MOUNTAIN ECOLOGY

Apart from the general accounts of naturalists such as MacGillivary (1855) in Scotland, the first scientific descriptions of British mountain vegetation were the work of Robert Smith (1900) and Marcel Hardy (1906) who, inspired by the developing continental school of phytogeography applied the new techniques to the Scottish Highlands. In particular Smith's paper on the north Perthshire district was destined to become a classic work on British plant ecology, and remains, almost a century later, a definitive article, particularily on arctic/alpine communities, and formed the basis for chapter 13, written by his brother W. G. Smith, for "Types of British Vegetation" published in 1911 and edited by Arthur, later Sir Arthur Tansley. Marcel Hardy's contribution was the recognition of the importance of the differences in vegetation between the east/central highlands and the western highlands. Indeed he drew an approximate boundary between these two regions - a boundary that is still known as "Hardy's Line".

Further regional studies of Scottish mountain vegetation were made by Crampton - a geological surveyor - (1911). In Caithness, and again by Crampton and MacGregor (1913) in eastern Sutherland, where Crampton elaborated his ideas on "stable" and "unstable" or "migratory" plant associations (Crampton, 1912) with special reference to mountain habitats. In the period between the wars little work was done in this field, with the notable exception of Price-Evans' (1932) studies on Cader Idris, Watson's (1925) account of bryophytes and lichens from arctic/alpine vegetation - both incidentally following Robert Smith's classification - and Leach's (1930) work on non-calcareous British screes. Indeed, when 'The British Isles and their Vegetation' was published in 1939, Arthur Tansley, as well as summmarising this work, still had to rely largely on W. G. Smith's excellent 1911 account of mountain vegetation based on the pioneer work of his brother Robert. Since 1948 when Watt and Jones, both members of the Cambridge University expeditions to the Cairngorms in 1938/9, drew attention to the paucity of information on the mountain vegetation of the British Isles, interest has been aroused and several contributions to knowledge in this field have appeared.

Three of these contributions were studies of specific vegetation types in the Cairngorms based on the work of those same expeditions (Metcalfe 1950, Burges 1951, and Ingram 1958), while Pearsall's book in the Collins' New Naturalist series entitled Mountains and Moorlands provided in 1950 a more general account. A further valuable piece of work was that of Poore in 1955 on the Breadalbane district of Perthshire, which marked a shift in emphasis in British montane studies from the traditional ecological approach exemplified by the work of the Cambridge botanists, towards a phytosociological approach akin to that of the Scandinavian, German, and Swiss/French schools of the continent. This work of Poore was the basis of a paper published in 1957 where, together with McVean, he set out to formulate what they called a "new approach to Scottish mountain vegetation" and in which they first discussed the principal ecological factors at work in determining vegetation development with special emphasis on what they term "hitherto neglected factors" such as snow cover and oceanicity, and to assess the relative roles of these factors they drew comparisons with the mountains of Scandinavia. In this article the methods of vegetaion description and classification developed by Poore in Perthshire, and which are essentially phytosociological, were applied to a wider range of mountain vegetation in Scotland. This paper leads on automatically to the excellent monograph published by the Nature Conservancy in 1962 in which McVean, this time in collaboration with Derek Ratcliffe (who had worked on the Carnnedau mountains in north Wales) extends the phytosociological approach to representative areas covering the whole of the Scottish Highlands. Their work also forms the basis of the chapters covering mountain vegetation in the book edited by Burnett, entitled "The Vegetation of Scotland" and published in 1964.

Although, the application of phytosociological techniques to the Highlands has brought the classification of mountain vegetation in this country in line with work on the continent the emphasis of detailed study shifted for a time from the ecology of the communities to their phytosociology. It is true, of course, that the resultant lists provide an invaluable reference system of vegetation units, but in habitats where environmental factors play such a large part in determining vegetation pattern it is a pity that the main emphasis has been sociological. Nevertheless, several useful chapters are included in the Nature Conservancy monograph on appropriate habitat factors. Indeed mountain landscapes represent an environment where the interrelationships between plants and their habitats are all pervading, and where stable and dynamic habitats exist in juxtaposition. At the outset, therefore, we need to summarise efficiently the major directions of variation in the vegetation and indicate the underlying causal relationships between the environment and that vegetation. In this task there is no better starting point than Poore and McVean's classic 1957 paper in the Journal of Ecology.

