraki; 43°25'S, 170°08'E) which in 2014 reached 3724 m elevation. The treeline elevation ranges from about 1500 m in the north to 900 m in the far south (Cieraad et al. 2014). The permanent snowline similarly decreases north to south, being about 2400 m in the north and 2000 m in the south (Mark and Adams 1995). At least 68 vascular species reach 2000 m or more, mainly in the Southern Alps (Mark and Adams 1995). Only one species (*Ranunculus grahamii*) reaches 2800 m and two (*Hebe haastii*, *Parahebe birkeyi*) extend to 2900 m elevation. Three species reach 2400 m (*Chinohebe thomsonii*, *Leptinella pectinata*, *Ranunculus buchananii*), 17 occur between 2100 and 2300 m, and 45 reach 2000 m. Three of the six high-elevation species (2400 m or more) belong to the Scrophulariaceae, two are in the Ranunculaceae, and one is in the Asteraceae (Mark and Adams 1995).

Comparing upper-elevation limits, treelines, and upper limits of closed vegetation in different areas

Upper-elevation limits

This was a topic explored by von Humboldt (1817, 1845–1862) by constructing diagrams to show the elevational ranges of major vegetation belts on mountains at different latitudes from the Andes, Tenerife, Alps and Pyrenees, Lapland, and the Himalaya. He distinguished four broad elevational zones globally – tropical, temperate, boreal, and arctic – and seven elevational ranges for the northern Andes (von Humboldt et al. 2009). Von Humboldt clearly considered the treeline to be a global phenomenon, a major life-form boundary that he used as a common bioclimatological reference level. He then positioned other elevational vegetation belts relative to the treeline reference level (Körner 2012).

Körner et al. (2011) develop this general idea further to delimit seven thermal belts on Earth's mountains – nival, upper alpine, lower alpine, upper montane, lower montane, warm with freezing, and warm without freezing – with the thermal treeline as the global reference level (Körner 2007). These seven belts are clearly not applicable world-wide for all mountains but in terms of the uppermost elevational

limits of vascular plants, there are two important belts and the treeline. Körner et al. (2011) define the nival belt with a growing-season mean temperature $<3.5^{\circ}\text{C}$ and a growing-season duration of <10 days, whereas the upper limit of the alpine belt is set at the growing season >10 days and <54 days and growing-season mean temperature of $>3.5^{\circ}\text{C}$ (see also Gottfried et al. 2011). The transition from potentially forested to treeless terrain is defined by an empirically determined minimum growing-season duration of 94 days and a growing-season mean temperature of 6.4°C (Körner and Paulsen 2004, Körner et al. 2011, Körner 2012, Paulsen and Körner 2014).

Körner (2007) presents a simple but elegant conceptual global model of the treeline, the alpine belt, and the nival belt based on a global database of potential forested area derived from a minimum moisture requirement for tree growth and the cold limit of tree distribution based on treeline ecology and biogeography (Körner and Paulsen 2004, Paulsen and Körner 2014, Körner 2020). In the Körner (2007) model I use here, the potential forested area has a temperature $\geq 6.5^{\circ}\text{C}$ for ≥ 100 days a year, whereas the upper limit of the alpine belt has a 3-month growing-season mean temperature $<6.5^{\circ}\text{C}$ but $>3^{\circ}\text{C}$. The nival belt has a growing-season mean temperature $<3.5^{\circ}\text{C}$ and a growing season <10 days (Körner 2012). Körner (2007) emphasises that such a database and resulting conceptual model cannot show every local detail or topography and climate, but that the overall picture (Figure 3) accords with general ecological observations such as the equatorial depression of treeline due to high cloudiness and thus reduced temperature

