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Linking Geology and Biodiversity

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Foreword

Geology has strong ties with biodiversity, in that the nature of the substrate, as usually determined by the nature of the underlying rock, is a key factor in determining the distribution of habitats and species. An obvious example of this is the distribution of chalk grassland habitats with outcrops of chalk.

As a signatory to the Convention on Biological Diversity drawn up at the World Summit held in Rio de Janeiro in 1992, the UK Government has a commitment to promoting and protecting biodiversity. This commitment has been focused through the identification of priority habitats and species and the development of a series of national targets which aim to maintain or enhance their conservation status. These have been published as part of the UK Biodiversity Action Plan (UKBAP). Biodiversity action groups have been set up locally and regionally to identify and promote how local initiatives can play a part in achieving the national targets and also enhance local biodiversity.

This report investigates the links between biodiversity and geology. Some work had already been done in looking at how standard geological site management practices can benefit biodiversity and how some priority species may be associated with types of geological outcrop (report produced for English Nature - *Geological conservation – benefits for biodiversity ENRR 561*). This report takes this a step further, looking specifically at the link between rock type and biodiversity across England and thus how the achievement of biodiversity targets can be assisted through a better understanding of geology.

The outcome is an examination of the key factors influencing and determining ecosystems, illustrated by examples of the links and factors from a number of countries, including England, to illustrate the work that has been done elsewhere. It is therefore a useful examination of this aspect of ecosystem studies and provides an extensive bibliography for those wishing to look at the subject in more detail. This report, along with *English Nature Research Reports*, No. 561 and *English Nature Research Reports*, No. 502 (Learning from the past to influence the future), has been summarised in a booklet by English Nature *Geology and Biodiversity – making the links*, available from the English Nature enquiry service.

This is a research report and its findings have not necessarily been adopted as English Nature policy and practice.

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1. Introduction

Since the Earth Summit at Rio in 1992 there has been a significant surge in interest in the diversity of life (for which the term biodiversity has been coined), largely related to its conservation in light of concerns over its loss. Within England, the Rio Summit provided further impetus to conserving the wide range of remaining semi-natural habitats and the species that these support. As part of this drive the concept of Natural Areas was introduced and developed by English Nature.

In total, 97 terrestrial and 23 maritime Natural Areas covering the whole of England have been recognised and described. These areas effectively represent sub-divisions of England, each with a characteristic association of wildlife and natural features and provide a way of interpreting the ecological variations of the country in terms of natural features, illustrating the distinctions between one area and another. Each Natural Area has a unique identity resulting from the interaction of wildlife, landforms, geology, land use and human impact. Natural Areas have been identified using information from a range of sources including geological maps, landscape accounts, agricultural treatises and recent data on the distribution of habitats and species.

While the focus of Natural Areas has been on the habitats and species that characterise them, it is apparent both from their extent and the names that have been applied to them that Natural Areas are intimately associated with, and reflective of, underlying geology and physical geography. Comparison of the Natural Area map with that of a geological map of the country (see Figure 1) shows a distinct correlation between the defined areas and geological outcrops (eg the granite of Dartmoor and the Tertiary sands and gravels of the New Forest). This is suggestive that at some fundamental level there are factors at play, which connect the geology and physical geography of an area with its biological diversity and ecological interest. If this is the case, then the fact that almost 100 Natural Areas have been described not only provides an indication of the great diversity of landscape and habitat types present within England but also mirrors the great geological diversity of this country.

The concept and definition of Natural Areas is not based on a rigorous scientific approach, but upon observation, description and our ability to define and appreciate change in the landscape around us. That we can determine what are apparent linkages between physical and biological factors without resorting to scientific analysis suggests that these linkages are manifest and real. We may be able to appreciate the subtleties of change from one area to another and have over many millennia probably accentuated the natural differences through management of the land, but the questions remain as to how these differences have arisen and in what way does geology contribute to the ecological complexity that we observe. This study sets out to clarify and document how geology may influence biodiversity, enable a greater understanding of the interactions that occur to be gained and hopefully en route provide a more substantive appreciation of something that we already know.

2. Factors influencing the relationship between geology and biodiversity

The role of geology in the development of the characteristic landscapes of England and the presence and distribution of wildlife, particularly vegetation, has been a topic of debate and discussion amongst natural historians and ecologists for hundreds of years.