In formulating their new approach to Scottish mountain vegetation in this paper they maintain that most mountain communities are part of a climax mosaic each being determined and maintained by powerful habitat factors. Evenso, they consider that in each community there is some cyclic change or microsuccession, but that because the distribution and relative positions of communities to one another is so closely related to contemporary habitat factors these communities are unlikely to stand in any developmental relationship to each other, that is, there is no macrosucession between them.

Because of the great variety of habitats within a mountain area, each showing different combinations of environmental factors - some of which are actually very favourable to plant growth, the mountain flora is relatively rich in total and the variety of small communities very great in spite of the general severity of the mountain environment as a whole. Although undoubtedly true, this variety of communities and the extremely interesting and distinctive flora, including for example, arctic, alpine, and arctic/alpine elements, must not be overstressed, for as Pearsall has pointed out, the commonest form of vegetation in the mountains of Britain is some sort of stunted grassland, which with moorland and bog occupy by far the largest area of land and represent the sum of the effects of an inclement climate, a rainwashed and leached soil derived in the main from acid soil parent materials, and no doubt a uniformity that has resulted fron almost continuous cropping by sheep and deer. Nevertheless, it remains true that it is the existence of such a variety of communities as those of flushed sites, of colonising scree slopes, of exposed summit plateaux and ridges, and of those areas of prolonged snowlie, all maintained by an intimate interrelationship between plant and environment that makes the vegetation of mountains so interesting to study.

Poore and McVean (1957) consider that most Scottish mountain communities fit into a framework made up of the following five ecological factors.

1. Altitudinal Zonation
2. Oceanicity
3. Snow Cover
4. Base Status
5. Moisture

Although we will consider all of these factors, here we will rearrange them, for each forms part of a factor complex which has three main dimensions.

1. A Climatic Dimension
2. A Physiographic Dimension
3. An Edaphic Dimension

The first two of these dimensions of what can be called the mountain environment complex are difficult to separate and we shall find that climate and physiography are factors that are often interrelated at both meso and micro scales, while it is also sometimes difficult to separate physiographic and edaphic effects. Nonetheless we shall start by considering the climatic dimension.

1. The CLIMATIC Dimension.

1.1. The Mountain Climate.

The mountains and uplands of Britain are so sharply differentiated in meteorological terms from the lowlands that they may be regarded justifiably as possessing their own particular mesoclimate. As a generalisation this is primarily expressed as a combination of low temperatures, severe wind exposure, excessive precipitation cloud and humidity, low evaporation and continuous ground wetness, a defficiency of sunshine and poor visibility, and persistent winter frost and snow cover. Meteorological records collected at altitude are particularily scanty, although the Ben Nevis observatory in the early part of the century, the Caingorm weather survey in the 1950's, and more recently the Institute of Hydrology and the Heriot-Watt University automatic weather stations on the summit of Cairngorm itself, as well as installations associated with the Scottish skiing industry have provided some information.

1.1.1. Radiation.

There is a mean standard radiation increase with altitude of about 10% $1000m^{-1}$. The intensity of summer season radiation receipts compensates to a certain extent for its brevity - an advantage which could obviously apply during clear fine spells especially near the summer solstice and during the longer daylight periods operating in northern Britain and Scotland. Unfortunately this maximum occurs too early in the year for significant growth (with the notable exception of early flowering and truely mountain plants at high altitudes). This is because ground conditions usually delay soil warming until late summer, especially in wet, peaty, or snowlie areas, and of course by this time daylength is shortening rapidly. .