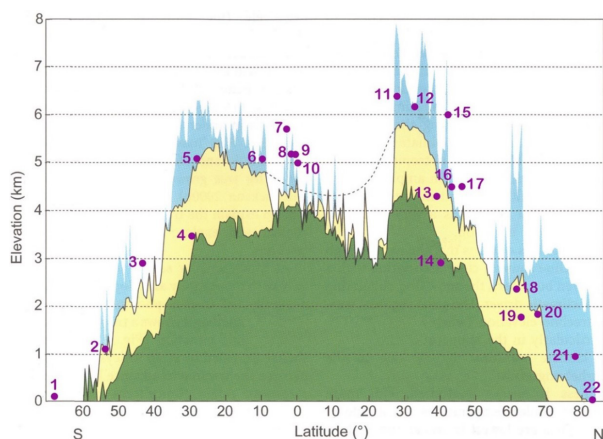


Figure 3. Elevational and latitudinal occurrence of the highest occurring vascular plants in 22 regions ranging from 69°S to 83°N (Table 3) plotted on Körner's (2007) diagram of the latitudinal distribution of the maximum elevation of land area, modelled elevational position of the treeline, and the upper limit of the alpine belt (yellow). The nival belt is shaded blue and the potential forested area is green. The area between about 8°S and 25°N shown by the broken line only has small areas in the alpine and nival belts. For further details about how this diagram was constructed, see Körner (2007). Note the parallel trends in the biological treeline limit with the physics-driven snowline (Körner 2012).

(Körner 2012). Note that the definitions used here in the Körner (2007) model for the upper limit of the alpine belt differ slightly from the definitions for this limit given by Körner et al. (2011). In Figure 3 the elevational and latitudinal occurrences of the highest occurring vascular plants in 22 regions (Table 3) are plotted onto Körner's (2007) model. As expected all but one (Mt Olympus (14)) lie within the alpine (6) or nival belts (15). Mt Olympus (summit 2917 m asl), the only region where the highest vascular plant (*Festuca olympica*) is not positioned on Figure 3 in the alpine belt, has its treeline at about 2750 m, the highest in the Balkans and in Europe as a whole. Körner's (2007) conceptual model is very broad-scale and it makes several assumptions. It is, of course, no substitute for detailed field observations and data-loggers (e.g., Körner and Paulsen 2004) but it provides a useful tool to depict and compare the upper-elevation limits of vascular plants globally.

Treelines and upper limits of closed vegetation

Grabherr et al. (1995) present not only elevational limits of plants in tropical, subtropical, and temperate mountains in East Africa, South America, and Europe but also the upper limits of continuous vegetation. In Table 4, I summarise information of the highest elevation (HE) of the mountains considered in Table 3, along with the highest known elevational limits of vascular plants (PL) on mountains in the major mountain regions within the tropical, subtropical, and temperate zones, as well as the potential climatic treeline (TL; based on Körner 2007, 2012, Paulsen and Körner 2014), the highest elevation when closed vegetation (VL) ('grassline' of Bürlí et al. 2021) occurs, and the ratios of PL/TL, PL/HE, and PL/VL. The data sources used in Table 4 include Grabherr et al. (1995), Körner (2003, 2012), publications cited earlier for the basic upper-elevation limits for vascular plants in particular mountain regions, and my own field observations, particularly for the closed vegetation limit ($\geq 40\%$ vascular-plant cover).

Despite the considerable variation in the HE, PL, TL, and VL values for different areas, there are no large differences between the mean values for PL/HE (0.85–0.90) or PL/VL (1.12–1.25) (Table 4). There is, however, a gradient in the mean PL/TL values with a mean of 1.89 for mountains in the temperate zone, 1.52 in the subtropical zone, and 1.40 in the tropical zone, indicating that the uppermost elevation limit of vascular plants relative to the treeline is highest in the temperate zones followed by the subtropical zone and the tropical zone. The lower mean values for the tropical and subtropical zones may result from the difficulties of delimiting the climatic treeline on tropical East African mountains and on tropical and subtropical Andean mountains.

Hedberg (1951, 1965) recognises three main vegetation belts on the high East African tropical mountains, above the lowland savannah or scrub, there is the montane forest belt consisting of tall trees such as *Juniperus procera*, *Podocarpus* spp., and several broadleaved trees. On Mt Kenya this

Table 3. The highest known elevations of vascular plants in 22 regions arranged from south to north along with the species concerned and the broad climatic zone the regions occur in. The numbers refer to the records shown on Figure 3. In the table, + signifies that one or more additional species have been found at the elevational limits. These are listed in the footnote to the table.

