THE MOUNTAIN FLORA OF LAKELAND

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After the Scottish Highlands, Snowdonia and Upper Teesdale come next in fame as districts for mountain plants in Britain. The Lake Country of Cumberland, Westmorland and Lancashire North of the Sands is less celebrated by far, though only the first region has a greater number of vascular mountain species. The poverty of many hills and the scarcity of those species which attract the greatest interest probably accounts for the poor reputation of the Lakeland fell flora and the relative neglect which it is accorded. One admits that there are woefully few places with a good assemblage of notable plants; moreover, these are either fairly remote or else they include difficult ground. Even so, the number of species adds up to quite an imposing list.

The Lakeland fells were quite well explored for plants by the end of the nineteenth century, and though the last sixty years have produced many new localities for various species, only one completely new discovery has been made during this period. Within the last few years, there has been proof that several species were unjustifiably presumed extinct in the district, whilst the finding of new stations for some plants would indicate that knowledge of distribution is not yet complete. The main sources of information on plant distribution are the three local floras (Baker, 1885; Hodgson, 1898; and Wilson, 1938), but data for the hills are mostly scattered and there is no single account of the mountain plants of the whole region.

I have seen all the plants named in Table 2 growing on the Lakeland fells, with the exception of *Cystopteris montana, Phleum alpinum, Poa balfourii, Vaccinium uliginosum, Veronica serpyllifolia* subsp. *humifusa* and *Euphrasia frigida.* The last two species have been observed recently by other botanists. A few species claimed for Lakeland seem to me to be best regarded as doubtfuls, and likely to have been recorded either in error or through confusion; they are *Cardaminopsis petraea, Gnaphalium supinum, Luzula spicata, Juncus trifidus* and *Cystopteris montana* (the Skiddaw record).

The term "mountain plant" as here applied to Lakeland is arbitrary, and used to indicate those belonging essentially to the hills, instead of referring to definite geographical groups such as Arctic-Alpine. It denotes the species which, in this district, have their headquarters above 1,000 ft., though some of these extend to low levels as well. By this definition, there are included with the exclusively high-level plants others such as *Antennaria dioica* and *Lycopodium clavatum,* which occur on heaths in the lowland country of southern England.

Nomenclature is according to the following works:

VASCULAR PLANTS

List of British Vascular Plants, by J. E. Dandy. London. 1958.

MOSSES

An Annotated List of British Mosses, by P. W. Richards and E. C. Wallace. *Trans. Brit. Bryol. Soc.,* **1**. 1950.

LIVERWORTS

An Annotated List of British Hepatics, by E. W. Jones. *Trans. Brit. Bryol. Soc.,* **3**: 353-374. 1958.

LICHENS

Census Catalogue of British Lichens, by W. Watson. Cambridge. 1953.

AN ECOLOGICAL BACKGROUND

Lakeland forms a single, well-defined geographical region, and sub-division is best made according to valleys and mountain groups, for the county boundaries are meaningless in any account of its natural history.

The distribution and abundance of mountain plants in Lakeland is governed, as elsewhere in Britain, mainly by altitude and soil conditions. Most of the species need a cool climate for their existence, and this condition, more than any other, is implicit in the environment at high levels. Scafell Pike, Scafell, Helvellyn and Skiddaw exceed 3,000 ft., and there are many peaks rising to 2,500 ft. or more. Taking 1,500 ft. as the level at which mountain plants become numerous in this region, there is thus a fairly broad altitudinal (i.e. climatic) zone available to the group. Within this zone, rock and soil type have a great influence on distribution of these plants.

The rocks of the high fells consist mainly of the Borrowdale Volcanic Series, Skiddaw Slates, and large igneous masses of granite and syenite. All these parent materials are predominantly acidic, only the first group containing basic rocks in any quantity, and then very locally. Under a rainfall which exceeds 100 ins. annually on most of the high fells, and tops 150 ins. in the Gable-Bow Fell area, the soils derived from acidic rocks are strongly leached and base-deficient. Even on the basic rocks, leaching is so pronounced that podsolisation is resisted only by some form of flushing (cf. Pearsall, 1950). The majority of the mountain plants are calcicole, and this group is most richly represented on the Helvellyn range, where calcareous rocks outcrop more extensively at high altitudes than in any other massif.

The deep, crag-girt, north and east facing coves of the Helvellyn, Fairfield and High Street ranges, and the great ravines cleaving the flanks of the Scafell range, together harbour nearly all the calcicole species which occur in the region and so form the best hunting-grounds. There are a few good crags on the Pillar, at the head of the Buttermere valley, in the Vale of Newlands, and in Langdale; but most of Copeland Forest, the Great Gable area, the Coniston Fells, the High White Stones group and the Bowfell range, show the poverty of the acidic Borrowdale Volcanic rocks. This Series contains a good deal of calcareous material in Borrowdale itself and in the Vales of Naddle, St. John, Ullswater, Longsleddale and Swindale, but at too low an altitude to support most mountain species. The Skiddaw Slate hills, including Skiddaw, Blencathra, the Grasmoor-Hobcarton group, Robinson and Hindscarth, are barren ground; whilst the Buttermere and Ennerdale syenite, and the Eskdale granite, together occupying a large area of the western fells, are equally unproductive.

The rich Borrowdale Volcanic cliffs contain relatively large amounts of calcium, either as solid calcite in cavities and veins of varying size, or in combined form in the various mineral components, e.g. hornblende. Such rocks, particularly those containing free calcium carbonate, are often softer than the acidic materials of the Series, and break down faster to give base-rich soils. Even on the same crag, however, the rock type is often mixed and the incidence of flushing variable, leading to quite sharp changes in soil base-status locally (cf. Hora, 1947). Sometimes, hard acidic lavas are flushed from calcareous rocks above and show soil conditions more typical of the latter. Even on Helvellyn there are no extensive exposures of uniformly rich rock such as occur on Snowdon or Ben Lawers, and search has to be made for the good patches in the crags. On the Scafell Range, from Glaramara to Wasdale Screes, the basic rocks occur mostly along the shatter belts of fault zones, where there has been strong impregnation with calcium carbonate and ferric oxide. These shatter belts are susceptible to weathering and erosion, so that their tracks are often marked by deep, stream-cut ravines, whose steep and crumbling sides, with their reddish, calcite-bearing rocks, provide suitable habitats for the mountain calcicoles.

The predominant upland communities, acidic grasslands, reflect not only a prevalence of strongly podsolised soils, but also the influence of sheep-farming over a long period. Land management has greatly impoverished the natural vegetation of the fells. Woods have been destroyed wholesale and the tree-limit artificially depressed, whilst fire and the grazing of sheep over every accessible square foot of ground have greatly reduced or locally eradicated ericaceous and herbaceous communities, and granted supremacy to the grasses, rushes and bracken. The mountain calcicoles, having mostly but slight tolerance of competition and/or grazing, have become restricted to situations where steepness of the ground satisfies the need both for open habitats and protection from sheep. Some species do not suffer from the attentions of sheep, and these occur along rill and stream sides, and in open flushes, as well as on the more precipitous ground.

Some calcifuge mountain plants have probably become scarce because they belong to the heath communities which suffer so much from burning and grazing; their restriction to rocky ground is thus an unnatural condition. Others need open habitats and are confined to places where instability prevents the development of closed vegetation.

Palaeo-ecologists have shown that a montane vegetation was everywhere widespread in Britain during Late-glacial times, so that the present mountain flora of Lakeland has become relict in three ways. First, the rising temperature and advancing forests of the Post-glacial Period drove these plants to high levels, whilst the gradual deterioration of the soils under a wet climate and finally, the management of the hills for sheep, have greatly restricted their distribution within the existing montane zone (cf. Godwin, 1949).

THE FLORA

(a) SPECIES OF BASIC ROCKS AND SOILS

Certain plants appear faithfully wherever basic cliffs occur, whereas others are irregularly distributed, often in widely scattered places, and in the extreme case, have only one or two stations. Between these extremes are species of intermediate rarity. Nearly every basic cliff in Lakeland lying above about 1,200 ft. may be relied upon to hold *Sedum rosea, Oxyria digyna, Thalictrum minus, Galium boreale, Rubus saxatilis, Alchemilla wichurae, Cochlearia alpina, Saxifraga aizoides, S. hypnoides, Euphrasia rivularis* and *Asplenium viride.* These plants vary much in abundance locally, and while their soil requirements are rather similar, their typical micro-habitats show some variation. The first six are particularly sensitive to grazing and so are more or less confined to crag-ledges, rocky stream-sides, or (occasionally) screes. The need for open habitats restricts *Asplenium viride* to rock faces, and a preference for shade keeps it mainly in crevices and recesses. *Cochlearia alpina, Euphrasia rivularis* and the two Saxifrages grow equally well on damp, broken slopes, in flushes, and beside rills, and are often more plentiful in these situations than on the main cliffs. *Saxifraga aizoides* and *S. hypnoides* grow locally as pioneers on earthy screes, as in Wasdale, and have colonised in abundance the quarry spoil below Honister Crag, forming distinct tufts with an unusually compact growth.