1.1.2. Temperature.

Mean temperature, of course, decreases as elevation increases, and in Britain temperature lapse rates can be amongst the most rapid in the world. The Meteorological Office adopts a standard lapse rate of mean temperature of $6^0C\ 1000m^{-1}$, but that for maximum temperatures appears to be greatest, $8\text{-}10^0C\ 1000m^{-1}$ implying cool afternoons and summers in mountain areas thereby limiting growth potential. Lapse rates vary with latitude and longitude, with altitude aspect and topography, type of air mass, time of day, and season of the year. In addition to lapse rates temperature variation in the mountains is much greater than in the lowlands, while the sensible temperatures as far as plants, animals, and man are concerned, are frequently lower than the air temperatures because of the general increase in wind velocity with altitude. Indeed wind is a climatic parameter of the profoundest importance in the mountain environment. Because the effects of surface drag diminish with altitude through the first kilometre or so of the free atmosphere there is a common wind velocity gradient of approximately 1m $s^{-1}\ 100m^{-1}$ and this velocity gradient is, at least in summer, is steeper for higher wind speeds. Over the highest mountains wind velocity may be further increased as air is accelerated through the gap between the mountain summits and a temperature inversion that commonly occurs at about 1600m (5000ft) forming an effective lid to the lower atmosphere. The resultant jetting can produce gusts of very high velocity indeed. The general increase in windiness and turbulence with altitude therefore accentuates the biological impact of temperature lapse rates as well as producing mechanical stress and abrasion. It also accentuates the effect of topography in terms of shelter and exposure, and is closely concerned with the accumulation of snow.

1.1.3. Precipitation.

The dominant components of rainfall are cyclonic and orographic and, of course, it increases with altitude - indeed some workers have suggested a linear relationship. Cloud cover and atmospheric humidity also tend to increase with altitude contributing to the wetness of the environment. As a result radiation inputs are much reduced, and diurnal and seasonal warming are seriously delayed and surface and air temperature ranges reduced. As a corollary sunshine quantities are reduced especially in late summer and early autumn. Snow frequency and intensity also increase with altitude as does the risk of blizzards and prolonged snow cover, while the length of the frost free season decreases. As well as significantly increasing the albedo and altering the radiation balance prolonged snowlie has a number of significant effects on plant growth and ecology, some of which we shall consider later.

1.1.4. Oceanicity.

Britain is a series of islands and its climate is influenced by the effect of the surrounding seas. This effect is recognised in the concept of oceanicity used by Poore and McVean, although attempts to quantify oceanicity, and its opposite continentality are less than satisfactory. Within an area such as the Scottish Highlands the index of oceanicity increases westwards with maximum values along the western Atlantic seaboard, while the east central Highlands are markedly more continental.

1.2. The Response of Plants and Animals to the Mountain Bioclimate

Perhaps the first effect of the mountain climate on plant growth to consider is the impact of low temperatures. In Britain the lower altitude and more maritime climate of our mountains is offset by the very steep temperature lapse rates and by the importance of the combined effect of low temperatures and high wind speed - the wind chill effect (the name given to heat loss from the surfaces of organisms ignoring radiation effects). The net result is for sensible temperatures to simulate the more extreme air temperature values associated with higher altitudes. This meagre supply of warmth at least in part explains why woody plants, especially the tree and shrub species disappear as altitude increases, for the ripening of wood requires more heat than is available. Although it is true that certain mountain dwarf shrubs, such as ***Empetrum*** and ***Vaccinium***, do reach considerable altitudes they actually make up a very small proportion of the total flora of the higher mountains. Temperatures are greatest, of course, close to the ground, and this is one reason for the prevalence of low growing plants with prostrate, rosette, cushion, and carpet growth habits - all variants of the *chamaephyte* life form with the perenating buds close to the ground. *Hemicryptophytes* are also strongly represented by grasses, sedges, and rushes, for here, again, the apical meristem is virtually at the ground surface. In addition, the marked dwarfness of vegetative growth displayed by montane species with these growth habits, coupled with the dense crowding of individuals in cushions and carpets produces mutual shelter and conserves heat, while the parabolic arrangement of leaves in rosette plants serves to concentrate radiation.

Wind also has a direct mechanical and abrasive effect and most mountain vegetation shows an intimate relationship with the site factors of shelter and exposure that we shall consider in more detail when examining the physiographic dimension of the mountain environment, particularily in relation to the effects of microtopography on plant growth, although, of course, animals also respond by well developed avoiding behaviour seeking sheltered feeding and resting sites, and especially in winter, migrating to lower altitudes. In addition to its mechanical effect, wind also affects plants through its contribution to evapotranspiration and a high proportion of mountain plants show, to some degree, xerophytic or xeromorphic features to regulate moisture loss. However, these adaptations are only partly a response to the desicating winds, for many mountain soils are immature, freely draining sands and gravels with scant moisture holding capacities, and this coupled with the increased intensity of radiation receipt at high altitudes on clear summer days, can place plants under severe water stress. Furthermore, for much of the winter water may be unavailable as ice or snow and the plants experience a physiological drought.