No.	Species	Elevation (m)	Region	Climatic zone
1	<i>Colobanthus quitensis</i> (+1) ^a	80	Alamode Island (Antarctica)	Polar
2	<i>Nassauvia pygmaea</i> (+20) ^b	1100	Mt Shipton (Tierra del Fuego, Chile)	Temperate
3	<i>Hebe haastii</i> (+1) ^c	2900	Southern Alps (New Zealand)	Temperate
4	<i>Helichrysum milfordiae</i> (+4) ^d	3482	Thabana Ntlenyana (Lesotho)	Subtropical
5	<i>Pernettya prostrata</i>	5100	Chilean Andes (Chile)	Subtropical
6	<i>Nototriche caesia</i>	5050	Peruvian Andes (Peru)	Tropical
7	<i>Helichrysum newii</i> (+2) ^e	5700	Kilimanjaro (Tanzania)	Tropical
8	<i>Draba aretioides</i>	5185	Chimborazo (Ecuador)	Tropical
9	<i>Pentacalia chimborazensis</i>	5185	Mt Antisana (Ecuador)	Tropical
10	<i>Arabis alpina</i> (+1) ^f	4970	Mt Kenya (Kenya)	Tropical
11	<i>Saussurea gnapholodes</i> (+1) ^g	6400	Mt Everest (Nepal, Tibet)	Subtropical
12	<i>Draba altaica</i>	6150	Ladakh (India)	Subtropical
13	<i>Saxifraga oppositifolia</i>	4265	Mt Elbert (USA)	Temperate
14	<i>Festuca olympica</i>	2917	Mt Olympus (Greece)	Temperate
15	<i>Thalycospermum caespitosum</i>	6000	Tian Shan (central Asia)	Temperate
16	<i>Veronica minuta</i>	4500	Caucasus (Russia)	Temperate
17	<i>Saxifraga oppositifolia</i>	4506	Dom de Mischabel (Switzerland)	Temperate
18	<i>Ranunculus glacialis</i>	2370	Jotunheimen (Norway)	Temperate
19	<i>Poa flexuosa</i>	1792	Jamtland (Sweden)	Temperate
20	<i>Ranunculus glacialis</i>	1827	Kebnekaise (Sweden)	Temperate
21	<i>Papaver dahlianum</i>	940	Svalbard (Norway)	Polar
22	<i>Saxifraga oppositifolia</i> (+1) ^h	20	N Greenland	Polar

a *Deschampsia antarctica*; b *Acaena magellanica*, *Azorella selago*, *Cardamine glacialis*, *Cerastium arvense*, *Colobanthus subulatus*, *Deschampsia atropurpurea*, *Epilobium conjugens*, *Hamadryas megallanica*, *Leucheria hahnii*, *Moschopsis rosulata*, *Nassauvia lagascae*, *Nassauvia magellanica*, *Oxalis enneaphylla*, *Poa alopercurus*, *Senecio alloephyllus*, *S. humifusus*, *S. magellanicus*, *Stipa rariflora*, *Taraxacum gilliesii*; c *Parahebe birkeyi*; d *Euryops decumbens*, *Helichrysum pagophilum*, *Heliophila alpina*, *Senecio barbatus*; e *Senecio meyeri-johannis*, *S. telekii*; f *Helichrysum brownie*; g *Lepidostemon everestianus*; h *Papaver radicum* agg.

belt is differentiated into three distinct zones – a montane rainforest zone, a bamboo zone, and a *Hagenia abyssinica*–*Hypericum lanceolatum* zone. There is then an ericaceous belt dominated by low forest or scrub of *Philippia* spp. and *Erica arborea*. Above this more-or-less continuous ericaceous tree or scrub vegetation, there is the alpine belt with *Dendrosenecio* spp., *Lobelia* spp., other ‘giant rosette plants’ (Hedberg and Hedberg 1979), and *Helichrysum* spp. and *Alchemilla* spp. low scrub (Coe 1967). Hedberg (1955) proposes that the “forest limit, or tree line, cannot be used with profit in East Africa because of the giant *Senecios*” (= *Dendrosenecio*). “Although these must undoubtedly be classified as ‘trees’, they belong to a very special life-form, apparently adapted to the afro-alpine climate, and on some mountains, e.g., Ruwenzori and Mt Kenya, they seem to reach to upper limit of phanerogamic plants” (see also Hedberg 1964, Grimshaw 2001). In the East African mountains, the treeline is about 4000 m if one accepts the giant *Dendrosenecio* spp. are trees: if not, the treeline is set at the upper limit of *Erica arborea* which can grow to 6 m tall, and is about 3000–3500 m.