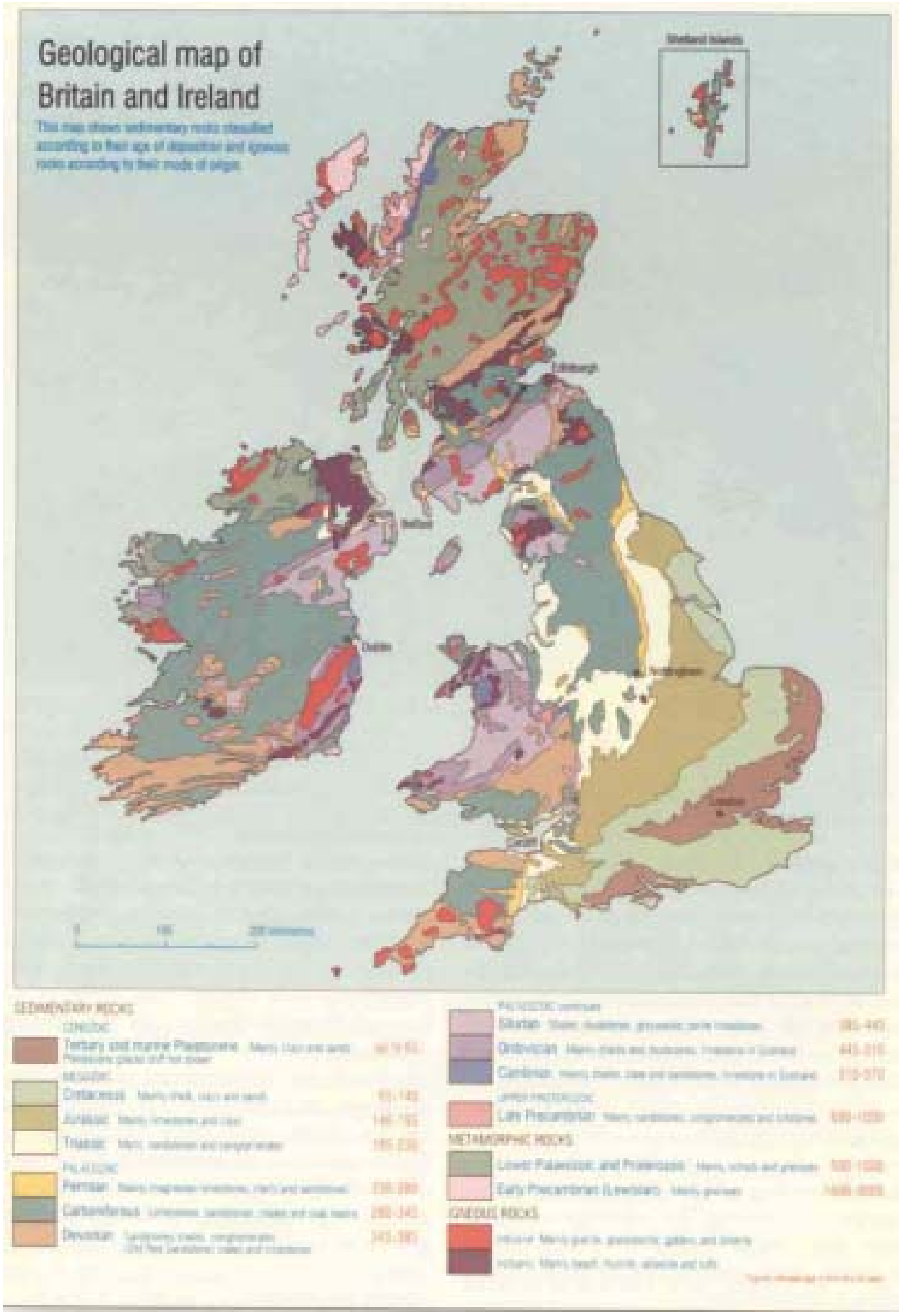

Figure 1 Geological map of the British Isles. NERC Copyright.

Certain associations between rock types and flora have probably been observed and considered since the first naturalists started to document and describe the plantlife of specific areas. However, by the end of the 19th century and beginning of the 20th century, advancements in natural history studies and the development of ecology as a science led to more explicit links between geology and wildlife being made. Much of this advancement came through the work of Victorian and Edwardian naturalists in the description of the floras of English counties and attempts to explain the distribution of plants and floristic regions or areas.

This work was built upon and enhanced by the emergence of ecology and the desire to provide a scientific foundation for the observed distribution of specific plant assemblages and floras. As Hopkins (2003) notes, the work of a number of Cambridge botanists in describing the floras of areas of differing geology and from this the development of ideas on the factors controlling floral differences was crucial in forging the notion of distinct linkages between geology and plant life.

These early studies and many subsequent ecological studies have revealed the complexity of relationships between the physical and biological components of ecosystems and habitats. Within this complexity of relationships it is apparent that geology plays an important role in delineating the ecology of an area, through both its contribution to the formation of soils and its influence on topography. However, it is by no means the definitive shaper of the distribution of plants and animals and the ecological diversity of the English countryside that we see today. Certainly, climatic variations from south to north and west to east play a significant role in the development of vegetation types and man's influence has been paramount in defining floral and faunal abundance, extent and distribution. Trying to determine the specific (if any) linkages between geology and wildlife (notably plant life because of its direct relationship with soil type), however, has often proved difficult and complicated even though it is apparent that such an association exists.

It would appear that no general studies have been undertaken to try and determine the contribution of controlling variables on the distribution of the English flora in order to determine to what extent geology actually plays a role in this aspect. However, while not entirely representative, such a study has been undertaken for the State of Wyoming in the United States of America (Reiners 2002).

The natural environment of Wyoming is, to a very large extent, geologically controlled. Rocks and sediments of all geological ages compose the mountain ranges, their bordering cuestas (scarp-slopes) and the structural basins lying between the ranges. These substrates provide a broad range of geochemical and physical substrates for plant growth. Reiners (2002) undertook a statistical analysis of the spatial distribution of a cross-section of the flora of Wyoming in relation to nine climatic variables, the basic vegetative cover types, and three geologically derived variables: bedrock type, surficial geology, and soil. The relationships between species distributions with these variables were tested by classification tree analysis, a method permitting the assessment of importance of the environmental variables. The study found that bedrock type was one of the controlling variables in about 80% of the cases and was the first determinant for distribution in about 21% of the cases. Thus, the study demonstrated that geology is a dominating feature in the distribution of plants in environments ranging from rolling plains, dissected basins, cuesta complexes and sedimentary and crystalline mountains. Whether such a study could also be undertaken for the far more modified (through human intervention and management) English habitats is debatable. However, it may be possible to select semi-natural vegetation types (eg NVC communities) on a Natural Area basis across the country and compare with similar climatic and geological variables at a relatively broad level.

The general conclusions from the study highlighted above, and a number of other ecological studies, are that geological influences on flora and fauna can be split into two basic areas: the direct influence of rock type itself and the indirect role that it plays in soil formation and the development of structures that influence the distribution of plants and animals at a range of scales. There are limited examples where it can be shown that the direct influence of rock type has a significant effect on plant presence and distribution. Generally these examples relate to groups of organisms and species which directly attach to a rock face (eg lichens and some vascular plants) and for which direct contact with the rock and its utilisation forms an integral part of the life cycle (eg uptake of mineral nutrients). However, even in these cases, lichens can modify the local chemistry and the rock outcrop may act as more of a physical structure than a specific substrate requirement for growth.

Rohrer (1983) found that higher plant and bryophyte species composition is similar on rocks that differ greatly in their chemistry, while Rune (1953) has shown that serpentine rocks support lichens and other plants that normally grow on both calcareous and siliceous rocks. Some species of the fern *Asplenium* are much more dependent on the accumulation of organic material rather than rock chemistry as they grow equally well on limestone and granite. Similarly, yew *Taxus baccata* and *Phyllitis scolopendrium* show the same lack of affinity for rocks of a particular chemical composition. Cox (1945) has shown that many species of *Rhododendron* associated with acidic bogs and heaths are also abundant on limestone cliffs in China.