One of the main effects of climate as a whole, however, is the great reduction in growing season. In more continental areas many mountain plants have a pitifully short time at their disposal for the production of stem, leaf, flower and fruit. The explanation is to be found in the frugal growth rate of these plants and the labourious and patient preparation stretching back over several seasons of slow vegetative growth until sufficient reserves are available to facilitate intense and rapid growth culminating flowering and seed setting. Indeed many plants of the mountains enhance their capacity for survival by avoiding the need for outcrossing altogether by becoming self fertile, sometimes obligate cleistogamy (eg ***Trollius europæus***, the globe flower), or by reproducing entirely vegetatively by means of bulbils, as in the case of ***Polygonium viviparum***, most species of ***Saxifraga***, the saxifrages, and the viviparous grasses ***Festuca ovina*** ssp ***vivipara***, ***Deschampsia alpina***, and ***Poa alpina***. In Britain absolute low temperatures and the persistance of winter snow in restricting the growing season are only really important in the east central Highlands of Scotland and in specialised snowbed habitats. Nevertheless, elsewhere the common delay in ground warming has a similar effect, and the growing season lapse rates, that is, the increasing reduction in growing season duration with increase in altitude, are very high in oceanic Britain compared with a more continental area such as the Swiss Alps.

Truely snow determined vegetation (**chionophilous**), therefore, only occurs in Scotland with the first signs of the effect of snowlie being discernable in the Southern Uplands and corresponding to an average of >70 days with snow lying, but the main area for snowbed vegetation is the east central Highlands, particularily the Cairngorm massif. The first effect of snowlie is to afford protection from very low temperatures in winter as the base of the snow is effectively isothermal maintaining a constant environment at or about 0°C. Protection is also afforded against the damaging effect of wind. The extent and duration of this protection diminishes outward from the centre of the snowpatch and is paralleled by a concentric zonation of vegetation until truely exposed habitats that are always blown free of snow are reached beyond the extent of snow accumulation. These habitats may contain species that habitually avoid snowlie and are therefore known as snow hating or chionophobus species. The price paid for this protection is, of course a greatly reduced growing season for most species must wait until ablation of the snow occurs in the spring or summer before effective growth can occur. Some species, however can actually thrive under snow as long as sufficient light and air reaches them. For example ***Pleuroclada albescens***, ***Saxifraga stellaris***, ***Sibbaldia procumbens***, and ***Gnaphalium supinum*** have all been seen with green leaves, presumably photosynthesising under snow in mid winter.

Certain additional properties of snow patches are actually advantageous - for example, the surface of the snow traps and holds debris, both mineral and organic, carried by the wind in winter. This debris concentrated as the snowpatch contracts by ablation in the early summer and is let down on to the vegetation and ground surface when the snow melts away, thereby enriching the nutrient supply of the habitat. (In Scandinavia this process has created problems of environmental pollution for anticyclonic circulation patterns have brought airbourne pollutants from as far afield as the Ruhr, and the concentration of this fallout in snowbeds has severely damaged sensitive communities of bryophytes.) Ablation of the snow also redistributes precipitation and snow melt irrigation both maintains the moisture status and base status of the habitat in summer, although, saturation by water, the temperature of which is only just above freezing, may further delay increase in soil temperatures. On the other hand the bowl shape of many sites of snow accumulation tends to enhance their capacity to trap radiation once the snow has gone. Many species characteristic of sites with prolonged snowlie are intolerant of competition by more vigorous species and this partially explains their presence in the specialised and often unsaturated habitat provided by snowbeds. However, it must be remembered that conditions of extreme exposure also maintain a plant community equally characteristic of an unsaturated open habitat so that several species occur in both snowbeds and exposed sites (eg ***Salix herbacea***, the least willow). For this reason total plant assembleges rather than individual species are better indicators of late snowlie.