In parts of the tropical and subtropical Andes, the limits of the climatic treeline can be unclear because of what Körner (2003) calls the ‘*Polylepis* problem’ and, as with the giant rosette plants in East Africa, high-elevation giant rosette vegetation dominated by *Espeletia hartwegiana* (Körner 2003, 2021). In parts of the Andes, *Polylepis besseri*, *P. racemosa*, *P. sericea*, *P. tarapacana*, *P. tomentella*, etc. (Rosaceae) can be 3.5 m tall, 30 cm in girth, and grow up to 4810 m asl in Bolivia (Hoch and Körner 2005) or 5000 m in Peru (Montesinos-Tubée 2013). *Polylepis* spp. may occur as ‘outposts’ amongst boulders and block-fields beyond what one would conventionally consider a treeline (Körner 2003, 2012). It is unclear if they are present because of the unusual habitat, the so-called ‘shelter’ hypothesis (Körner 2003), or if they are historical relics (the so-called ‘remnant’ or ‘fossil’ hypothesis; Körner 2003). These two hypotheses may be interrelated as block-fields can be impossible to graze, can be sheltered from fire, and can provide shelter for seedlings. Grubb et al. (2020, Appendix S6) discuss low-stature forest of *Polylepis* on the northern side of Antisana (Ecuador) that reach 4500 m (Sarmiento 2002) and are

Table 4. Data on the highest elevation (HE), highest vascular plant limit (PL), potential climatic treeline (TL), and highest elevation with closed vegetation (VL) and values of PL/HE, PL/VL, and PL/TL and means for these values for tropical, subtropical, and temperate zones. These are based on publications cited above and personal field observations. When more than one value is available for an area, the values given here are means for mountains within the area (e.g., Scandinavia – Norway, Sweden)

	HE (m)	PL (m)	TL (m)	VL (m)	PL/HE	PL/VL	PL/TL
Tropical							
Andes	6263	5185	3800?	4600	0.83	1.13	1.36
East Africa	5895	5700	4000?	4500	0.97	1.27	1.43
<i>Mean</i>	<i>6080</i>	<i>5445</i>	<i>3900?</i>	<i>4550</i>	<i>0.90</i>	<i>1.20</i>	<i>1.40</i>
Subtropical							
Andes	5400	5200	3000?	4600	0.96	1.13	1.73
Southern Africa	3482	3482	2700	3300	1.00	1.06	1.29
Himalaya	8848	6400	4200	5500	0.72	1.16	1.52
<i>Mean</i>	<i>5910</i>	<i>5027</i>	<i>3300</i>	<i>4465</i>	<i>0.90</i>	<i>1.12</i>	<i>1.52</i>
Temperate							
North America	4401	4265	2000	3800	0.97	1.12	2.13
South America	2488	1100	600	1000	0.44	1.10	1.83
Scandinavia	2469	2370	1200	1800	0.96	1.32	1.98
Central Europe	4545	4506	2000	3480	0.99	1.29	2.25
Mediterranean Europe	2917	2917	2750	2350	1.00	1.24	1.06
Asia	7439	6000	3800	5000	0.81	1.20	1.58
New Zealand	3724	2900	1200	2000	0.78	1.45	2.42
<i>Mean</i>	<i>3998</i>	<i>3437</i>	<i>1935</i>	<i>2776</i>	<i>0.85</i>	<i>1.25</i>	<i>1.89</i>

largely confined to ‘protected sites’, mainly on scree and in block-fields but at lower elevations on damp or well-drained ground in gullies. Ellenberg (1979) and Lægaard (1992) propose that *Polylepis* forests once covered low-alpine vegetation but were destroyed by burning and grazing. Pollen evidence (Willie et al. 2002) suggests that low-alpine areas below c. 3700 m were once forested and destroyed by human activities but that higher elevations may not have been forested. This and other palaeoecological studies provide support for the ‘remnant’ or ‘fossil’ hypothesis whereas field observations strongly support the ‘shelter’ hypothesis. Smith (1976) shows that *Polylepis sericea* seedlings sown into Venezuelan low-alpine vegetation died in the absence of shelter during the drier part of the year, irrespective of whether competition from the existing plant cover had been removed or not. In all probability the ‘*Polylepis* problem’ of Körner (2003, 2012) results from a complex interaction of historical, ecological, and chance factors.

Ecological studies at high elevations

Introduction

Ecological research is very demanding and is thus relatively rarely attempted for a variety of reasons. Besides the obvious practical issues of accessibility and extreme conditions, one of the major problems is the microscale topographical and climatic variation in high-elevation areas above or beyond the treeline. Scherrer and Körner (2010, 2011) and Scherrer et al.