A few mountain plants have a fairly wide distribution in Lakeland, but are absent from many places where conditions seem suitable in every way. *Saussurea alpina* has a good many scattered localities, but grows sparingly in most of these: Helvellyn and the Pillar are its best stations and here some good clumps occur. This is a plant of high levels, occurring mostly above 2,000 ft., and on the damp soils of shady, flushed ledges. *Polystichum lonchitis* occupies similar habitats, though it tends to be rooted in sheltered crevices and corners, and evidently once had a number of stations in the eastern half of the district. Though probably never a plentiful plant in any locality, the rarity of the Holly Fern has been magnified by the depredations of fern collectors. It still survives sparingly in at least three old haunts. *Thalictrum alpinum, Juncus triglumus, Epilobium alsinifolium* and *Myosotis brevifolia* are plants of rather wet flushes and rill-sides, though all but the last occur on many rock-ledges. None needs particularly rich soils but all are local. The first two grow mainly at high levels, but the second pair descend to 500 ft. in the Vale of St. John.

Saxifraga oppositifolia, Silene acaulis and *Minuartia verna* have their main strongholds on the Helvellyn Range, though the first grows very finely and plentifully on certain crags of the Scafell Range. All fare best on rather dry, crumbling, calcareous rocks, though the Purple Saxifrage commonly appears in a more attenuated form on wet ledges and in basic flushes. Moss Campion sometimes occurs on steep banks at the broken cliff-foot, and the Purple Saxifrage grows in at least one earthy scree, but both are confined to steep, unstable ground. *Minuartia verna* is locally plentiful in close-cropped, rich turf on the upper Westmorland slopes of Helvellyn, but steep rocks are its more usual place.

The last eight plants all tend to favour rather open habitats, where competition is slight, and this tendency is pronounced in nearly all the remaining mountain calcicoles, most of them rarities.

Among the plants particularly associated with dry calcareous rocks elsewhere in Britain are *Draba incana, Potentilla crantzii, Dryas octopetala* and *Ajuga pyramidalis*. In Lakeland, all four belong to steep and rather exposed rock faces, always of strongly calcareous material. Alpine Cinquefoil grows on at least eight different crags, mostly rather sun-exposed, scattered over central Lakeland, and *Draba incana* also occurs sparingly in eight stations, chiefly on the eastern fells. *Dryas octopetala* was first found by James Backhouse, jun., in 1869 on Helvellyn. It still grows in very small quantity on a crag of the Helvellyn range and a single good clump was found on the Scafell range by the writer in 1957. *Ajuga pyramidalis* is even more impressive in its rarity, a robust cluster being known from just a single ledge in the High Street Range, where it has hung on since its discovery by Backhouse 90 years ago. None of these four species belongs to particularly high altitudes, for all their localities lie between 1,000 and 2,500 ft.

By contrast, several other calcicoles appear to owe their rarity at least partly to their requirement for high elevations, for most of their localities lie above 2,300 ft. Their chief, or only, stations are accordingly on the Helvellyn Range. This group includes *Saxifraga nivalis, Cerastium alpinum, Salix lapponum, Carex atrata, Poa alpina, P. balfourii, Phleum alpinum, Euphrasia frigida, Veronica serpyllifolia* subsp. *humifusa* and *Cystopteris montana.* The habitats of these plants differ in detail, but all occur on north to east facing rocks or broken slopes, and very sparingly. (I have not seen the last five and am judging by the records.) *Poa glauca* has been seen on Helvellyn only at about 2,800 ft., but has a better colony at 2,000 ft. on the Coniston Fells. *Thlaspi alpestre* would appear to be confined to a similar altitude on Helvellyn, where it is very scarce, but the Fusedale record probably refers to a lower level. *Polygonum viviparum,* a strangely rare plant in Lakeland, might be placed in the same group, for it is known only from a few places on Helvellyn and on Bowfell, all above 1,800 ft., though on limestone near Shap it descends well below 1,000 ft. This plant grows on rather wet, bare ledges and in the richer grass-lands adjoining the cliffs or on exposed summit slopes.

The remaining three species of the present group all have a curiously restricted and discontinuous distribution in Britain. *Sedium villosum* has a very few Lakeland stations, mostly in wet, basic flushes at moderate elevations in the eastern half of the district. Another Pennine plant, *Potentilla fruticosa,* was discovered on Helvellyn by James Backhouse, jun., but has evidently not been seen there since. It still grows very locally on the shaded crags of Wasdale Screes and the Pillar, on moist ledges, in rock crevices and sometimes in tall herbaceous communities. The growth is not nearly as luxuriant as on the banks of the Tees, but there are some good clumps.

Woodsia ilvensis was found in several places, chiefly on the eastern fells, by Victorian fern-hunters, but its present status is obscure. At least one colony still survives in the District, and may well be the finest remaining in Britain. The growth varies from one year to another and is evidently best during a wet summer, when many fronds reach 7 ins. in length. There are about a hundred plants, and during a favourable season, one clump, with over a hundred fronds, has a diameter of 10 ins. or more. The habitat consists of dry, earthy and moderately basic rocks with a very sparse plant growth otherwise. The recorded stations of *Woodsia ilvensis* are evidently all above 1,500 ft., but probably do not exceed 2,500 ft. There are compelling reasons why no locality can be given for the described colony.

(b) Tolerant species

The remainder of the mountain flora consists of plants which grow on both calcareous and non-calcareous materials, and those which are confined to the latter.

The most famous of Lakeland plants, *Lychnis alpina,* may be put in the first group. Long known from Hobcarton Crags in the Grassmoor group, this species grows on dry, acidic Skiddaw Slates on the sun-exposed walls of gullies at 2,000-2,300 ft. The other reported station on the Coniston Fells has never, to my knowledge, been re-discovered. *L. alpina* still adorns the rocks of Hobcarton, though the many pilgrims have taken a toll, and the best clumps are now mostly in awkward places. Over 130 plants were counted recently, at the height of the flowering time, but the total population probably does not exceed 150 individual clumps. The blooms vary from white to the predominant deep pink, and the growth is much more luxuriant than in the Clova station. Its associates are such commonplace taxa as *Vaccinium vitis-idaea, Cryptogramma crispa, Solidago virgaurea* and *Festuca vivipara.*

Raven and Walters (1956) have described the Hobcarton habitat of the plant, and their evidence suggests a connection between its presence here and an unusual quality of the rock, notably the occurrence of a vein with pyrites. Other botanists had suggested previously that *Lychnis alpina* has an unusual mineral requirement, but magnesium was mentioned as the critical ion. The plant grows on serpentine in Clova, and Fernald (1907) believed it to belong essentially to the flora of magnesium-rich rocks (including serpentine) in the New England mountains. Knaben (1950) says it grows on nearly all serpentine outcrops in Norway.

Pyrites is widespread in Lakeland and characteristically associated with other minerals in veins, so it seemed possible that more than one ion might be in abnormally high concentration. Samples of the soil on which *L. alpina* was actually growing, and from the crumbling banks below an unusually rotten, yellowish-brown seam of rock in the middle of the main colony, were analysed in an attempt to discover any peculiar chemical properties. The analyses (Table 2) disclose that two samples, especially B, are rich in manganese, which is the predominant exchangeable cation. Soil B also has more available iron than is usual, but iron-bearing rocks are so widespread in the district that this cannot be regarded as a distinctive feature. The usually predominant ion, calcium, and to a lesser degree, magnesium, sodium and potassium, are all in low concentration, and there may well be significance in the relatively high proportion of manganese rather than in the absolute amount. The pH values are fairly low and soil chemists have shown that manganese is more readily available in acidic than basic soils.

It is interesting that *Grimmia atrata,* a moss said to be particularly associated with copper-bearing rocks (Martensson and Berggren, 1954), grows abundantly with *Lychnis alpina* on Hobcarton Crags. In two samples copper is the predominant cation after manganese, but is only in average concentration compared with most soils: sample No. 6 from Helvellyn shows a larger amount. It is, however, rather suggestive that this rare moss grows on at least two copper seams in the Coniston Fells, where the other *L. alpina* station lies. Perhaps magnesium, copper, manganese, iron and even other metals are mutually replaceable as critical ions in the physiology of these plants. Again, it could be that the relatively high combined concentration of manganese, iron and copper is the decisive factor concerned in the occurrence of *L. alpina* at Hobcarton Crags. Pigott (1958) has, however, pointed out that the pyritic rocks favoured by "copper-mosses" in this country give soils rich in sulphate. No analyses of this anion were made for the Hobcarton samples, but the pH values do not show the high acidity usually associated with high concentration of sulphate.