1.3. Altitudinal Zonation of Vegetation and Climate.

Perhaps the most important overall manifestation of climatic control of mountain ecology is to be seen in the almost ubiquitous phenomenon of altitudinal zonation of plant and animal communities reflecting the gradient of increasing climatic severity with increasing altitude on a mountain. The theoretical datum line for the study of such mountain zonations is the climatic forest limit, or altitudinal treeline. Both of these terms, however, need further definition if we are to understand this most import ecological boundary. In the first place we are really dealing with two lines and a zone of transition or **ecotone** between them. The lower of these lines is the forest limit, or the timberline, as it is often called, which is the upper limit of erect tree growth occuring at forest densities. Beyond this line the trees thin out growing as small groups or as scattered individuals. They are often dwarfed, semi-prostrate, exhibit the flagform or **krummholz** growth habit, or are in some other way deformed. The upper limit to this transition zone is the treeline (sensu stricto), where tree growth ceases entirely. On mountains outside the tropics it has been concluded that the primary cause of the damage that limits the altitudinal extension of tree growth is winter dessication. In continental climates this is due to the freezing of soil water coupled with the intense radiative heating of plant organs exposed above a winter snow cover. In more oceanic mountains in the temperate zone it is persistent strong wind flow particularly in winter that promotes the high evapotranspiration that leads to dessication. However, winter dessication, itself the prime cause, relates back to the conditions experienced during the previous summer because short growth seasons at altitude do not allow the leaves to mature fully. Cuticles remain thin, cells are incompletely lignified, and tissues retain a high water content with little transpiration resistance. In this condition leaves are highly vulnerable to dessication when, in winter, high evapotranspiration losses are compounded by physiological drought.

In Scotland it is difficult to establish either the natural climatic forest limit, or the potential treeline, because over much of the Highlands forest has been cleared and where treelines exist they display none of the features described above which typify natural altitudinal treelines, and they occur at lower altitudes than would be the case under natural conditions because of anthropogenic interference. In the Cairngorms, for example the anthropogenic upper limit of tree growth is usually c. 490m except at Creag Fhiaclach in Glen Feshie where the only really natural treeline in the Highlands occurs at c. 640m. Here twisted and contorted pines (***Pinus sylvestris*** spp ***scotica***) grow amongst junipers that, at the treeline, extend as a distinct **Sub-Alpine Zone** juniper scrub that appears to have escaped the burning that presumably destroyed it elsewhere. Though patchy, this scrub grows quite densely in places and the bushes reach heights of a metre or more, while their spreading low branches turn upward at the tips, and the leaf characteristics relate the shrubs more closely to ***Juniperus communis***, rather than to the prostrate dwarf juniper, ***Juniperus communis*** spp ***nana***.

In Scandinavia the birch, ***Betula tortuosa***, occurs above pine, spruce, or deciduous forest forming the Sub-Alpine Zone. Within it areas of juniper, willow, or even grassland occur. The latter may be natural features wherever exposure is great, or snow cover sustained, but some are associated with summer grazings and the sites of saeters. In Scotland this birch belt is fragmentary and of uncertain status because of the existance of secondary birch wood that has replaced oak and pine. The Cairngorm juniper scrub alluded to above, some of the upper birch scrub in the west and central Highlands as well as the northern birchwoods of Sutherland probably belong to this Sub-Alpine Zone, with its lower limit lying at around 640m in the east central Highlands, but descending to 100-150m in the west and perhaps to sea level in the northern Highlands. We can broadly conclude that a shrub zone succeeded the forest at higher altitudes over much of the Scottish Highlands. This was probably composed of:

> Juniper scrub on the well drained acid hills of the east and centralHighlands.
>
> Willows (***Salix lanata, S. lapponum, S. myrsinites, S. aurita S. repens***) on wetter and more eutrophic soils. nb. good example of such willow scrub on Durness Limestone in Inchnadamph.
>
> Dwarf juniper scrub (spp ***nana***) on the Torridonian sandstone, Cambrian Quartzites, and granites of the west and north.
>
> [The dwarf birch, ***Betula nana***, may have been an important constituent of the scrub growing on bogs in this Sub-Alpine Zone]

Again, in Scandinavia, mountains are divided above the Sub-Alpine Zone into three regions; **Low Alpine, Middle Alpine, High Alpine.** Here the Low Alpine Zone is predominantly one of dwarf shrubs. The dwarf juniper, dwarf birch, and dwarf arctic willows being most important in the lower part of the zone and distributed according to their edaphic preferences (juniper and birch associated with drier and poorer soils, the willows with wetter and richer soils or sites flushed by snow melt irrigation). Higher up they give way to the ericoid dwarf shrubs; ***Vaccinium, Empetrum, Arctous, Arctostaphylos,*** and of course ***Calluna*** sometimes associated with Low Alpine ***Nardus*** grasslands. For example in the Sogn Mountains of Norway juniper gives way at about 900m to the ericoid shrubs which in turn ascend to about 1100m. Here there is a change to Middle Alpine communities consisting of snowbed assembleges, and heaths of ***Juncus trifidus, Festuca ovina, and Carex bigelowii***.