(2011) worked in alpine areas in the Swiss Alps, Norway, and Sweden and in arctic areas on Svalbard, using high-resolution infrared thermometry and miniature data-loggers. They show considerable spatial and temporal variation in plant-surface and ground temperatures for many plots on slopes of contrasting exposure. In the Swiss Alps, Scherrer and Körner (2010) demonstrate variation of 7.2 K in seasonal mean soil temperature, 10.5 K in surface temperature, and >32 days in growing-season duration. Scherrer et al. (2011) show substantial variation in soil temperatures (at 3 cm depth; 2–3 K) depending on slope exposure, within slopes of 3–4 K due to microtopography, and within 1 m² plots of 1 K as a result of plant-cover effects. Their results – based on a total of 889 1m² plots covering an elevation range of 200 m on one south-south-east slope and 400–600 m on the north-north-west and west slopes – indicate that a topographically induced mosaic of microclimate conditions is associated with local-scale plant distribution. Microtopography can mimic temperature differences of large elevational or latitudinal gradients over very short horizontal distances. In many high-elevation areas it is not elevation but the microclimate near or at ground-level that may be most critical, and that microclimate does not or hardly at all correlates with elevation. In such areas plant stature, topography, and seasonal snow-cover may interact to create local-scale temperature conditions that deviate greatly from extrapolations from standard weather records (Körner and Hiltbrunner 2018; see also Körner 2007, Wundram et al. 2010, Körner 2021).

In this section I review three ecological studies in high-elevation areas: (1) assessing possible factors limiting colonisation and survival, (2) demonstrating new sources of obtaining nitrogen using ‘snow-roots’, and (3) documenting the coldest places where angiosperms can live.

Factors limiting colonisation and survival

Experimental transplants in eastern Ladakh (34°N, 78°E) by Klimeš and Doležal (2010) involved transplanting fourteen species from 5800–5850 m to a control site at the same elevation and to edaphically suitable sites at 5960 m (sparse subnival vegetation), 6030 m (elevational limits), and 6160 m (beyond elevational limit). After two years, only five species survived at 5960 m, two at 6030 m, and none at 6160 m. Dvorský et al. (2016) performed a similar transplant over six years from 5750 m to 5900 m (upper limit of vegetation) and 6100 m (beyond elevational limit). In the first three years, plants survived at 6100 m, supporting the hypothesis of dispersal and/or recruitment limitation. These three years coincided with substantial warming. However, no species survived after 2013 at 6100 m, probably due to the extreme snowfall in 2013. These two unique experiments suggest that the upper elevational limits of vascular plants are not set by any physical barrier such as lack of available habitat but instead by the physiological tolerances of the species and episodic extreme climatic events influencing critical factors such as growing-season duration and suitable soil temperature, as well as nutrients, wind, exposure, presence of soil, and physical soil disturbance. Doležal et al. (2016, 2018) revisited in 2013 populations after ten years and permanent plots after four years. They showed that several species including *Saussurea gnaphalodes* had shifted up to about 6150 m, about 150–250 m above the limit of continuous plant cover, in response to warming. The impact of warming, however, interacted with increased precipitation and soil disturbance. The extreme summer snowfall in 2010 may have led to a substantial decrease in plant cover in both alpine and subnival vegetation with a compositional shift towards plants favouring wetter habitats (e.g., *Koenigia islandica*, *Pegaeophyton scapiflorum*). Simultaneous increases in precipitation and summer temperature resulted in rapid snow-melt and frequent night frosts, leading to multiple freeze-thaw cycles detrimental to many subnival species (e.g., *Aphragmus oxycarpus*, *Draba oreades*, *Poa attenuata*, *Saussurea hypsipetala*). These long-term results suggest that plant responses at very high elevations to ongoing climate shifts are complex, multi-dimensional, species specific, and spatially variable (Doležal et al. 2016, Doležal et al. 2018).

These conclusions are elegantly reinforced by the detailed study by Doležal et al. (2021) on the annual growth and recruitment of *Potentilla pamarica* over 60 years in the dry steppe, wet alpine, and cold subnival zones between 5250 and 5900 m. In the steppe, recruitment increased with high late-winter snowfall and decreased with high summer

temperature and growth increased with high summer precipitation. In contrast, in the alpine and subnival zones, warm winters and summers favour growth and recruitment whereas snow-rich winters reduce them. Age distribution shows the highest density of healthy populations in the alpine zone and ageing populations in the steppe and subnival zones. Accelerated warming in the 1990s limited growth and recruitment in the dry steppe areas whilst favouring plant growth in the alpine zone. Recruitment in the subnival zone was low due to concomitant extreme snowfall. As Doležal et al. (2021) conclude, their results in Ladakh (see also Doležal et al. 2016, Doležal et al. 2018) show the high vulnerability of the high-elevation Himalayan flora and vegetation to climate change and “Continuing trends of extreme snowfall events at higher elevations and droughts at lower elevations may lead to species range contraction”. These Ladakh experimental and monitoring studies highlight the complexity of predicting alpine plant responses to climate change in the Himalaya (cf. He et al. 2019, Anderson et al. 2020, Hamid et al. 2020, Wang et al. 2021).