A number of studies emphasise that local variations in the nature of cracks, crevices and solution hollows may be of much greater importance than the overall variation in chemistry imposed by the rocks themselves. Hora (1947), reports that few cliff species show clear site selection based on the chemistry and pH of the substrate, but that there is enormous variability of pH values among microsites only a few centimetres away from each other. Lundqvist (1968) has shown that on acidic rocks, calcareous materials go into solution and make the acid surface more alkaline, while on alkaline rocks, humic material acidifies the alkaline-rich soils and make them more neutral. This finding is supported by evidence presented by Cox and Larson (1993) which shows that the pH between rocks of large-block talus at the base of limestone cliffs is very high initially, but drops as low as 4.6 once organic matter accumulates to a significant degree. Siliceous rocks such as gneiss may contain traces of calcium which accumulates in crevices and hence these crevices often support calcicole plants. Some soils sampled on limestone cliffs in England possess up to 700mg calcium/gram of sample, but still have pH values between 6.8 and 7.5 (Rodwell 1992).

There would, therefore, appear to be evidence indicating that there is no or only limited control of vegetation by rock chemistry. However, this is not entirely the case and there are examples showing direct control. Jarvis and Pigott (1973) report that *Lychnis viscaria* only shows good growth on limestone cliff faces that are high in phosphorous. Lichens as a group seem to be controlled more by rock type or chemistry than any other group of organisms. Boyle, McCarthy and Stewart (1987) show that lichen communities can be good predictors of substrate chemistry and others have shown that granite rocks have a very different lichen flora from limestone rocks in the same geographical area. What has not been shown, however, is whether these distinctive communities reflect the chemistry of the rocks of some other property such as small-scale weathering patterns.

Photo 1. Lichens growing on a granite boulder, Isles of Scilly
Photo R. Cottle

The physical structure of rocks and their role in influencing biodiversity can probably be more easily demonstrated, although even here the influence of other physical and biotic factors is important. This relationship is not a direct one but is manifested through landforms which may either be wholly characteristic of a certain rock type (eg limestone karst) or more readily formed from some rocks than others (eg cliffs and bluffs). A limestone or sandstone cliff in a landscape of otherwise low or non-descript relief will provide different habitat conditions and support an ecosystem that is at variance to the surrounding area. In this sense, the structural nature of the rock and its influence upon landform can be said to be having an effect on biodiversity. However, even in this case the actual ecological interest that the feature supports will be determined by a large number of other factors other than geology such as aspect, relief and climate.

Although direct relationships may be few and far between it is apparent from the various studies that have been undertaken, and our observations of the landscapes around us, that broad associations and relationships do exist. For instance, the landscape and ecological changes associated with an eastwards journey from the granite uplands of Dartmoor to the undulating landscape of the Devon redlands formed in Triassic sandstones and marls is readily apparent. The problem is trying to define what this association is and at what level it operates. Geology is undoubtedly a key determinant, and some authors have argued that it is a prime factor in influencing plant and animal communities. The following sections highlight those factors which, together with geology, are considered important in determining and influencing ecological interest and diversity. This is not a comprehensive assessment of the effects of these varying factors, but is provided to show the various linkages that exist, particularly with respect to the role that geology has in interacting with or modifying them.

2.1 Soil formation

2.1.1 Parent material and weathering

Most higher plants do not show preferences for igneous, sedimentary or metamorphic rocks per se as preferred habitats (see discussion in Sections 4-6). It is mostly the weathered products of rocks, ie soils that may influence vegetation type and its distribution. However, soils do reflect the type of parent material, both in physical properties such as texture, colour and weatherability and in chemical content.

There would appear to be no universal agreement on the definition of what constitutes a soil. Geologists and engineers see soils as soft, unconsolidated rocks. The entire profile of weathered rock and unconsolidated rock material, of whatever origin, is then soil material. Most pedologists (scientists who study soils) confine soils to the portion of the regolith (all superficial material above fresh bedrock) supporting plant life and dominated by soil forming processes. The issue of definition can be circumvented if exposed hard rocks are defined as soils. This means that 'the soil' includes all material that is affected by physical and chemical processes and, to a far lesser degree, by biological processes.

It is very difficult to assess the role of parent material (ie the rock or deposit from which soil is derived) in soil formation. Parent material often only provides the framework within which other factors and processes operate. The term lithospheric material is often used, or preferred, as this denotes more of a dynamic situation to that of parent material, with soil formation occurring on and being influenced by depositional material.

Birkeland (1984) stresses that the influence of parent material appears to be greatest in the early stages of soil formation and under more arid conditions. As formation progresses then other factors such as climate and biota come more into play and gradually replace the influence of the parent material. The length of time that the soil has been forming is also significant. However, there are a number of what can be taken as generalised cases where some rock types and materials can control the evolution of soils to a relatively great degree.

The process by which soils are depleted of base elements and compounds and become acidic (podzolisation) takes place best on acidic rocks or parent material, such as sandy or crystalline deposits/rocks. Rocks with a high carbonate content inhibit podzolisation as the high base content keeps pH high and prevents the translocation of aluminium and iron. Soils formed on limestone are an example of this type, and are typically thin, fine-grained and have a sharp contact with the bedrock. Soils such as this tend to be the insoluble residue left following dissolution of the carbonate, although there is growing evidence to indicate that some of the material is often of aeolian (wind derived) origin. Another example involves volcanic rocks that are rich in feldspar and ferromagnesian minerals, which weather to provide abundant oxides and hydroxides of iron and aluminium in the soils derived from them.

Parent material also influences soil properties through the process of weathering and through the influence of the weathered material on subsequent soil forming processes, with some rock types being more susceptible to weathering processes than others.

Physical weathering is important in the early stages of soil formation. This is brought about largely through the process of temperature change and its effects on the crystalline nature of different rock types. As rock is a poor conductor of heat the effects of diurnal heating are confined to the surface layers and not transmitted freely through the rock. With the concentration of heat in the upper layers the surface of the rock tends to expand more than the rock at depth and this may lead to the creation of stresses in the rock. The assumption that a process such as this operates has been held to explain the flaking off of sheets of rock parallel to the surface of the rock, a process known as foliation and which is particularly prevalent in granite. Most igneous and metamorphic rocks are composed of different minerals, which, because of different specific heats, expand at different rates. Such expansion and contraction leads to minute internal fracturing within the crystals that make up the rock and lead to particulate disintegration.