Continuity between these Scandinavian zones and those that can be distinguished in Scotland is evident in a similar Low to Middle Alpine Zone transition from dwarf shrub heaths; ***Calluna, Empetrum, Vaccinium, Loiseleuria*** to snowbed vegetation, or to communities dominated by grasses, and grass like hemicryptophytes such as ***Juncus trifidus, Festuca vivipara, Luzula spicata, Deschampsia flexuosa.*** In Scotland the Low Alpine Zone can be sub-divided into a dwarf shrub sub-zone, and an upper moss sub-zone. The latter is so called because of the widespread dominance of ***Rhacomitrium lanuginosum***, and indeed the name ***Rhacomitrium*** sub-zone could equally be substituted to replace the equivalent ***Empetrum/Vaccinium*** sub-zone used on the continent even though these dwarf shrubs do occur wherever shelter is provided by intermediate snowlie. Few Scottish mountains, however, have large areas of Middle Alpine Zone vegetation, and it is doubtful if any reach true High Alpine Zone conditions, although, exposure on the highest summits limits continuous vegetation cover in a similar way to raw soil parent materials and low temperatures do in continental regions, and produce High Alpine conditions in the Ben Nevis range, the Cairngorms, and elsewhere.

The overall altitudinal zonation of vegetation in the Scottish Highlands can be summarised as follows:

III MIDDLE ALPINE ZONE
Juncus trifidus heaths ***Festuca vivipara/Gymnomitrium*** comms. Snowbed communities.

II LOW ALPINE ZONE
b. **Moss Sub-Zone**
Dwarf shrubs still present. ***Rhacomitrium*** 'heaths'
Empetrum/Vaccinium communities.
a. **Dwarf Shrub Sub-Zone**
Ericoid dwarf shrub heath, rarely dwarf juniper, birch, or willow scrub.

I. SUB ALPINE ZONE
Potential birchwood, birch scrub, juniper, or willow scrub. Now: ***Calluna*** moor
Festuca/Agrostis,
Nardus, and/or
Trichophorum/Molinia Grassland, or Blanket bog.

The altitudinal limits of these zones become depressed towards more westerly and more northerly sites and the zones become simultaneously wider, so that the Low Alpine Zone in particular becomes more important in Scotland than in Norway. This is because of the depression of the treeline due to increased exposure, the great extension in bog covered ground, and because of the relatively higher altitude at which temperature becomes limiting for dwarf shrub growth.

2. The PHYSIOGRAPHIC Dimension.

The physiography, or topography of a mountain area influences the vegetation and animal communities mainly indirectly acting through climate, through soils, and through drainage regime. These effects can best be considered at different scales as those due to macro and those due to micro relief or topography.

2.1. Microtopography.

The major importance of microtopographic variation is expressed through the relative degrees of shelter and exposure provided by any particular site, and operates mainly through the microclimatic growth environment of the individual plant. Both minor undulations of the ground surface, sometimes associated, as we shall see, with patterned ground and solifluction forms, and more major breaks of slope, often reflecting geological structure are mirrored by patterns in the vegetation with closed communities giving way to open discontinuous cover as exposure increases. Sheltered sites not only protect the plant from wind, dessication, and low temperatures, but also from surface erosion by wind, rain and sheet wash. As well as being liable to such processes of surface erosion exposed sites are blown free of extensive winter snow cover so that the plants are partially exposed and the snow cover is only temporary and such sites therefore provide habitats for snow intolerant or chionophobus species. Individual boulders and rock outcrops also support on their lee sides more profuse growth, while blockfields and block scree provide in the gaps between the blocks particularily well sheltered habitats for taller herbs, grasses and ferns. Mountain cliffs, crags and corrie walls also provide sheltered if not always stable niches for plant growth. Even the more robust plants afford shelter to those of lower stature which often gives wave like patterns even in closed communities, as for example in the ***Calluna/Arctostaphylos*** heath where the bear berry grows forward and in front of the more robust heather, or where in a similar situation the heather affords protection to the bilberry.