Snow-roots and nitrogen uptake

Onipchenko et al. (2009) report the discovery of specialised ‘snow-roots’ on *Corydalis conorhiza*, a snow-bed plant growing at 2800 m in the northern Caucasus (Russia). Besides providing detailed anatomical evidence, they show using experimentally added ¹⁵N that the snow-roots form extensive networks of specialised aboveground roots within the snow and acquire nitrogen directly from the snow. Snow-roots differ anatomically from conventional soil-roots (0.5–0.7 mm diameter) in being very fine (0.1 mm diameter) and having very few cell rings and no clear differentiation into epidermal and cortex cells. The inner root section has a ring of endodermal cells with thick, cork-like walls. Snow-roots form dense networks that cover large areas under the snow, rather like a filamentous alga (see Figure 1c and 1d in Onipchenko et al. 2009). They disappear on snow-melt, explaining why these snow-roots had not been noticed before. Further studies by Onipchenko et al. (2014) show that snow-roots are true winter organs that start to grow early in winter. They require winter surface and soil temperatures continuously close to or slightly above freezing. Excavations of snow-beds show that snow-roots are present in January and in May, as well as in July when Onipchenko et al. (2009) made their initial studies. An obvious question is do other snow-bed plants have snow-roots?

Onipchenko et al. (2021), following an observation of “root-like structures in the snow” in an obscure 1948 publication about snow-beds in the Aragat Mountains in Armenia, investigated snow-beds at 3300 m on Mt Aragatz in the Lesser Caucasus in Armenia. Using a combination of field observations, anatomical studies, and DNA barcoding, Onipchenko et al. (2021) present very strong evidence for snow-roots in six species in five families and some evidence for snow-roots in two additional species. The species with very strong

evidence are *Carum caucasicum* and *Chamaesciadum acaule* (Apiaceae), *Gagea pusilla* (Lilaceae), *Minuartia aizoides* (Caryophyllaceae), *Ranunculus aragatzii* (Ranunculaceae), and *Sibbaldia procumbens* (Rosaceae). Like *Corydalis conorhiza* (Papaveraceae), all these species except *G. pusilla* are eudicotyledons. The two species that probably have snow-roots are *Poa alpina* (Poaceae) and *Taraxacum stevenii* (Asteraceae). Current knowledge shows snow-roots being present in nine species in seven families, all occurring in the Caucasian mountains *sensu lato* including mountains in Turkey and Iran. Onipchenko et al. (2021), failed to find snow-roots in the Slovakian Tatra, the Swiss or Italian Alps, or in the Chinese Himalaya. However, they report fine, whitish, aboveground nets (roots?) within patches of *Claytonia lanceolata* (Montiaceae) at the edge of snow-beds in the Montana Rockies in North America.

Clearly there is very much to be discovered about how widespread snow-roots are both geographically and taxonomically and what features of snow such as its nitrogen content, atmospheric nitrogen loading, and/or oxygen availability are responsible for the development of snow-roots (Onipchenko et al. 2021). As Körner (2003, p. 62) concludes “snowbeds represent a rather specific part of the alpine life form from subtropical to polar latitudes, with microenvironmental peculiarities and the co-occurrence of a variety of plant response types with respect to stress resistance, development and biomass production. Over very short distances and periods of time we find extreme changes in life conditions – a natural ‘experiment’ which will continue to provide promising opportunities for the study of plant adaptation”. Snow-roots clearly provide such exciting opportunities.