The other main process of physical weathering is crystallisation (either through the action of the freeze-thaw of water or expansion of crystal salts). Freeze-thaw operates under climatic conditions where water freezes into ice causing expansion. For the operation of freeze-thaw there have to be joints and/or small-scale intergranular fractures present within the rock. Effectively these attributes apply to all rock types. A number of conditions have to be fulfilled for freeze-thaw to operate to full effect, including the presence of cavities within the rock. Within soft rocks such as chalk, which is essentially porous, there is considerable space for the retention of water. When this freezes and then thaws chalk can almost undergo complete disintegration. The crystallisation of salts is similar in action to that of freeze thaw whereby salts may become dissolved in the moisture penetrating rocks and then be re-crystallised having a disruptive mechanical effect. Such effects have been demonstrated in Magnesian Limestone, where calcium and magnesium carbonates react with sulphuric acid in the atmosphere (acid rain) leading to the production of magnesium sulphate which is very soluble and will re-crystallise in dry weather.

Despite the potentially significant effects of physical weathering (eg formation of scree slopes in glaciated mountain areas) the formation of soil is far more influenced by chemical weathering. Chemical weathering comprises a number of processes, including solution, carbonation, hydration, oxidation and reduction. Solution is particularly important in the breakdown of carbonate rocks and is dependent on environmental factors such as temperature and pH. The rate of mineral weathering depends on chemical composition, crystal shape and size and degree of crystal perfection. Weathering rate is governed by available surface area and, therefore, large minerals are harder to weather than several small minerals occupying the same volume. A knowledge of rock mineralogy allows rocks to be placed in their order of susceptibility to chemical weathering. For instance, the ranking for igneous rocks, in order of decreasing resistance, appears to be granite>syenite>diorite>gabbro>basalt. For sedimentary rocks the following appears to hold; sandstone>siltstone>dolomite>limestone>chalk.

If weathering has been intense and the landscape stable, considerable thicknesses of weathered material, known as the weathering profile, may develop with specific characteristics related to the nature of the rock being weathered. The weathering profile will vary considerable from place to place because of variations in rock type and structure, topography, rates of erosion, groundwater conditions and variations in climate. In the early stages, the nature of the weathering profile will be particularly determined by the parent material and the way that it weathers. Weathering profiles have been examined most thoroughly for igneous rocks and in tropical to sub-tropical climates. This work demonstrates that generally there is an upward-fining sequence with an increase in the abundance of clay minerals up the profile. Profiles on sedimentary rocks can be extremely variable, but the general principles still apply. Most profiles exhibit trends of decreasing particle size and increased clay content towards the surface. Profiles on carbonate rocks are usually just the insoluble portion of the rock, such as quartz, chert, iron and manganese oxides and some clay minerals. Weathered residues on chalk are usually thin because of the rock's purity.

Many soils develop in transported materials and it will be the characteristics of these transported materials that will influence the development of the soil. This is important in the context of the English landscape, much of which is covered by material that has not been derived simply from the progressive weathering of the underlying rocks. In many areas the soils have formed from deposits of glacial clays, silts and sands that were derived from areas tens or hundreds of miles away and transported by ice sheets during the Pleistocene. Thus, the gently rolling chalk hills of parts of Norfolk are covered with thick deposits of boulder clay deposited by ice sheets and sandy soils of aeolian origin which now support the characteristic heathland vegetation of the Brecks. Other such deposits include alluvium deposited by rivers over their floodplains and some coastal deposits such as shingle and sand.

2.1.2 The influence of climate

The climate of a region has both direct and indirect effects on the formation of soil. Directly, climate acts as a key determinant in defining the moisture and temperature regimes the soil is subject to as it develops and indirectly it plays a role in the processes of erosion, transport and deposition.

Water acts as the basis for many of the physical, chemical and biochemical processes that operate within soils. The moisture content of soils influences leaching and weathering rates, and temperature dictates the rate at which these reactions and processes take place. It is believed that the rate of chemical weathering of soils doubles for every 10^{o}C increase in average temperature.

Climate can act upon soils indirectly through influencing the type, extent and nature of vegetation and inorganic input into soils. Growth rates of vegetation increase with temperature and humidity, as does the rate of organic decay. Maximum decomposition occurs between 25 ^{o}C - 35 ^{o}C, therefore an increased rate at which organic material is incorporated into the soil.

Climate, and its influence on vegetation, also acts indirectly on soils through altering or dictating the surface wash rates of water, the mass and intensity of rainfall and the rate of aeolian erosion.

2.1.3 Biota

It is argued by Fitzpatrick (1986) that nearly every living organism, be it bacteria, plant or animal can affect soils and the way in which they develop. The biota creates, adds and transforms the organic materials that form soil. They can transfer and transform mineral materials and facilitate the operation of many soil processes.

The influence of organisms on soil formation depends upon the niche they occupy and upon their life strategies. Decomposers, such as bacteria, live in the surface organic horizon and ingest organic material. Burrowers live below the surface in the mineral horizon and ingest both mineral and organic material. Grazers eat vegetation on the soil surface. Predators can live in or on the soil surface and prey on the other biota. With the exception of predators, these organisms affect soil directly through the transformation of organic matter, predators act indirectly by returning organic material to the soil through excretion.

The type and nature of vegetation cover has an important influence on soil formation and structure, and in a number of cases may appear to be the most important soil influencing factor, largely due to the interaction of plant roots which extract water and nutrients, with the fall of leaves, and other organic debris enriching the soil in various ways. Different plant communities have varying effects on the soil. Deciduous trees have deep root systems drawing nutrients from depth and so tend to counteract leaching. Their leaves decompose readily to recycle nutrients and add humus to the soil. A wide range of organisms live in the soil beneath deciduous trees. Coniferous trees, on the other hand, lead to acidification, partly by locking up nutrients in the fallen needles that may take years to decompose, and partly due to the organic acids, tannins and polyphenols that are washed off the bark and needles by rainfall and thus cause podzolisation. Soils under conifers therefore accumulate litter and peaty layers that are too acidic for many soil organisms to survive in, which in turn reinforces the system as the decomposers are not present in the soil. Heather moorland affects soils in a similar way to conifers. Grassland recycles nutrients rather like deciduous woodland, but with shallower root systems, leaching may become more prevalent and the soils gradually lose nutrients and become more acidic. Studies carried out on grassland and forest soils in America show that all soils tend to have an equally high content of organic matter at the surface, but the distribution with depth varies according to vegetation type. 'A' horizons under trees, as a rule, are generally thin and organic matter content decreases with depth. Grassland 'A' horizons tend to be thick and organic matter content remains high.