Open communities of plants are characteristic of extreme exposure and can occur even at lower altitudes particularily on ridges, but are best developed and most widespread on the highest summits as for example the ***Juncus trifidus*** of the Cairngorm plateau with their distinctive circular or crescentic tussocks and associated flora of the mountain, or stiff sedge ***Carex bigelowii***, and the least willow ***Salix herbacea***. These tussocks are dynamic, undergoing a cycle of development, the course of which depends on whether the site is one of net erosion, or accretion of gravel and sand. In the northwest Highlands this community is replaced by the even sparser vegetation cover of the related ***Juncus trifidus/Festuca vivipara*** so called erosion surface community. The accompanying map shows the distribution of these two communities in relation to the frequency of gales (recorded here as the number of days with gale force winds logged at meteorological station altitudes ie. these represent the minimum figures, because the incidence of gales at the higher altitudes at which these communities occur will be much greater).

Apart from the generalised effect of microtopography in terms of shelter and exposure, specific topographic features form particular and specialised habitats for plant growth. Perhaps the most important are the ledges and fissures of mountain cliffs, blockfields and block scree, screeslopes and gravel slides, patterned ground and solifluction features, and drainage and seepage lines - the so called wet flushes. All of these relatively small scale features tend to interact with microclimate, but their peculiarity as plant habitats is also associated with, certainly in some cases, their inherent instability and dynamic nature, or with their effects on soil moisture and soil nutrient status. Because of this we will consider them further when we turn to the edaphic dimension later.

2.2. Macrotopography.

Macrotopography of course effects the overall mesoclimate of a mountain massif - indeed the geomorphological character of mountain physiography is very important - whether the massif has been intensively glaciated with oversteepened slopes along glacial troughs with deeply incised corries with near vertical head walls with sharp ridges and frost shattered peaks. Such a landscape though dependant on the intensity of erosion, will also partly reflect the lithological response to erosion exhibited by different rock types - as in the Lake District with the contrast between the rugged physiography developed on the Borrowdale volcanics and the more subdued forms developed on the Skiddaw slates. Such intense dissection is characteristic of parts of North Wales. the Lake District, and the Southwest Highlands (eg. the Knoydart Penninsula, and Glencoe). Further north in the Northwest Highlands the mountains are mere remnants with much of the landscape reduced to the lower elevations of the 'knockan and lochan' topography of Sutherland. In central Wales, the northern Lake District, and particularily in the Grampians the landscape is more subdued for erosion has left broad plateaux at high altitudes, especially in the Cairngorms. True, steeply incised corries and glacial troughs eat into the margins and through these highland surfaces, but low angle slopes are more widespread forming a more subdued and rounded landscape of dissected plateaux with a considerable depth of mountain top detritus mantling the solid rock and allowing, albeit immature, soil development.

Now, the significance of these contrasts in mountain scenery lies in their effect on the areal extent of different habitats and hence plant communities. For example, the prevalence of snowbed vegetation in the Cairngorms, although partly a reflection of the greater elevation, the lower temperatures and greater snowfall of this part of the 'continental' east central Highlands, it also reflects the large area of suitable gathering grounds from which snow can drift and the large area of suitable depressions and lee sites at the correct altitude for snow accumulation. Equally the extent of exposed summit vegetation is much greater in the Grampians and Cairngorms than in either the west, or northern Highlands. Two further and important manifestations of the effect of macrotopography on the mountain mesoclimate are the interaction of slope angle, length and orientation on the effect of the climatic complex we call aspect, and the effect of macrotopography on momentum flux or air movement. In mountains, steep and near vertical slopes produce complex patterns of shadow reducing on the one hand and increasing on the other the effective radiation receipt of north and south facing slopes repectively, and this contrast can become very significant in terms of ground warming, snowmelt, length of growing season, humidity, and so on and thereby result in distinct patterns of vegetation response to aspect. Macrotopography also controls the development of 'katabatic' and 'anabatic' diurnal patterns of air movement, while cold air drainage especially in spring and early summer can also regulate vegetation through the development of frost hollows and frost pockets.