The coldest place where angiosperms can live

As discussed above, the colony of *Saxifraga oppositifolia* near the summit of Dom de Mischabel in Switzerland is currently the highest known vascular

plant in Europe (Körner 2011). The thermal conditions near to the summit of Dom (4543 m) for the growing season were recorded by a miniature data-logger and compared with results from 5960 m in the Himalaya (32°N) and 450 m on Svalbard (78°N) (Table 5; Körner 2011). During the growing season of 2008/09, Dom experienced 66 days with a daily mean temperature >0°C at 2–3 cm below ground. Degree hours (°h) >0°C summed to 4277 °h corresponding to 178° days. The absolute minimum winter temperature was –20.9°C and the absolute maximum was +18.1°C. The mean temperature for the growing season was +2.6°C and all plant parts experienced temperatures below 0°C every night, even during summer (Körner 2011). Körner (2011) concludes that in comparison with climate data from other extreme habitats in the Alps (3460 m; 46°N), Himalaya (5960 m; 32°N), Arctic (78°N), and Antarctic (69°S), the Dom environment represents what is probably the coldest place for vascular plant life on Earth. The likely limit for vascular plant growth to persist, once established, may be 60–70 growing-season days with at least one hour >3°C or a daily mean >0°C in the uppermost rooting zone, and a seasonal mean top-spoil temperature of about 2.6°C for about 180 degree days >0°C over the entire growing season (Körner 2011).

In Aurland, western Norway, Odland and Birks (1999) compare vascular species richness in 100 m elevational bands from sea-level to 1764 m with inferred mean July air temperatures for each band based on a standard lapse rate of 0.57°C per 100 m change in elevation (Laaksonen 1976). They did a similar analysis using the species data of Jørgensen (1932) from the Jotunheimen mountains in south-central Norway. Both areas show a decrease of 30 species per 1°C decrease in mean July air temperature. The vascular plant limit in Jotunheimen is 2370 m, where the estimated mean July air temperature is 2.2–2.3°C, close to the measured values for soil temperature near the summit of Dom of 2.6°C for the growing-season mean and 2.8°C

Table 5. Soil temperature records (2–3 cm depth) from Svalbard (450 m), near the summit of Dom de Mischabel in Switzerland (4543 m), and north-west Himalaya (5960 m) for the growing season 2008/09 (from Körner 2011). The lowest recorded values are shown in bold.

Record	Svalbard	Dom	Himalaya
Absolute minimum (°C)	-13.0	-21.0	-20.0
Absolute maximum (°C)	12.0	18.1	11.8
Growing-season mean (°C)	4.8	2.6	4.0
Mean of warmest month (°C)	4.7	2.8	-
Duration of growing season (days)			
a) First to last day when $T_{\max} \geq 3^{\circ}\text{C}$	47	72	82
b) First to last day when $T_{\text{mean}} > 0^{\circ}\text{C}$	58	73	82
c) No. of days when $T_{\max} \geq 3^{\circ}\text{C}$	46	62	80
d) No. of days when $T_{\text{mean}} > 0^{\circ}\text{C}$	51	66	81
No. of hours in c) with $T_{\max} \geq 3^{\circ}\text{C}$	893	585	1085
No. of hours in d) with $T_{\text{mean}} > 0^{\circ}\text{C}$	1189	1053	1684
Degree days in c) (°d)	99	103	144
Degree days in d) (°d)	210	178	290

for the mean of the warmest month (Körner 2011). As discussed in the introduction to this section, local conditions of soil temperature, surface temperature, duration of the growing season, and exposure (slope and aspect), may be critical in determining local plant distribution at very high elevations (Körner 2011, Körner and Hiltbrunner 2018, Körner 2021). The local environmental conditions where *Saxifraga oppositifolia* grows near the summit of Dom may represent “the life conditions at what is possibly the coldest place for angiosperm plant life on earth” (Körner 2011).

An ignored von Humboldt legacy

In all the many recent celebrations, reviews, books, and so forth of von Humboldt’s many and diverse achievements and writings, I have not found any mention of the Humboldt Cantata (MWVD2), also known as the Welcome or Greetings Cantata. It was composed specially by Felix Mendelssohn (1803–1847) in 1828 for the Natural Scientists Congress (attended by about 600 delegates) in Berlin, which was organised by von Humboldt and his brother Wilhelm. At the opening session of the Congress on 18 September 1828, Mendelssohn directed the Cantata and Alexander von Humboldt gave an address on the social utility of science (Todd 2003, 2005). The Cantata has an unusual scoring of a four-part male choir with four soloists (two bass, two tenors) accompanied by two clarinets, two trumpets, two horns, low strings (cello and double bass), and timpani. It consists of seven parts, solo and duet numbers, and recitatives and lasts for about 25 minutes (Todd 2005). The text follows the progress of the natural world from chaos to unity and the development of the ‘glorious world’ and the Lord is asked to “bless the strivings of the united forces” (Todd 2003, 2005). It has, as far as I know, rarely been performed since 1828, although performances are recorded from 1930, 1959, 2004, 2006, 2009, 2012, and 2019. Although it was recorded by the Leipzig Gewandhaus Orchestra under Riccardo Chailly in 2009, this recording has not been released.