Though *Alchemilla alpina* is so plentiful on basic rocks, it is best included in the present group, since it flourishes also on relatively base-deficient soils. A plant of wide tolerances, it is surprisingly little affected by sheep-grazing. Whilst growing in the utmost profusion on many of the high crags, it is no less abundant on some grassy slopes and soily screes, often at much lower levels. Though the second most plentiful mountain plant in Lakeland, *A. alpina* has a patchy and, at first sight, rather puzzling distribution. It grows abundantly on Dove Crags, Grasmoor, but is otherwise very scarce on the Skiddaw Slate, and though common on many of the Borrowdale Volcanic fells, it is noticeably sparse in some parts, such as Langdale and Eskdale.

The distribution of this plant is to be explained largely by its soil requirements, though its absence from apparently suitable substrata remains mysterious. *A. alpina* is not completely acid-tolerant in Lakeland, though many of its soils are base-poor by agricultural standards. It appears to avoid acidic "mor" soils and to favour either skeletal types in which podsolisation is resisted to some extent by steepness of the ground or frost action, or those which are periodically enriched by flushing during wet weather. From these rather low nutrient levels, the plant grows successfully as base-status increases to saturation point. The need for something better than the poorest soils probably explains its general absence from the Skiddaw Slate, Buttermere syenite and Eskdale granite, as the soils derived from these parent materials are usually more mineral-deficient than those formed from the Borrowdale Volcanic rocks.

This point is nicely shown in the Newlands Valley, where the dividing line between the last Series of rocks and the Skiddaw Slate runs obliquely up the slope of Eel Crags, with the Borrowdale Volcanic uppermost. *A. alpina* is abundant on the last parent material, but occurs on the Skiddaw Slate only where this receives at least intermittent drainage from the igneous rocks above. The soils derived from the Slate are evidently too poor normally to support the plant. Again, Robinson above Buttermere is a Skiddaw Slate hill but has some rather calcareous patches of this rock in one place. *A. alpina* is abundant on these lime-bearing outcrops, but quite absent from the acidic rocks which form the bulk of the mountain. Some of the hard, flinty volcanic ashes of the Borrowdale Series likewise yield soils of nutrient value too low for *A. alpina*. Within Lakeland, this plant may thus be used, to some extent, as an indicator of the better mountain soils.

Salix herbacea and *Carex bigelowii* often grow together, and occur in all the major fell groups, though the latter is the more plentiful and widely distributed. Both belong to the *Rhacomitrium* heath of high summits and spurs, and are almost the only mountain plants of the barren, stony and windswept summits, where they occur in extreme dwarf form on the poorest of soils. They are, however, equally typical of elevated cliffs, both acidic and basic, and attain a relatively luxuriant growth on the sheltered rock ledges. *Carex bigelowii* grows successfully in closed grass and dwarf shrub communities, and in shallow, high-level bogs, down to 1,800 ft., whereas *Salix herbacea* is confined to more open, drier soils, and has not been seen below 2,150 ft.

Saxifraga stellaris is a common plant of the damper soils, usually with a rather low nutrient content, and is one of the few mountain species to occur plentifully on the Skiddaw Slate. Moist rocks, stream-sides, small rills, flushes and springs are its chief habitats, but it grows sparingly on exposed, rather dry, summits and screes. Fine, robust clumps occur in many damp, shaded rock crevices, and it is sometimes associated with others of its genus on the more basic rocks. Hawkweeds are abundant on some of the high-lying cliffs, and could form the subject of a separate account, but the distinctive *Hieracium holosericeum* deserves special mention. A true montane plant, this species is rare and confined to crags at over 2,000 ft. on several widely separated hills. It needs very open, dry rock ledges, and often grows on exposed faces with only the very sparsest accumulation of soil in tiny crevices. Whilst it would seem to flourish in habitats which are acidic and base-deficient, the parent rock is not necessarily the poorest. *Antennaria dioica* and *Orthilia secunda* are best included under tolerant species, since their substrata vary from moderately acidic to decidedly basic. *Antennaria dioica* is rather local, growing occasionally in grassy and heathy pastures, but most finely and abundantly on base-rich rocks at moderate elevations, as on the crags above Honister. *Orthilia secunda* occurs over the rather narrow range of altitude from about 1,000 to 1,700 ft. and is not a plant of high levels. Its habitat is usually the dry crevices of shattered rocks in damp places, such as gullies and ravines, in Borrowdale, the Vale of Legburthwaite and Mardale.

The trio of coastal species, *Silene maritima, Armeria maritima* and *Plantago maritima* all qualify for inclusion in the mountain flora, and belong to the present ecological group. The first is the most widespread and abundant, ranging from river and lake-side shingle to high-lying screes and cliffs at 2,600 ft., on markedly acidic to slightly basic materials. It grows very finely on certain crags of the Scafell Range. Whereas this species favours the drier rocks, *Armeria maritima* grows usually on rather moist, shaded crags and has not been seen below 2,300 ft. It occurs sparingly on several hills, on rocks slightly enriched by flushing. *Plantago maritima* is abundant on rather moist, basic ledges of Honister Crag, but grows by sandy tracks in Ennerdale.

(c) Calcifuges

Last are those plants which belong mainly to acidic heath or bog communities. *Arctostaphylos uva-ursi* and *Empetrum hermaphroditum* have scattered localities, mainly on fairly stable screes and broken cliffs. Both grow on fairly dry, acidic soils with a "mor" surface humus, but the former is mainly a plant of moderate elevations (below 2,000 ft.) and belongs to open Callunetum, whereas the latter grows chiefly above 2,000 ft. and is associated more with *Vaccinium* spp. *Empetrum hermaphroditum* does, however, grow well on the screes of Riggindale Cove at only 1,200 ft. Both plants are likely to have been eliminated from many former localities by fire and sheep, but their absence from many suitable and undisturbed cliff ledges cannot be thus explained. *Arctostaphylos uva-ursi* still grows abundantly on the rocky western slope of Grasmoor, its trailing mats there mixed with heather and juniper, forming a community similar to that widespread in parts of the Highlands.

Vaccinium uliginosum, a frequent plant of montane heaths and bogs in Scotland, is recorded only from Grisedale Pike, High Street and Great Mell Fell in Lakeland. Probably all these localities lie above 1,500 ft., but this species occurs in a number of places just beyond Lakeland, in peat-mosses and moors at surprisingly low levels: near Carlisle it descends to below 100 ft. The dwarf form of juniper, *Juniperus communis* subsp. *nana,* grows on cliffs and broken ground on several hills, mostly above 1,500 ft., but is linked by intermediate forms to the ordinary shrub which produces thickets on many lower hillsides. *J. communis* subsp. *nana* is not merely the montane habitat form of *J. communis,* for equally stunted plants, still clearly nearer to the latter, commonly occur in exactly the same kind of place as the true dwarf, and even alongside it, up to fully 2,500 ft. The high-level juniper populations are evidently mixed and there is a taxonomic and ecological problem to be solved.

Lycopodium annotinum has scattered localities along the Langdale slopes of the Bow Fell range, mainly in rather damp, rocky grassland, but is unknown elsewhere in Lakeland. The three other club-mosses, *L. selago, L. alpinum* and *L. clavatum* are all widespread and often common—typically in dry, acidic grassland —and frequently grow in close association. All descend to very low levels, but whereas the other two reach the highest tops, *L. clavatum* seldom occurs much above 2,000 ft.: they are less strictly montane than *L. annotinum.* Though so common on Pennine moors, *Rubus chamaemorus* is rare in Lakeland, its few stations being high on the fells in the eastern half of the region—the Skiddaw Group, Matterdale Common and the High Street Range. Here it grows sparsely in the shallow *Eriophorum* blanket-bogs, hardly below 2,000 ft., and flowers sparingly or not at all.

The remaining calcifuge, *Cryptogramma crispa,* has strong claims to rank as a mountain plant, though its distribution extends to low levels. Famous as a scree pioneer, it is present everywhere in this rôle, from the base to the summits of the hills. Some earthy screes are smothered with a profusion of *C. crispa* and *Alchemilla alpina* but support few other vascular plants. Rock ledges and crevices are another habitat, but there the Parsley Fern does not luxuriate as on the loose talus slopes below. It is often plentiful in dry *Festuca-Agrostis* grassland, especially on rocky slopes with patches of scree, and such a community is sometimes seral. Occurring as it does on all the acidic rocks of the region, this is the most widely distributed of all the Lakeland mountain plants, and nowhere in Britain does it grow more finely.