2.1.4 Summary

It is apparent that the characteristics of any particular soil type represent the influences and interactions of a number of key physical and biological components and processes. The nature of the parent material (ie the bedrock or derived geological material) is but one of these components. The influence of parent material on soil formation will vary depending on the nature of interaction and strength of influence of the other factors. In this way, it may be that in certain instances (eg scree slopes, arid environments) bedrock comes to play a more significant role on overall soil formation and as a consequence the type of vegetation that a soil may support. Evidence for this is presented in more detail in some of the following sections on specific rock types and their floral associations.

2.2 Climate

The climate of Britain results from a combination of several factors but notably latitude, altitude and the position of the Island off the coast of mainland Europe and the influence of the warming waters of the Gulf Stream. The northern part of England tends to be wetter and cooler, which in part reflects its general greater relief (which is also reflective of its geology and geological history) and latitudinal difference. The south and west tend to have a relatively mild climate in comparison, which is particularly reflected in the winter by the fact that some coastal areas experience no frosts.

Mean annual rainfall varies from 600mm in the east to over 2400mm in the north and west over areas of high relief (eg the Lake District and Dartmoor). Temperature variation also shows a similar pattern with southern England experiencing elevated mean temperatures over the entire year in comparison with northern England. Average daily sunshine levels of more

4.5-5.0 hours on the south coast and 4.0-4.5 over much of southern and eastern England reduce to 3.5-4.0 hours over much of northern England and areas of higher relief eg Dartmoor in southern England.

At a broad level these climatic variations do undoubtedly influence the ecology of an area. Thus a broad distinction can be made between vegetation and fauna that predominates in the wetter and milder conditions of the west to that which occurs in the more arid and continentally influenced climate of the east (eg the greater abundance and diversity of ferns and mosses in the west). It is perhaps at a local level that the influence of geology on climate comes into play through local and often abrupt changes in relief. The classic example is the influence of a hill range on rainfall/moisture, where greater rainfall occurs on west facing slopes (in the UK) as moisture precipitates out as air cools as it is forced upwards. As air descends eastern slopes, precipitation reduces and these slopes are said to be in the 'rainshadow'. This difference in localised rainfall pattern can have a significant effect upon vegetation composition and growth.

Climate interacts with various other physical factors at all scales from the broad-scale regional level described above to the scale where small variations in topography can influence local climatic conditions and hence vegetation type and structure. Geology and more specifically topography plays an important role in the development of microclimates and in this sense some rock types are more likely to lead to variations in microclimate as a direct result of their ability to influence topography.

A good example of the influence of topographically controlled microclimate on vegetation comes from a detailed study of sandstone ravines in the Saxon part of Switzerland (Beer 2002). Detailed ecological work in this area has shown that the ravines have a reducing and delaying effect on temperature fluctuations. This effect increases in deep and narrow ravines. During cold fronts, the bottoms of the ravines are warmer than the plateaus and reefs. During warm fronts, the bottoms are colder than plateaus and reefs. Temperature also varies between the bottoms of the ravines and the plateau surface depending on the time of day and year with the bottoms being noticeably colder (up to 10^{o}K) than the plateau surface during the summer. The distribution of vegetation within the ravines appears to be strongly influenced by the microclimatic conditions, among other factors such as soil, relief and competition. The proportion of northern, mountain species is much greater in the ravines than on the plateau surface, where species reflective of drier and drought resistant conditions are more prevalent. These differences are particularly reflected in the distribution and diversity of bryophytes which would appear to have a narrower tolerance of ecological conditions (ie they are more specific) than many higher plants. Similar associations occur throughout the British Isles, where small differences in microclimate caused by abrupt changes in topography, may influence the composition and distribution of plant communities at a very localised scale.

Thus, although there are broad differences in the climate across the country which have a clear influence on vegetation, local modification due to relief, in part reflecting geological substrate and history, can play an important role. This aspect is further explored in the following section.

2.3 Relief and topography

The correspondence between the relief of an area and its underlying geology is often so close that the nature and the arrangement of the rocks are fundamental in the development of landforms. The structure of rocks affects the general pattern of relief, while the lithology (the specific makeup of a rock type) of individual beds influences relief in detail. However, rock type in itself is not the only controlling factor and there are areas where relief does not seem to be greatly affected by rock type.

Where beds of differing resistance are involved in folding or faulting, the processes of erosion may cause the pattern of the outcrops to be reflected in the relief. Thus, alternate resistant and non-resistant beds in a gently dipping series may be etched out by erosion to form a typical scarp and vale landscape, like that of the London Basin of southern England. Much also depends on the history of erosion of any particular region.

The resistance of an individual rock type to erosion depends on a number of factors. Its effective ability in forming relief depends largely on the lithology of adjacent rocks and on the time over which erosion has acted. Two sets of factors may, therefore be separated: those governing the resistance of the rocks (hardness, permeability and minor rock structure such as jointing) and those governing the effect of resistance on relief (influence of adjacent beds, the structure of the strata (eg angle of dip) and the length of the period of erosion).

In practice, the various ways in which rocks affect relief may rarely be isolated. As no single rock type remains homogeneous over considerable distances and many of them change to a marked degree, it is difficult to generalise about the effects of rocks on relief. As an example, there is a common conception that granites form upland areas of rounded relief in Britain. This holds true for many igneous intrusions, but not for all. In southwest England the granite intrusion forming Dartmoor has a maximum elevation of 600m, while much more subdued granite relief is found on the eastern side of Bodmin Moor, where the granite rises to about 180m above the surrounding Devonian sediments. The eastern part of the St. Austell granite affects the relief to a very limited extent. Whether this is due to there being only a slight difference between the resistance of the granite and that of the surrounding rocks is uncertain as the whole area was affected by marine erosion during the Pleistocene and there may have been too little time since this period of planation for subaerial erosion to expolit the lithological differences.