3. The EDAPHIC Dimension.

The soils of the mountains of britain of course mainly reflect the dominant influence of the climatic and parent material factors of soil formation. The influence of the former is to affect the rate of weathering to control the potential for leaching and translocation and to act through the occurrence of waterlogging to influence the accumulation of organic matter. In addition wind exposure and freeze-thaw remain locally important today and also influence mountain soils. The generally western and northern distribution of mountains in the British Isles coincides more or less with the distribution of the older, more resistant , siliceous, and acidic rock types and these dominate as sources of parent material for soil development. Deeper soil profiles are mainly associated with glacial, fluvio-glacial, and periglacial superficial materials derived from these rocks.

Although it is true that a distinct assemblege of soil types can be recognised and justifiably termed montane, some of these types are of wider distribution at altitudes that should more strictly be defined as upland while some are also found extensively as lowland soil types. In consequence in the following account of montane soil types the terms of reference will be broadened slightly to take account of this behavoir.

Raw mineral soils, and peaty rankers are the typical British mountain soils characteristic of a very cold wet climatic regime and are best developed on the exposed high summits and summit plateaux of Snowdonia, the Lake District, and the Central Highlands of Scotland.

Acid peats, peaty podsols, and peaty gley soils, constitutes a moorland soil association is a suite of soil types characteristic of a cold wet climatic regime over a much wider area than would be strictly defined as mountain viz. through the spine of Wales, the Pennines, the Southern Uplands, and north and west Scotland.

Iron humus podsols characterise a cold but drier regime, that is much more continental than the last, and are developed on very siliceous, permeable parent materials, and as such are only really widely developed on the hills and mountains of the east central Highlands, particularily the eastern Grampians.

Brown rankers, brown podsolic, and acid brown earth soils make up a marginal upland soil association in well drained situations while the essentially lowland group of soils, the non-calcareous gleys, could also, be added to this list for they too ascend into the uplands where drainage relationships are appropriate.

In the mountains, however, base rich soils are maintained largely by irrigation (flushing) with water that is strongly charged with ions removed from the rock and/or other soil by leaching, and by throughflow, or by mechanical instability due to gravity (screes, talus, colluvium), or to soil frost phenomena producing sorting, mixing, heave, and movement (geliturbation, solifluction). On any one parent material, therefore, most differences in soil base status are due to the varying incidence of such enrichment processes. Even on base rich rocks leaching usually produces base defficient soils unless this opposite tendancy is at work. So, in general, it can be said that on sloping ground, the composition of the rock and soil through which drainage water has percolated, or from which rock, regolith, or soil partcles have been contributed, is at least as important as the actual soil parent material at any particular site.

Sites which are particularily characterised by such enrichment are closely correlated of course with particular features of the microtopography of mountain areas, and because moisture status and base status are the most important influences affecting the floristic composition of the vegetation, these sites are also correlated with particular plant assembleges. These distinctive combinations of site microtopography, soil enrichment, and plant associations add to the diversity of the small scale mosaic of mountain habitats. Traditionally these habitats have been known as montane rills, and wet flushes, where they are characterised by irrigation along discernable drainage or seepage lines, and dry flushes where they are characterised by enrichment by solid particles, as for example in the case of screes. Solifluction features such as terraces may provide combinations of these habitats, with unstable but dry flush conditions existing on the terrace tread, while the emanation of drainage water at the base of the terrace riser leads to wet flushing. Finally, however, it must be emphasised that these sites and the habitats they represent can occur at a wide variety of scales, from for example a small fissure in a rock free face, to sizeable spring and stream heads forming large flushed areas. In the Scottish Highlands and particularily in the Cairngorms the distribution of such micro habitats is further complicated by their relationships with sites of late snowlie, which of course are themselves sites of enrichment.

From the ecological point of view perhaps the most interesting feature of these enriched habitats is that they provide habitats for some of the rarer montane species which require exchangeable calcium levels of >30mg 100g-1 oven dry soil and pH values usually in excess of 5 - the calcicoles - or exchangeable calcium levels in excess of 300mg 100g-1 oven dry soil and a pH >6. (see the attached lists).