PLANT COMMUNITIES

Some Lakeland mountain plants grow on more or less bare rocks with little or no other vegetation, but others belong to distinctive cliff-ledge communities which, though small in area, are relatively constant in composition from one site to another. On basic rocks the character of these "hanging gardens" is given not only by the mountain element, but also by the accompanying and equally constant assemblage of plants which are better known in lowland woods and damp meadows, or along moist roadside verges, in northern Britain. The two groups together form a tall herbaceous growth similar to the communities of subalpine birch and willow scrub in the mountains of Scandinavia. This type of vegetation is best developed on calcareous crags with large, stable and damp ledges, as on Honister Crag about the old quarry workings, and on some rich cliffs at higher levels. It is strikingly represented in an elevated gully of Blea Water Crags, above Mardale. A middle section of this gully has broad, gradually inclined sides, but steep rocks on all approaches bar access to sheep and deer. The bed of the cleft and its broken sides are smothered in a rank growth of tall herbs, giving some indication of the vegetation natural to these moist, base-rich soils before the advent of hill-farming (soil analysis, Table 2, No. 6).

Mountain plants are not particularly well represented at this station, however, and for ledges rich in these species, the Helvellyn range is the best place. The following list, drawn from a series of north-east and east facing cliffs at 2,600-2,800 ft. on Helvellyn, gives some idea of the vegetation on the bigger ledges with a well developed layer of mull-humus soil. It is a composite list, though a few ledges have most of the species named.

Alchemilla alpina	f.	*Geum rivale*	a.
A. glabra	a.	*Heracleum sphondylium*	f.
Anemone nemorosa	f.	*Lathyrus montanus*	o.
Angelica sylvestris	f.	*Luzula sylvatica*	a.
Cochlearia alpina	f.	*Oxyria digyna*	f.
Crepis paludosa	a.	*Ranunculus acris*	f.
Deschampsia cespitosa	a.	*Rhinanthus minor*	o.
Festuca rubra	a.	*Rubus saxatilis*	o.
F. vivipara	a.	*Rumex acetosa*	f.
Filipendula ulmaria	a.	*Saussurea alpina*	f.
Galium boreale	l.	*Saxifraga hypnoides*	a.
Geranium sylvaticum	f.	*Sedum rosea*	a.

Solidago virgaurea	a.	*Mnium hornum*	a.
Succisa pratensis	f.	*M. punctatum*	f.
Taraxacum officinale	f.	*M. undulatum*	a.
Thalictrum minus	f.	*Philonotis fontana*	f.
Trollius europaeus	l.	*Plagiothecium denticulatum*	f.
Valeriana officinalis	o.	*Polytrichum alpinum*	f.
Atrichum undulatum	o.	*Pseudoscleropodium purum*	o.
Brachythecium rutabulum	f.	*Rhacomitrium lanuginosum*	a.
Breutelia chrysocoma	f.	*Rhytidiadelphus loreus*	a.
Campylium protensum	o.	*R. squarrosus*	a.
Ctenidium molluscum	a.	*Sphagnum plumulosum*	f.
Dicranum majus	f.	*S. subsecundum*	f.
D. scoparium	a.	var. *auriculatum*	
Drepanocladus uncinatus	o.	*Thuidium tamariscinum*	a.
Eurhynchium praelongum	f.	*Lophocolea bidentata*	a.
Hylocomium splendens	a.	*Tritomaria quinquedentata*	f.
Hypnum cupressiforme	a.	*Plagiochila asplenioides*	o.

Similar ledges elsewhere on the fell have *Chamaenerion angustifolium* and *Silene dioica.* Elsewhere in Lakeland, rarer members of such a community include *Potentilla fruticosa, Cirsium heterophyllum, Vicia sylvatica, Aquilegia vulgaris* and *Rosa pimpinellifolia,* whilst at lower levels *Vicia sepium, Trifolium medium, Centaurea nigra* and *Epilobium montanum* are added to the list. In the Highlands, *Salix lapponum* often grows in tall herb communities, but the survivors on Helvellyn occupy rather bare rocks.

Whilst all the species listed above may grow in more open and unstable rock habitats, a characteristic assortment of mountain plants and lowland associates belongs solely to such places, though its members commonly inhabit the less crowded edges of ledges covered with tall herbs. The list below was compiled for the same range of Helvellyn crags and refers to the more specialised calcareous rock habitats, such as small ledges, pockets, crevices and steep slabs—all those places where gravity keeps soil development to its earliest stages. It does not represent a community in the usual sense, but merely a group of species kept in association by a common need for a more or less basic substratum and relative freedom from competition. In Lakeland, a few of these plants always grow in intimate contact with the rock surface and some of the mosses are strictly rupestral. Whereas the herbaceous ledge vegetation is usually associated with rather moist conditions, the open rock-face habitats vary greatly in wetness, and on sun-exposed cliffs may be very dry.

Alchemilla alpina	a.	*C. flacca*	f.
A. wichurae	f.	*C. panicea*	a.
Asplenium viride	o.	*C. pulicaris*	a.
Campanula rotundifolia	f.	*Cerastium alpinum*	r.
Carex atrata	r.	*C. holosteoides*	f.
C. demissa	f.	*Cystopteris fragilis*	a.

Euphrasia rivularis	f.	*Bryum pseudotriquetrum*	a.
Festuca rubra	a.	*Campylium stellatum*	f.
F. vivipara	a.	*Cratoneuron commutatum*	f.
Hieracium spp.		*C. filicinum*	f.
esp. *H. anglicum*	f.	*Ctenidium molluscum*	a.
Juncus triglumis	o.	*Distichium capillaceum*	o.
Linum catharticum	f.	*Ditrichum flexicaule*	f.
Minuartia verna	f.	*Encalypta ciliata*	o.
Poa alpina	o.	*Fissidens adianthoides*	f.
Polystichum lonchitis	r.	*F. cristatus*	f.
Potentilla crantzii	r.	*F. osmundoides*	f.
Saxifraga aizoides	f.	*Grimmia apocarpa*	a.
S. hypnoides	a.	*G. funalis*	o.
S. nivalis	r.	*G. torquata*	f.
S. oppositifolia	f. -a.	*Hypnum callichroum*	o.
S. stellaris	f.	*H. hamulosum*	o.
Selaginella selaginoides	a.	*Isopterygium pulchellum*	f.
Silene acaulis	f.	*Mnium marginatum*	f.
Thalictrum alpinum	f.	*M. orthorrhynchum*	r.
Thlaspi alpestre	r.	*Neckera crispa*	f.
Thymus drucei	a.	*Orthothecium intricatum*	o.
Amphidium lapponicum	r.	*Plagiobryum zierii*	f.
A. mougeotii	a.	*Plagiopus oederi*	o.
Anoectangium compactum	a.	*Rhacomitrium ellipticum*	r.
Anomobryum filiforme	f.	*Tortella tortuosa*	f.
Bartramia ithyphylla	o.	*Riccardia pinguis*	a.
B. pomiformis	o.	*Frullania tamarisci*	f.
and var. *crispa*	o.	*Tritomaria quinquedentata*	f.
Brachythecium plumosum	f.	*Preissia quadrata*	f.

(Soil analysis. Table 2, No. 4.)

Various other basic cliffs of the Helvellyn range provide such notable additions to this list as *Dryas octopetala, Draba incana, Polygonum viviparum, Poa glauca, P. balfourii, Antennaria dioica, Armeria maritima, Orthilia secunda* and *Anthyllis vulneraria*; on other hills *Ajuga pyramidalis* and *Plantago maritima* belong to a similar variety of open rock habitats. The basic cliffs of Helvellyn and other high fells commonly have *Salix herbacea* and *Carex bigelowii,* but these are equally typical of acidic rocks and soils. Sudden changes in edaphic conditions account for the abundance of common calcifuges on the rich cliffs, but at least some of these plants appear to tolerate basic soils. Most of these species typical of acidic rocks, particularly the bryophytes, have been omitted from the above lists.

Calcareous flushes on the slopes have a distinctive type of vegetation. Such places appear as small, bare stony patches of ground, with water trickling over the muddy soil, which usually has a very open plant growth. An example on the north face of

Catchedicam is listed below; it contains species of the rock ledges which are unaffected by sheep-grazing.