Limestones develop more distinctive relief features than any other type of rock, primarily as the result of the jointing of the rock, its permeability and its solubility in water containing carbon dioxide or humic acids. The lithology of limestone is also significant, as hard, well-jointed limestone possess different features from those of soft limestones such as chalk. The geomorphology of limestone outcrops and the formation of typical karst scenery is discussed further in Section 10.2.

However, in general terms, the resistance of a rock type to erosion (ie the relative hardness and permeability) is the fundamental factor in determining relief. The effect of rock hardness on resistance to erosion is impossible to measure. However, providing that all things are equal, including chemical weathering, it is the harder rocks that will generally form higher ground. A classic example of this is the Precambrian rocks of the Malvern Hills which rise abruptly from the softer Devonian and Triassic sediments of the surrounding plains. At a larger scale, the older, harder rocks of the north and west of Britain form higher ground (eg the Pennines) than the younger and softer rocks of the south and east (eg the Chalk and Tertiary sands and gravels).

Relief, in itself, at the scale exhibited in England probably has only limited influence upon flora and fauna, and this influence is probably largely manifested through climate. The general rule of thumb is that a rise of 300m equates to a 4^0F drop in temperature. For the majority of England it is therefore unlikely that there are significant differences in vegetation and ecology due to changes in relief mediated climatic variation. However, its effects are apparent in areas like the Pennines, the Lake District and Dartmoor where there are significant differences in altitude (up to 600m) and geological structure/outcrop between adjacent lowland and upland areas, and hence average temperatures.

2.4 The recent past

The natural features and semi-natural habitats that form the modern landscape of England have, in geological timescales, been significantly modified in the relatively recent past. Although many of the structural elements of the country owe their formation and foundations to geological processes of great antiquity (eg the Alpine mountain-building phase of approximately 25 million years ago) it is the events of the last 1 million years that have been most influential in defining the present-day landscape.

The repeated advances and retreats of ice sheets and glaciers over the last million years or so have acted as a giant exercise in the erosion and re-distribution of surface sediments and deposits. The glaciers and ice sheets stripped away soil and weathered rock from the uplands leaving many areas of almost bare rock, with mounds of debris known as moraine. All of northern England and much of the Midlands and eastern England was glaciated at some time during this period, leaving behind large-scale erosional features such as glacial hollows and trough-like U-shaped valleys in areas like the Lake District.

In the lowlands, ice sheets and their extensive meltwater streams deposited vast quantities of sediment with a great variety of composition and texture, often derived from source bedrock at some distance from the site of eventual deposition. The kames, drumlins, till sheets and lake deposits often give rise to interesting but confused drainage patterns as sediments were laid down in environments with very different controls to those of the present day. This means that coarse sediments may be located in hollows with no drainage exits, leading to the formation of groundwater gleys or peat. Thus, in many parts of England, areas of varying bedrock geology are now carpeted by sands, gravels and glacial tills that bear little resemblance to the underlying bedrock and in may instances effectively drown out any specific influence that these rocks may have had on the local vegetation. In some areas individual rocks or aggregations of rocks are present which clearly bear no resemblance to the local geology, having been transported into an area through the action of ice and water. These so-called erratics are generally not extensive enough to have an influence, except perhaps at a micro-environmental scale, on floral and faunal patterns.

Photo 2. Glaciated landscape, Svalbard. Parts of Northern Britain may have once looked like this following the retreat of the last ice sheet.
Photo R. Cottle

Although the repeated advance and wane of the ice sheets has had a significant influence on the distribution of sediments across the English landscape, the vegetation that we see today is in part reflective of the physical and chemical nature of the rocks and sediments in the locations where they were deposited. Thus, In many parts of northern and eastern England and some parts of southern England there is not a simple and defining relationship between bedrock geology and the overlying veneer of sediments and soils. The mass transportation of sediments from a wide variety of sources during the Pleistocene has complicated the geological fabric of the country. Glacially derived clays therefore overly limestones, sandstones and igneous rocks in the Midlands and aeolian derived sands occupy hollows and valleys on the chalk. These deposits effectively mask and alter the potential influence of the bedrock on the surface soils and associated vegetation. What this leads to is a blurring and blending of formative characteristics and boundaries, so that the interactions between bedrock and surface deposits in effect increases the diversity of soil condition and type and in turn the complexity of the floral and faunal assemblages that any one area may support.

2.5 Man's influence

Without doubt the influence of man and his ability to change the environment has been paramount in determining the extent and distribution of the habitats that we see today. The vegetation of England has been altered by human activity for thousands of years, resulting in a heavily modified or cultural landscape. Much of the habitat diversity present within the English landscape is the product of many generations of management, including livestock grazing, burning, cultivation, woodland management and infrastructure development. Without man's intervention, influence and management the vast majority of the land would revert to climax lowland woodland. Most habitats in England are described as semi-natural, and effectively comprise native (and exotic) plants and animals and natural features that have been substantially altered by human activity. Only a few truly natural and unmodified habitats still exist, usually where human exploitation is impractical, for example inland cliffs, mountain tops or steep and inaccessible areas around the coast.

Human activity has, to a large extent, masked and modified the effects that geological and physical processes have had (and are still having) upon our flora and fauna. However, an argument can be made that man's use and modification of the land over the past 10,000 years has actually resulted in a greater distinctiveness between regions and areas of differing geological outcrop. Prior to the large-scale clearance of woodland from the majority of lowland and upland England by the early colonists it is likely that the ecological differences between areas would have been more difficult to discern than today. Subtle differences in woodland composition would have existed and would have reflected changes in soil permeability, structure and pH, all attributes to some extent controlled by underlying geology. However, habitat types such as heathland on sandy soils, lowland neutral grassland on clays and chalk downland would not have extensively occurred and these habitats, or the main species making up these communities, would have only been present as small-scale and integral components of the wider woodland landscape. It wasn't until man started large-scale deforestation and the widespread introduction of agriculture that some of these habitats appeared more widely in the landscape. Over time, certain soil types and areas would have been preferentially selected for specific agricultural practices and the structure of natural floral and faunal communities would have adapted to this management. Through this process certain areas would have gained more definable characteristics (eg the development of grassland and/or heathland in areas of more intense grazing) reflecting the physical ability of an area to sustain a specific management function. Thus, through the intermediary role of soils and relief, it is suggested that geology has had a significant influence on our management of the landscape and that human activity has in effect accentuated any inherent differences in the linkages between rock types and vegetation.