Von Humboldt’s reaction to the 1828 premiere is not known but the Cantata certainly brought Humboldt closer to Felix and Fanny Mendelssohn (Todd 2003, 2005). With von Humboldt’s increasing interest in magnetic observations, he constructed a copper hut in the garden of the Mendelssohn’s residence. Here, while Mendelssohn rehearsed a revival of Bach’s St Matthew Passion, von Humboldt was recording changes in magnetic declination, often at hourly intervals between 3 p.m. and 7 a.m. (Todd 2005). Within a few years, what had begun in the Mendelssohn’s garden as a modest laboratory became part of a “chain of geomagnetic observation stations” that stretched around the world, an early example of effective international collaboration (Botting 1973, Todd 2003).

Conclusions

Thanks to continued botanical exploration of the world’s mountains an immense amount of information

has accumulated since von Humboldt and Bonpland (von Humboldt et al. 2009) discussed elevational distributions and limits of vascular plants globally. Some higher plant families are well represented at very high elevations. They include the Asteraceae, Brassicaceae, and Caryophyllaceae. Several large families, such as Fabaceae, Lamiaceae, Cyperaceae, and Apiaceae, are absent or very poorly represented in high-elevation floras. It is surprising that despite *Saxifraga oppositifolia* growing in what might be the coldest place on Earth for vascular-plant growth and also being the highest vascular plant in North America, the second highest on Svalbard, and the northernmost plant in the Northern Hemisphere in Greenland, only one other *Saxifraga* (*S. lychnitis* var. *everestianus*) occurs at very high elevations (6350 m; Dentant 2018). Several *Saxifraga* species (e.g., *S. biflora*, *S. bryoides*, *S. cernua*) do, however, occur at moderately high elevations in various European mountain ranges.

Dentant (2018) notes that the five uppermost taxa found on Mt Everest all belong to clades that are very rich in cushion plants (Aubert et al. 2014). These clades account for 54% of the nival flora in the central Himalaya (Miehe 1987), 49% in the Hindu Kush, 46% in the Caucasus (Breckle et al. 2017), and more than 52% in the European Alps (Aeschmann et al. 2011). In the Late Miocene radiation of *Androsace* about 15 million years ago (Roquet et al. 2013, Boucher et al. 2016, Dentant 2018), the cushion life-form may have appeared independently in two uplifting mountain ranges – the Himalaya and the European Alps. New *Androsace* taxa (Dentant 2017, 2018) are being recognized and described, illustrating how much there is to be discovered about basic taxonomy at high elevations.

Detailed plant ecological studies in high-elevation areas are also revealing new and unsuspected features such as the critical importance of local-scale topography in alpine areas, the dynamics of high-elevation plants in the Ladakh Himalaya, the occurrence of snow-roots in the Caucasian mountains, and the environmental extremes that vascular plants withstand, as on Dom in Switzerland (see Dentant 2018 for additional examples). In preparing this review, I have been surprised how many detailed regional or national floras do not give any information on elevational ranges in, for example, North America, Australia, or North Africa. Such data are important ecological attributes about a species. Much effort is expended in documenting the geographical distribution of species but much less effort is given to documenting the elevational distributions and limits of species.

Dentant (2018) notes that “it seems timely to encourage a renewal approach to mountaineering, one which integrates awareness of scientific issues and a culture of data collection. Climate change and its consequences on biodiversity could be an interesting point of convergence between mountaineers and scientists”. People such as Eric Shipton, Bill Tilman, Norman Collie, Noel Odell, Sandy Wollaston, and Albert Zimmermann were all great mountaineers and explorers, but they also had a scientific background

and an interest in their environment. Their finds are a challenge to a new generation of scientifically trained mountaineers interested in our rapidly changing world and for botanists and ecologists who are also good climbers or mountaineers (e.g., Körner 2011, Dentant 2017, Marx et al. 2017, Dentant 2018). Alexander von Humboldt was primarily a scientist, but he had clearly had to have been a bold mountaineer to have reached about 5875 m on Chimborazo in 1802.

Von Humboldt would certainly have been excited, stimulated, and fascinated by all that has been discovered about high-elevation botany and ecology since 1802. The basic message from von Humboldt's legacy of high-elevation exploration and global biogeography is that there are still many basic and exciting things to be discovered in areas high above the trees.

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