Cardamine pratensis	o.	*Selaginella selaginoides*	o.
Carex demissa	a.	*Thalictrum alpinum*	f.
C. panicea	f.	*Viola palustris*	o.
C. pulicaris	a.	*Acrocladium sarmentosum*	o.
Cerastium holosteoides	o.	*Blindia acuta*	a.
Cochlearia alpina	f.	*Bryum pseudotriquetrum*	f.
Deschampsia cespitosa	f.	*Campylium stellatum*	f.
Euphrasia rivularis	f.	*Cratoneuron commutatum*	f.
Festuca rubra	a.	*Ctenidium molluscum*	f.
Juncus triglumis	f.	*Drepanocladus revolvens*	a.
Pinguicula vulgaris	f.	*Fissidens adianthoides*	f.
Ranunculus acris	f.	*Philonotis fontana*	a.
Saxifraga aizoides	a.	*Riccardia pinguis*	f.
S. oppositifolia	o.	*Scapania undulata*	a.
S. stellaris	f.		

Sedum villosum grows in similar flushes elsewhere on the Helvellyn range. On the slopes of High White Stones, more strongly calcareous flushes have a more luxuriant growth of mosses such as *Cratoneuron commutatum* and *Ctenidium,* and contain *Meesia uliginosa,* though they are less rich in mountain plants.

Springs situated high in the coves of Helvellyn are fed by rather poorer water and typically show an abundance of bryophytes, as in a list from Brown Cove.

Agrostis canina	f.	*Sagina procumbens*	o.
Cardamine pratensis	f.	*Saxifraga hypnoides*	a.
Cerastium holosteoides	f.	*S. stellaris*	a.
Chrysosplenium oppositifolium	ld.	*Stellaria alsine*	a.
Cochlearia alpina	a.	*Brachythecium rivulare*	a.
Deschampsia cespitosa	f.	*Bryum weigelii*	o.
Epilobium alsinifolium	f.	*Dicranella squarrosa*	f.
Festuca rubra	f.	*Mnium punctatum*	f.
Poa annua	o.	*Philonotis fontana*	a.
P. trivialis	f.	*Pohlia albicans* var. *glacialis*	o.
Rumex acetosa	f.	*Aplozia cordifolia*	f.
		Scapania undulata	a.

To these are added the following in Nethermost Cove.

Agrostis stolonifera	a.	*Sphagnum squarrosum*	o.
Ranunculus acris	o.	*S. subsecundum* var. *auriculatum*	f.
Bryum pseudotriquetrum	f.	*Chiloscyphus polyanthus*	f.
Drepanocladus exannulatus	f.	*Pellia epiphylla*	f.

Two plants recorded from this area (the first not seen recently), *Phleum alpinum* and *Veronica serpyllifolia* subsp. *humifusa,* grow in very similar spring communities in the Highlands. Such springs grade into richer flushes below, whilst in wet gullies they are often bounded by banks of *Saxifraga hypnoides*. (Soil analysis. Table 2, No. 5.)

Even on basic soils the grasslands are not usually rich in mountain species, but on many Borrowdale Volcanic hills, the *Festuca-Agrostis* pastures which receive intermittent irrigation with mineral-charged water are densely grown with carpets of *Alchemilla alpina*. The best example of an "alpine grassland" occurs very locally at about 2,500 ft. on Helvellyn, where normally dry slopes are flushed in places from calcareous rocks during wet weather. The sward has some affinity with the wetter flushes, but is characterised by the following.

Achillea millefolium	*F. rubra*
Agrostis tenuis	*Geum rivale*
Alchemilla glabra	*Thymus drucei*
Anthoxanthum odoratum	*Viola riviniana*
Campanula rotundifolia	*Ctenidium molluscum*
Festuca ovina	

Mountain species occurring in varying quantity are

Alchemilla alpina	f.	*S. hypnoides*	a.
Cochlearia alpina	a.	*S. oppositifolia*	o.
Galium boreale	o.	*S. stellaris*	a.
Juncus triglumis	o.	*Thalictrum alpinum*	a.
Minuartia verna	f.	*Viola lutea*	f.
Polygonum viviparum	f.	*Oncophorus virens*	r.
Saxifraga aizoides	o.		

All these species except *Oncophorus virens* grow more abundantly or more luxuriantly on rock ledges above.

Analyses of soil samples taken from these various eutrophic habitats are given in Table 2.

The calcifuge communities of the Lake Fells are poor in mountain plants, and since mention has been made of the vegetation types in which each species occurs there is no need for complete lists. These communities are adequately described elsewhere, e.g. Pearsall (1950): they range from the predominant acidic grasslands (the dry *Festuca-Agrostis* to the wet *Nardus-Juncus squarrosus* types) to *Calluna* and *Vaccinium myrtillus* heaths, *Calluna-Eriophorum* bog and *Rhacomitrium* heath.

Northern Plants

In addition to the mountain species, there are plants with a widespread distribution in the northern half of Britain, both on the low ground—sometimes away from the hills—and on the mountains. Some of these have been mentioned in the account of the crag-ledge "communities", as for instance, *Trollius europaeus, Geranium sylvaticum* and *Cirsium heterophyllum.*

Others are more definitely restricted to the lower slopes of the hills, the mountain valleys or the foothill country, and are scarce or absent in the northern lowlands: these may be described as sub-montane, but the group as a whole is here termed "northern".

Primula farinosa is widespread and locally plentiful in the eastern half of Lakeland, chiefly in the dales of the High Street range, but within the fell country does not occur west of a line from St. John's Vale to Tilberthwaite. Drainage and heavy grazing have evidently reduced in extent the particular kind of calcareous marshy ground which it favours, but its frequent companions, *Parnassia palustris* and *Selaginella selaginoides*, are less exacting in their needs and more widely distributed over the district. The Grass of Parnassus appears in open communities on basic ledges on some of the high cliffs, though flushes and marshes on the slopes are its more usual place. It has a rather patchy distribution, whereas *S. selaginoides* is almost ubiquitous wherever wet, basic soils occur. Another much rarer plant of calcareous flushes, *Equisetum variegatum,* has been found only in Wasdale. *Sorbus rupicola* and*Dryopteris villarii* are notable and locally abundant plants of the limestone tract bordering the district to the south-east but very rare in Lakeland itself. The Rock Whitebeam has three good colonies on strongly calcareous rocks in Borrowdale and St. John's Vale, but *Dryopteris villarii* is known only from Honister Crag. Mr. F. Jackson has found two young clumps of this fern on rocks recently exposed by quarrying, and believes there is a parent colony, perhaps in an unapproachable part of the great precipice.

Asplenium septentrionale has a good many sites, well scattered over the district, but its hybrid, *A.* × *alternifolium,* is very rare and in small amount on only three or four crags. Whilst these ferns may well have a special mineral requirement (Raven and Walters, 1956), the Forked Spleenwort, at least, grows on markedly base-poor rocks of both the Skiddaw Slate and Borrowdale Igneous Series. *Cystopteris fragilis,* by contrast, is decidedly calcicole and may be found on nearly all the basic crags of the region, at all altitudes.

Among the plants characteristic of rocky mountain woods are *Melampyrum sylvaticum, Ciraea alpina, Impatiens noli-tangere, Melica nutans* and *Festuca altissima.* The first is recorded from a few woods, mainly in Borrowdale, presumably on acidic humus soils, whereas the rest are confined to fairly basic substrata. *Circaea alpina* and *Impatiens noli-tangere* grow as members of herbaceous communities on moist "mull" soils in mixed deciduous woods, with the former widespread and reaching 1,500 ft. on shaded cliff ledges. The Yellow Balsam is exclusively lowland and much rarer, its main localities being in the Windermere district, around Derwentwater and in the Duddon Valley. This is one of the distinguished plants of the district, for only here and in North Wales is it truly native in Britain. The two grasses are more or less confined to rocks, especially those in damp ravines. *Vicia orobus* has been recorded from woods near Ullswater, and grows very sparingly on cliff ledges in Wasdale and in fell meadows in Eskdale. *Salix phylicifolia* has scattered localities at low levels but ascends to the cliffs of Helvellyn at over 2,000 ft.

Two species belong mainly to the sub-montane pastures. *Meum athamanticum* formerly grew in a few places, but now appears to be extinct in Lakeland. *Viola lutea* (the blue-flowered form), on the other hand, is plentiful in some places, chiefly in dry grassland on moderately basic soils, but grows on a few of the higher crags.

Among the plants of acidic humus soils, *Listera cordata* is rather rare, on damp heathy slopes, and *Trientalis europaea* has been found only in Eskdale. The spongy *Sphagnum* bogs of the valleys and gently contoured hills produce a few species of note. *Carex paupercula* grows in a few swamps of this kind, and has *C. limosa* for company near Matterdale and on the Watendlath fells, whilst *C. pauciflora* is plentiful on parts of the Watendlath and Eskdale moors. *Drosera anglica* and *Hammarbya paludosa* occur in scattered places only, but *Vaccinium oxycoccos* is a widespread and usual species of these wet bogs. *Andromeda polifolia* is very local in Lakeland itself, in contrast to its abundance on the peat-mosses of the adjoining lowlands, but grows up to at least 1,500 ft. on the blanket bogs above Watendlath.