The previous sections have briefly explored the main factors that have, or have had, a key influence on the distribution and presence of habitats in England. As previously stated it is by no means an exhaustive discussion, but has been used to illustrate the potential influence that geology may have in determining certain ecological attributes. The following sections provide a more focussed discussion on the linkages that have been described for rock types and, in particular, vegetation so as to provide a more detailed picture of the influence that can be discerned at the broader level.

3. Rock classification

3.1 Introduction

Rocks are physical mixtures rather than chemical compounds without the fixed attributes of form, density, hardness and chemical composition of specific minerals or crystals. No two rocks are alike, and although they may be given the same name there will always be differences in the relative sizes, shapes and proportions in the minerals of which they are composed.

Rocks are generally classified on the basis of their textural features, especially grain size and mineralogical composition (see Table 1). Broadly, rocks are classified into one of three groups: igneous, sedimentary and metamorphic. All the common rocks are made of silicate minerals, with the exception of limestones, which consist of calcium carbonate ($CaCO_3$); but rock-forming minerals tend to occur in fairly well defined associations. Quartz, feldspars and micas are common constituents in all three main rock groups, whereas amphiboles and pyroxenes are rare in sedimentary rocks but common among both igneous and metamorphic rocks. Olivines and garnets are practically confined to igneous and metamorphic rocks, respectively, and calcite is widespread among sedimentary and metamorphic rocks but is not a major component of igneous rocks.

Table 1 Mineralogical composition (%) of main rock types showing the significant difference between the main groupings

Mineral	**Rock Type**						
	Granite	Basalt	Amphibolite	Schist	Shale	Sandstone	Limestone
SiO_2	70.8	49.0	49.3	63.3	62.4	94.4	5.2
TiO_2	0.4	1.0	1.2	1.4	1.1	0.1	0.1
Al_2O_3	14.5	18.2	16.9	17.9	16.6	1.1	0.8
Fe_2O_3	1.6	3.2	3.6	3.6	3.2	0.4	0.3
FeO	1.8	6.0	6.8	2.6	2.1	0.2	0.2
MgO	0.9	7.6	7.0	1.6	2.5	0.1	7.9
CaO	1.8	11.0	9.5	1.9	1.7	1.6	42.6
Na_2O	3.3	2.5	2.9	1.3	0.9	0.1	0.1
K_2O	4.0	0.9	1.1	3.1	3.0	0.2	0.3
H_2O	0.8	0.4	1.5	2.6	5.2	0.3	0.7
CO_2					1.0	1.1	41.6

As a result of the predominance of silicon over all the remaining elements the principal component in chemical analyses of common rocks, save limestone, is silica. Rocks rich in quartz and alkali feldspars (eg granites) contain a higher proportion of silica (SiO_2), potassium (K_2O) and Sodium (Na_2O) and less of the basic oxides (MgO, FeO and CaO) than rocks rich in plagioclase feldspar and pyroxene (eg basalts). While metamorphic rocks have chemical compositions similar to igneous and sedimentary rocks they may have quite different mineralogical compositions (the main exceptions are marbles and quartzites which are metamorphosed limestones and sandstones). Metamorphism is primarily a recrystallisation process, whereby elements are redistributed into new minerals; there is only very limited movement into or out of the rock and so the chemical composition remains essentially that of the original rock.

3.2 Igneous rocks

These rocks are formed when magma cools and solidifies. Magmas that reach the surface form volcanic, or extrusive, rocks and those that are emplaced within the crust form intrusive rock bodies of various shapes and sizes. An important chemical subdivision of igneous rocks is into acid, intermediate, basic and ultrabasic categories. The terms acid and basic are inappropriate, but stem from the idea that silicate minerals were salts of 'silicic acid'. The more silica in the rock, the more 'acid' its parent liquid. Acid igneous rocks contain sufficient silica for at least 10% of the rock to be quartz. Intermediate rocks have up to 10% quartz and basic rocks typically have no quartz; as all the silica is taken up in feldspars and other silicates.

3.3 Sedimentary rocks

Sediments and sedimentary rocks cover most of the ocean floor and about three-quarters of the continental land area, forming a veneer rarely more that a few kilometres thick upon the predominantly metamorphic and igneous continental crust. Most abundant are greywackes, sandstones, shales and limestones, of which the essential minerals are few in number, namely, quartz, feldspars, clay minerals and calcite.

The agents of mechanical weathering physically disrupt solid rocks exposed at the Earth's surface. Such agents include frost action, pounding by waves, differential expansion and contraction in deserts and the wedging action of growing plant roots. Further physical breakdown accompanies transportation by rivers, wind or by waves and currents along coasts. Individual particles become smaller and more rounded and minerals with good cleavage are rapidly reduced in size by repeated fracturing. These physical processes are largely responsible for determining the textural features of sedimentary rocks. Their mineralogical composition is largely the result of chemical weathering, which decomposes the minerals of igneous and metamorphic rocks and forms new ones.

Most of the aluminium in the minerals of the original rock goes into clay minerals and much of the silicon is retained in quartz, but the other principal constituents are mainly removed in solution, though they do not always travel very far. Iron is normally in the Fe^{2+} state in minerals; on weathering it rapidly oxidises to very insoluble Fe^{3+} and is precipitated in soils near the site of weathering as hydrated iron oxides. Magnesium, calcium, sodium and potassium usually stay in solution and end up in the oceans. However, variable amounts of all of these elements enter the structures of new clay minerals. Calcium is precipitated from seawater mainly by the action of marine organisms. It is precipitated mainly as calcium carbonate in the shells and skeletons of invertebrates, but also as calcium phosphate in the bony skeletons of fishes.