The more distinctly aquatic habitats have several species which belong chiefly to hill districts in Britain. *Juncus filiformis* and *Carex aquatilis* are plants of lake and stream-side respectively; the former known from several of the larger lakes. *Isoetes lacustris* is mostly a plant of the bigger lakes and *Subularia aquatica* favours the smaller, higher-lying tarns, whilst *Lobelia dortmanna* is equally typical of both kinds of place.

The Relict Nature of the Mountain Flora

Though the mountain flora of Lakeland is relict as a whole, there are all degrees of "relictness" and the distribution patterns of the various species differ widely. First, there is the group of species, including both calcicoles and calcifuges, which occurs in most places where conditions are suitable. Discontinuities in the distribution of these plants are therefore to be explained by the obvious barriers of unsuitable habitats. The occasional absence of species such as *Sedum rosea, Alchemilla alpina* and *Salix herbacea* from likely places would best be attributed to the element of chance which must always affect plant distribution, especially where migration is concerned. The limitations imposed by an obvious lack of suitable edaphic habitats and by biotic effects are here discounted; the present purpose is to examine the distribution of species which are often absent from apparently suitable places.

Palaeo-ecologists stress the importance of "historical factors" in the present distribution of plants, especially relict species. Included under this head are the effects of climatic changes following the end of the latest glaciation, involving the large-scale migration of types of vegetation and inevitably causing the disappearance of species from large areas where they were once common. When this effect is less extreme, plants survive but with a relict distribution, their few remaining localities being widely and often irregularly scattered: some species may be in the last stages of a retreat which will lead eventually to their extinction.

The history of the Late-glacial flora as drawn by Godwin (1949, 1956) shows that most of the montane plants of Lakeland must be regarded as relicts of a much colder climate, and they are restricted to the altitudinal zone where comparable conditions yet prevail. Even so, at the Post-glacial Climatic Optimum, the lower limit to this favourable temperature zone must have been at least several hundred feet higher than at present. With the fall in temperature during the Sub-atlantic Period, some of the montane plants may, in theory, have been able to descend slightly. It is likely, however, that some plants which *could* grow under the present cooler conditions near the tops of our highest hills were eliminated completely at the Climatic Optimum. Equally, though, others managed to hang on here and there at high levels during this time, yet they may have been unable to spread under "improved" conditions which still do not allow their ecesis. The Climatic Optimum thus seems to have been the critical period in determining the present relict distribution of many species. Though they extend to heights far beyond the tree limits, the mountain species of tall herb ledges are quite characteristic of high-level woodlands on basic soils. This group would be the least depleted by the warmer period of the Post-glacial, and, accordingly, its members are now mostly widely distributed and reach low levels. Formerly, a cover of forest and scrub extended to at least 2,000 ft.—possibly much higher—and this growth must have eradicated plants which need open habitats.

A good illustration of this point may be seen at Wolf Crags on Matterdale Common. Here, the broken and rather low-lying cliffs are strongly calcareous in places, but their mountain flora consists of only a few widespread species. One rock face at 1,600-1,700 ft. is smothered with a relict patch of scrub, including a dense growth of *Prunus padus*. Perhaps because of the shade, true mountain species are missing from this face, but there is a fairly rich herbaceous flora typical of basic woodlands at lower levels. The other faces, on which scrub growth is sparser or has disappeared, have been recolonised by those high level species which had managed to survive in the vicinity, and the woodland flora has in turn lost ground.

Even on precipitous ground, tree and scrub growth is thus quite likely to have eliminated the more exacting mountain species up to 1,700 ft., replacing them with a woodland flora; while in earlier times the effect probably extended to well over 2,000 ft. in places.

This competition effect is distinct from the direct damage some species may suffer due to increased temperatures. Within the woodland and scrub zone, these competition-intolerant plants must have become restricted—if they survived at all—to steep, rocky ground where trees could grow only sparsely. Only above the tree-limit are there likely to have been many suitable refuges for such species: the great screes of the present day would not then be available as they are mostly recent features, caused by human abuse of the land.

The present patchy distribution of species such as *Saxifraga oppositifolia, Silene acaulis, Thalictrum alpinum, Polystichum lonchitis, Saussurea alpina* and *Juncus triglumis* may therefore be explained by their disappearance from hills which were not sufficiently high or rugged to give refuges from either the warmer climate or the blanket of trees at the Climatic Optimum. Even if the need for altitude or an open habitat were satisfied, calcareous substrata were also a prime requirement. The plants of the above list occur mostly on the massifs which possess the combination of high altitude and calcareous rock, though here they may occur at quite modest elevations (see Table 1, at end), suggesting downward migration as the tree-limit fell. These species are often absent from the lower hill-ranges, even though habitats suitable in soil and elevation occur now, for no favourable refuges were available at the maximum extension of the tree zone.

Some of the rare Lakeland mountain plants appear to have limited powers of spread under present conditions, though they seem able to maintain their existing populations. Some of these, such as *Dryas octopetala,* are abundant in the Highlands, and there set good seed in quantity. Others, including *Ajuga pyramidalis,* are nowhere plentiful in Britain, and their rarity may be due partly to a poor capacity for dispersal, even under optimal conditions. By contrast, some common species are certainly able to spread by seed, though their effective dispersal range may be small. Nearly all the widespread calcicoles have colonised in quantity the bare rock-faces of abandoned quarries, as on Honister Crag, Ill Bell and Erne Crag at Rydal. The newly exposed surfaces evidently have a higher lime-content than those long-weathered. The first locality provides an unusual spectacle by way of illustration, for the ruined cabins and retaining walls of the old railway so cleverly built across the great cliff are festooned with growths of *Sedum rosea, Oxyria digyna, Cochlearia alpina* and various Saxifrages and ferns. High on Helvellyn, the dump of an old lead mine is studded with clumps of Purple Saxifrage, and this plant has colonised the site of a fairly recent rock-fall on the Scafell range. In all these cases, parent populations on the adjacent rocks have supplied the seed. The mountain plants restricted to the highest levels perhaps do not set viable seed under present conditions, or it may be that their populations are too small and seed production therefore insufficient to allow spread. These are the true relicts.

Some of these rarities may still be declining in quantity. One of the Helvellyn colonies of *Salix lapponum* has a poor stunted growth, with small leaves: there are many dead twigs, and the willow has an unhealthy look compared with a few larger bushes elsewhere on the hill. It has not been rediscovered in its old locality on Catchedicam and may have died out there. Many of the plants of *Potentilla fruticosa* on Wasdale Screes show numerous dead twigs in their crowns, though often with plenty of leafy growth on the lower parts of these branches. In this case, perhaps recovery followed a severe check caused by some exceptional condition such as an unusually long drought.

Patton (1923) has made the very feasible suggestion that plant disease may well be important in deciding the survival or extinction of montane species. Such a factor is likely to be the more significant for rare species, and infection is more probable when a plant is growing under unfavourable conditions. Many chance extinctions may have come about through such an agency.

The connection between the occurrence of mountain plants and a cold climate is implicit, but Dahl (1951) has analysed this correlation in detail for Scandinavia, suggesting the possibility of critical maximum summer temperature as a limiting factor. Since the critical temperature is not the same for all species, different plants will have different lower altitudinal limits in the same district. The varying altitudinal ranges of the Lakeland species (see Table 1) may well be due to this effect, i.e., species confined to high levels cannot survive under the relatively high critical temperatures of others which extend much lower down the hillsides. The figures given may not represent a strict sequence of critical temperatures—only the general trend. The two extreme groups—those occurring below 1,000 ft. and above 2,500 ft.—certainly seem to show differentiation with regard to critical maximum summer temperature.

Many species are too rare to indicate their true lower altitudinal limits, but such boundaries are fairly well defined in plentiful plants, e.g. *Sedum rosea, Oxyria digyna, Carex bigelowii* and *Salix herbacea*. The lower limits of these four species show a gradual descent with distance north in Britain—a trend consistent with the idea of limiting temperatures, though humidity effects have not been ruled out as a possible controlling factor. Most of the mountain plants which occur below 1,000 ft. in Lakeland descend to sea-level in north-west Scotland. On the other hand, most of those confined to over 2,000 ft. in Lakeland do not descend below 1,000 ft. anywhere in the Highlands. Many of the plants listed in the upper half of Table 1 are plentiful in Scotland, and their rarity in Lakeland is probably due to the lack of cool enough summers, combined with a scarcity of suitable edaphic habitats. It is significant, too, that no species which has a lower limit of 2,500 ft. in the Highlands occurs in Lakeland. *Cystopteris montana* and *Salix lapponum* do not grow much below 2,000 ft. in Scotland, and in Lakeland have been found only above 2,500 ft.

on Helvellyn, their southernmost British station.

In contrast to the Scottish Highlands, Lakeland does not appear to have any vegetation which depends on a prolonged snow-cover during winter, and apart from one or two rare mosses such as *Dicranum starkei,* species associated with late snow-lie are absent. This is again an expression of the warmer climate.

As a point of interest, several species reach their lowest Lakeland elevation in Wasdale, but this may be due to the occurrence of suitable habitats at low levels as much as to the seaward position of the dale. *Alchemilla alpina, Saxifraga aizoides, Lycopodium alpinum* and *Cryptogramma crispa* reach the shore of Wastwater, whilst *Saxifraga oppositifolia* descends to 800 ft. on the slopes above.

Finally, although the scarcity of some species does not at first seem to be due to the lack of suitable climatic or edaphic habitats, they may have subtle special requirements. These plants are highly relict in Lakeland because their particular needs are seldom satisfied. *Lychnis alpina,* with its special mineral demands, is the outstanding example of this effect (see p. 7). In the Pennines *Thlaspi alpestre* and *Minuartia verna* are particularly associated with lead-mine refuse, and their restricted distribution in Lakeland may be due to their special soil requirements—perhaps the combination of lead and high base-status. Both grow on Helvellyn, which has lead-bearing and calcareous rocks. *Woodsia ilvensis* seems to favour an uncommon habitat, namely, dry, basic and very rotten rocks. Probably only a very few outcrops of Lakeland rock contain enough lime for *Dryas octopetala,* and both this species and *Potentilla crantzii* have a predilection for dry and often sun-exposed sites, whereas most high-lying calcareous rocks in the district are rather moist and shaded.

Scattered distributions of the above kind present, to some extent, an inscrutable problem, for one usually has to explain not so much why a plant grows where it does as why it is missing from other places which are apparently equally suitable. When all the obvious possibilities have been explored, the distribution of some plants remains inadequately explained. Species nearly always have a scattered distribution at the limits of their range, which over long periods is necessarily mobile—either extending or retreating. It follows that the flora of any district must have a number of rarities, since conditions are usually marginal for some species. The relative slowness with which most plants appear or disappear under gradually changing conditions ensures that only a proportion of the available habitats holds any species at its limits of range, but the actual places where the plant becomes established, or survives, depend largely on chance.

A COMPARISON WITH OTHER DISTRICTS

The nearest floristically-rich hills to Lakeland are the Northern Pennines, chiefly the districts of Upper Teesdale—Crossfell and Craven. The two regions have a good deal in common, for out of the 59 mountain species named for Lakeland, 41 occur in the Northern Pennines, and in the latter there are no more than 17 mountain plants which do not grow in the former. Both contain the only stations for *Potentilla fruticosa* on the British mainland; *Myosotis brevifolia* is known elsewhere only from the Moffat Hills and N. Yorks.; and other rare or very local plants common to both are *Phleum alpinum, Saxifraga nivalis, Dryas octopetala, Potentilla crantzii, Poa alpina, Minuartia verna, Thlaspi alpestre, Sedum villosum* and *Woodsia ilvensis* (believed extinct in its only Pennine locality). From the eastern distribution in Lakeland of certain species which are, or were, more common in the Pennines, such as *Minuartia verna, Draba incana, Sedum villosum, Polystichum lonchitis, Rubus chamaemorus* and *Primula farinosa,* it is tempting to suggest an eastern migration of part of the mountain flora into the first region.

The absence from the Northern Pennines of *Alchemilla alpina* and *Oxyria digyna* is remarkable, considering their abundance in Lakeland. It may be that the migrating periglacial flora was heterogeneous in composition in Northern England, lacking certain species locally, so that these two plants failed to reach the first region during the period when conditions for their spread were suitable. *Saussurea alpina* and *Silene acaulis* are two other surprising absentees from the Northern Pennines and it is equally unexpected that the Purple Saxifrage should be missing from the Teesdale area. Though its habitats are widespread in both, *Empetrum hermaphroditum* has a relict distribution in Lakeland and is completely absent from the Pennines.

In ecological character the two districts have much less in common, and Lakeland has no counterpart to Upper Teesdale, either in extent and type of calcareous habitats or in the number of exclusive rarities which it harbours.

Another adjacent area with a rich mountain flora, the Moffat Hills in Dumfriesshire, has 38 of the 59 Lakeland species and 7 others besides. Here again, *Alchemilla alpina* is absent and there is only a doubtful record of *Saxifraga aizoides,* a very plentiful Lakeland plant. The most southerly recorded stations in Britain for *Salix myrsinites* and *Carex vaginata* lie in this district. Formerly, the Moffat Hills were evidently the British headquarters of *Woodsia ilvensis,* and though collecting exterminated the fern in its best known localities, at least one respectable colony survives.

The absence of *Alchemilla alpina* and *Saxifraga aizoides* from Snowdonia is noteworthy, for this region shares 42 mountain species with Lakeland and claims only eight not in the northern district. The two areas are very similar in climate, topography and geology, but the great calcareous cliffs of Snowdon and the Glyders have a much more profuse and varied growth of plants than the best Lakeland crags. Lakeland rarities such as *Saxifraga nivalis, Dryas octopetala, Polystichum lonchitis, Carex atrata, Poa alpina* and *P. glauca* all grow more abundantly, though still very locally, on the Welsh hills. The difference is clearly due to the greater extent of suitable edaphic habitats in Snowdonia, for this district as a whole seems to have lost more of its original Late-glacial flora than has Lakeland—probably due to the slightly warmer climate. Helvellyn now has a greater number of mountain species than Snowdon, irrespective of their abundance. Snowdonia is the poorer region of the two in calcifuges, lacking *Rubus chamaemorus, Vaccinium uliginosum, Arctostaphylos uva-ursi* and *Lycopodium annotinum* (believed present once but now extinct). Five species common to Snowdonia and the Highlands, *Cerastium nigrescens, Cardaminopsis petraea, Deschampsia alpina, Saxifraga cespitosa* and *Woodsia alpina,* show an extra large disjunction in that they are missing from northern England and southern Scotland.

Some parts of the Scottish Highlands have an incomparably greater wealth of mountain plants than any of these more southern regions, and as a whole have no fewer than 65 species which do not grow in the Lake District. There is strong similarity, however, between Lakeland and some less rich districts of the southern and western Highlands, though the former lacks such widespread Scottish plants as *Gnaphalium supinum, Sibbaldia procumbens, Loiseleuria procumbens, Luzula spicata* and *Juncus trifidus. Potentilla fruticosa, Myosotis brevifolia* and *Euphrasia rivularis* are the only Lakeland species not found in the Highlands, and of the rest, only *Woodsia ilvensis, Lychnis alpina, Minuartia verna, Thalictrum minus, Saxifraga hypnoides, Silene maritima, Cryptogramma crispa* and the three common clubmosses do not grow more finely or abundantly in the Highlands.

Quaternary studies have established (see Godwin, 1956) that many British mountain plants occurred in Full-glacial and Late-glacial times far to the south of their present range. For instance, though now confined to the Scottish Highlands, *Betula nana* once occurred in Cumberland and Westmorland (D. Walker in *op. cit.*). Some of the floristic diversity between the various mountain regions in Britain is thus explained by the disappearance of species during the Post-glacial Period. This explanation cannot, however, justifiably be extended to cover *all* regional diversity in flora when the direct supporting evidence is lacking. There are, for instance, no grounds for assuming that *Alchemilla alpina* was ever present in the Pennines or North Wales during the Late or Post-glacial Periods, unless remains of this species can be found in either district. Strangely, despite the impressive body of information collected, British Quaternary studies have thrown very little light on the history of the species which are now most prominent in the Lakeland mountain flora.

As a final note it should be pointed out that some of the species mentioned are so rare that any collecting at all would create a serious threat to their chances of future survival. The danger is the greater in these days of easy access to the hills.

TABLE 2

EXCHANGE IONS AS MG./100 GM. SOIL
EXCH. IONS AS MG./100 GM. SOIL

Locality	% loss on ignition	pH	Na	K	Ca	Mg	Fe	Mn	P_2O_5	C
1. Hobcarton Crag A	15·0	4·4	3·3	8·0	6·6	2·4	2·4	10·4	3·5	8·
2. Hobcarton Crag B	6·8	4·0	1·4	5·6	3·5	0·3	7·7	21·4	0·2	9·
3. Hobcarton Crag C	4·7	5·2	2·2	6·6	6·8	2·1	0·5	2·5	0·3	2·
4. Nethermost Cove, Helvellyn A	20·3	6·1	6·7	15·4	295·6	34·3	0·3	—	0·9	4·
5. Nethermost Cove, Helvellyn B	17·0	5·8	4·7	9·9	99·7	7·9	—	6·9	0·8	2·
6. Blea Water Crags	19·4	5·5	4·9	21·2	185·0	14·6	—	—	0·3	12·
7. Wasdale Screes	—	6·27	—	7·06	264·4	—	—	—	10·2	—
8. Piers Gill, Scafell Pike	—	6·52	—	3·3	175·1	—	—	—	3·7	—
9. Brown Cove, Helvellyn	—	7·51	—	2·9	730·4	—	—	—	2·7	—

NOTES ON SOILS AND VEGETATION:

1. Dark brown friable loam in pockets and niches of rock face with *Lychnis alpina*.
2. Crumbling bank of raw ochreous mineral soil freshly disintegrated from rock face in *Lychnis alpina* gully.
3. Decomposed clayey seam in disintegrating rock face of *Lychnis alpina* gully.
4. Dark brown silty loam with mull humus, from rich chomophytic vegetation on steep calcareous rock face (locality list on p. 13).
5. Dark brown silty loam with mull humus from strongly irrigated banks with *Saxifraga hypnoides* and *Chrysosplenium oppositifolium.*
6. Dark brown silty loam with mull humus from ungrazed tall herb community on broad ledge of calcareous cliffs.
7. Red-brown silty loam from crumbling sides of gully occupying a shatter belt strongly charged with calcite and ferric oxide. *Saxifraga oppositifolia, S. hypnoides, S. aizoides.*
8. As in 7. *Saxifraga oppositifolia* and calcicolous mosses.
9. Finely comminuted debris of old lead-mine dump: a raw, unleached deposit evidently containing a large amount of calcite. Thickly colonised by *Saxifraga oppositifolia.*

I am very grateful to Miss M. C. Gray, The Nature Conservancy, for providing the soil data for samples 1-6. Mrs. V. Jones, University College of North Wales, carried out the analyses of samples 7-9, and she and Professor P. W. Richards have kindly allowed me to reproduce these data from their Biological Flora account of *Saxifraga oppositifolia* (*J. Ecol.*, **44**: 300-316) (1956).

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THE DISTRIBUTION AND ECOLOGY OF ARUM NEGLECTUM IN SOUTHERN ENGLAND AND WALES

By C. T. Prime, O. Buckle and J. D. Lovis

Part II.—DORSET, DEVON, CORNWALL, ISLES OF SCILLY, CHANNEL ISLANDS and WALES

The distribution of *Arum neglectum* (Townsend) Ridl. and *A. italicum* Mill. in the south-west of England does not present quite so simple a picture as that in Sussex and Hants. In fact, careful study of plants from Cornwall, the Channel Islands and Portland, Dorset makes it clear that the two taxa are not specifically distinct. This is also confirmed by observations on the Continent, and taxonomic revision is contemplated (Prime, *unpubl.*). For the purposes of this paper, however, the two names will still be used, to conform with current usage.

Since the first part of this account was written (Prime, Buckle and Lovis, 1955) considerable colonies of *A. neglectum* and *A. italicum* have been rediscovered at Portland, Dorset*. The plants are to be found in the hedges, under the protection of brambles, within the small walled fields (called "closes"), and also along the balks which mark the remains of an early mediæval field system. In fact, in some places, where cultivation has been discontinued owing to the increase of quarrying, it is possible to trace the original boundaries by the presence of the plants. *Arum* species were, at one time, used for their corms, and an early account quoted by Warren (1940), suggests that the plants were cultivated, though other accounts do not mention this. Whatever the truth of this, the plant has been in Portland for a long time. It is hoped to give elsewhere a fuller account of the early uses of the plants.

Devon (Vice-counties 3 and 4)

The earliest record of *A. neglectum* for Devon is from Fursdon, Egg Buckland, the home of T. R. Archer Briggs, who wrote (1888): "When first I found the plant here at Fursdon I quite expected to meet it elsewhere in the country around, but having failed to do so, now suspect that it has become wild in the immediate vicinity of this house through early cultivation in proximity to an ancient dwelling, the meadow below here, close to which the plant occurs, still bearing the name of Undertown". The plant still survives in the wild garden, under the partial shade of an oak, in a rather acid soil of pH 5·5, and it very probably owes its survival to the cutting and clearing of the undergrowth at intervals.

Many of the remaining records cited by Martin and Fraser (1939) are open to doubt. Those from Braunton may be in error,

*Some of these colonies were previously known to Mr. A. W. Graveson.

TABLE 1

DISTRIBUTION OF MONTANE PLANTS IN LAKELAND AND OTHER MOUNTAIN REGIONS

Lower Limit (ft.)	Species	1 Helvellyn	2 Fairfield	3 High Street	4 Scafell	5 Pillar	6 Gable-Honister	7 Derwent Fells	8 Grasmoor	9 Bowfell	10 High Raise	Coniston Fells	11 Snowdonia	12 Northern Pennines	13 Moffat Hills	14 Scottish Highlands
2,500	Cerastium alpinum	+	+										+		+	+
	Cystopteris montana	+														+
	Phleum alpinum	+												+		+
	Veronica serpyllifolia subsp. humifusa	+													+	+
	Salix lapponum	+													+	+
2,000	Armeria maritima	+			+	+	+	+	+				+	+		+
	Carex atrata	+		+	?								+		+	+
	Euphrasia frigida	+													+	+
	Hieracium holosericeum	+		+	+		+				+	+	+			+
	Poa alpina	+											+	+		+
	P. balfourii	+	+	+									+	+	+	+
	P. glauca	+											+	+		+
	Polygonum viviparum	+								+		+	+	+	+	+
	Rubus chamaemorus	+		+										+	+	+
	Salix herbacea	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	Saxifraga nivalis	+		+	+								+	+	+	+
	Lychnis alpina								+			+				+
1,500	Ajuga pyramidalis			+											+	+
	Carex bigelowii	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	Draba incana	+	+	+								+	+	+		+
	Dryas octopetala	+			+								+	+		+
	Juncus triglumis	+	+	+	+								+	+		+
	Juniperus communis subsp. nana	+			+	+	+		+			+	+			+
	Minuartia verna	+	+	+									+	+		+
	Polystichum lonchitis	+	+	+									+	+	+	+
	Potentilla fruticosa	+			+	+								+		
	Saussurea alpina	+	+		+	+	+			+	+		+		+	+
	Silene acaulis	+	+	+	+								+			+
	Vaccinium uliginosum			+					+					+	+	+
	Woodsia ilvensis	+	+	+	+								+	+	+	+
1,000	Alchemilla wichurae	+	+	+	+	+	+	+						+	+	+
	Arctostaphylos uva-ursi			+	+	+			+		+			+	+	+
	Empetrum hermaphroditum	+	+	+	+								+		+	+
	Euphrasia rivularis	+			+	+		+					+			
	Lycopodium annotinum									+						+
	Orthilia secunda	+		+				+			+			+	+	+
	Potentilla crantzii	+	+		+			+			+		+	+	+	+
	Sedum villosum	+		+							+			+	+	+
	Thalictrum alpinum	+	+	+	+	+	+			+			+	+	+	+
	Thlaspi alpestre	+		+									+	+		+
500	Antennaria dioica	+	+	+	+	+	+	+			+		+	+	+	+
	Asplenium viride	+	+	+	+	+	+	+		+	+	+	+	+	+	+
	Epilobium alsinifolium	+	+	+	+	+	+	+			+		+	+	+	+
	Myosotis brevifolia	+	+	+							+			+	+	
	Oxyria digyna	+	+	+	+	+	+	+		+	+	+	+		+	+
	Saxifraga oppositifolia	+	+	+	+					+	+		+	+	+	+
	Sedum rosea	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
−500	Alchemilla alpina	+	+	+	+	+	+	+	+	+	+	+				+
	Cochlearia alpina	+	+	+	+	+	+	+		+	+	+	+	+	+	+
	Cryptogramma crispa	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	Galium boreale	+	+	+	+	+	+	+		+	+	+	+	+	+	+
	Lycopodium alpinum	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	L. clavatum	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	L. selago	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	Plantago maritima			+			+						+	+		+
	Rubus saxatilis	+	+	+	+	+	+	+			+	+	+	+	+	+
	Saxifraga aizoides	+	+	+	+	+	+	+	+	+	+	+		+		+
	S. stellaris	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	Silene maritima	+	+	+	+			+	+	+	+	+	+		+	+
	Thalictrum minus	+	+	+	+	+	+	+		+	+	+	+	+	+	+
		54	34	42	36	26	25	24	16	21	27	22	42	42	40	57
		60											8	17	7	65 others