3.4 Metamorphic rocks

Metamorphism can be said to begin when temperature and/or pressure has risen enough to effect obvious changes of original igneous or sedimentary textures or mineralogy. Metamorphism is a solid-state recrystallisation process, but the presence of water is crucial as it acts both as a catalyst and as a kind of intergranular lubricant between mineral grains.

Rocks in the vicinity of igneous intrusions are literally baked by the heat given off by the cooling magma. The textures of contact metamorphic rocks are generally granular and unfoliated with randomly orientated crystals. Metamorphic rocks that are the product of high temperatures and pressures underlie huge areas of the Earth's crust and in the deeper parts of mountain building areas. These rocks are almost always foliated, possessing a directional texture defined by the alignment of minerals such as micas and amphiboles at right angles to the principal stress. There is a general increase of grain size with increasing metamorphic grade: gneisses and schists are coarser grained than phyllites which in turn are coarser than slates.

It can be seen from the above description that each of the main rock types has specific chemical and in many instances physical characteristics. These characteristics in turn may determine the way in which a rock weathers and the products of chemical weathering. As discussed in Section 2, the nature of the parent rock can be important in determining soil structure and character and as a consequence vegetation and habitat. This is particularly so with respect to soil chemistry and structure. This aspect is explored further in the following section, particularly in relation to one of the key issues that vexed the pioneer ecologists of the late 19th and early 20th centuries.

4. Plant-rock associations and the calicole-calcifuge issue

One of the fundamental issues that crops up in the discussion of the role of geology and its influence on plant life (and therefore, in turn, on habitat type and structure) is the so-called division into lime loving (calcicole) and lime avoiding (calcifuge) plants. This aspect of plant ecology has been widely recognised by naturalists for many years and is well appreciated by gardeners and horticulturists.

It is apparent from the work of early pioneers into the ecophysical study of plant-soil relationships that the division between calcicole and calcifuge plants is not a simple one and is complicated by a large number of factors. However, there are clearly broad relationships and interactions at work which, may be reflective of derived chemical and physical attributes (ie from the soil or parent rock), which provide us with the ability to determine the geology of an area by description and definition of the flora. Botanists and naturalists are able to do this without recourse to undertaking analysis of chemical parameters in order to determine the nature of soil pH etc. In effect the vegetation of an area may act as an indicator of the local geology or soil conditions, which as has been previously discussed can be significantly influenced by the type of parent rock from which the soil is derived.

Early studies of the British flora made by botanists such as Tansley showed that there were clear patterns of plant distribution between calcium-rich limestones and chalks, and acidic, siliceous rocks low in calcium. This pattern revealed itself as acid grassland, heathland and sessile oakwoods on acid rocks and calcareous grasslands and ash woods on limestone and chalk. The calcicoles comprise a much larger group of species (ie found only on calcareous rocks) than the calcifuges (eg species like common rock rose *Helianthemum nummularium*, squinancywort A*sperula cynanchica* and salad burnet S*anguisorba minor*). Lousley (1950), provided an assessment of the calcicole component of the British flora with his book on wildflowers of limestone and chalk. No such equivalent of the calcifuge flora appears to have been written, perhaps due to its comparatively impoverished nature and limited representation of species from the more prominent and 'showy' groups such as the orchids.

The many studies of British limestone vegetation provide a good example of the basis behind the calcicole-calcifuge division and the nature of plant-rock relationships. Grime and Hodgson (1969), identify some plant species as strongly calcicole (eg small scabious *Scabiosa columbaria*) and others as strongly calcifuge (eg wavy hair grass *Deschampsia* *flexuosa*), but recognise that there is actually a continuum of response by plant species. Some species such as white clover *Trifolium repens* have been shown to be ecotypically differentiated into races tolerant or intolerant to limestone (Snaydon 1962).

Kerner (1903), gives an account of the contrasts between calcicole and calcifuge plants grown reciprocally on limestone and siliceous (acidic) soils. Kerner concludes that reciprocal culturing did not change the phenotype and that the two substrates were toxic to non-native populations. In a similar vein, Tansley's (1917) study found that species interactions greatly altered the effect of soil type on plant growth. For example, where a calcicole species is handicapped as a result of growing on acid peat it is forced to compete with its calcifuge rival. A calcifuge species is handicapped during the seedling stage as a result of growing on calcareous soil, and is therefore unable to compete effectively with calcicole species. The study emphasised the significance of competition in modifying edaphic responses, and warns against reading too much significance into results obtained from plants studied in isolation.

Growth studies show that growing plants of acid soils on lime-rich soils result in a weak, yellow growth form, a condition known as chlorosis. Similarly, many calcicole species cannot be grown or grow weakly on acid soils. This indicates that the patterns of plant distribution clearly have a physiological basis. Work by a variety of researchers has found that there a complex set of chemical factors that influence growth and therefore distribution. However, what emerges from these studies is that calcium is not always a direct controlling factor in the presence or absence of calcicole and calcifuge plants. It appears that the main factor is that of pH, which affects the solubility of a range of important elements. On acid soils, many calcicoles cannot grow, as they are not able to tolerate the high levels of soluble aluminium. Chlorosis in calcifuge plants has been found to be due to the fact that on calcareous substrates, iron is insoluble and these plants cannot produce chlorophyll (which is iron based) hence leading to the yellow coloration (Grime & Hodgson 1969). Similarly, the availability of the main nutrients (nitrogen, phosphorous and potassium) has been found to be strongly influenced by pH. It is also clear from these studies that species form a calcicole-calcifuge spectrum, not two discrete groups, and a wide range of species typical of neutral soils (so-called mesophytes) occur. These include meadow species such as great burnet *Sanguisorba officinalis* and snake's head fritillary *Fritillaria meleagris* (Hopkins 2003).

The study of calcicole-calcifuge plant groupings provides a strong indication of the way in which vegetation may be intimately linked with soil chemistry and by linkage through to parent rock. This linkage and its component mechanisms are documented further in the following sections, which provide an analysis of linkages with respect to each of the main rock types.

5. Sedimentary rocks

As previously described, sedimentary rocks comprise a wide range of rock types with differing physical and chemical characteristics which, to a large degree, reflect the material from which they have been derived, the process of deposition and subsequent geological history. Because of differences in these factors all sedimentary rock types are unique, although broad groupings are clearly apparent (eg limestone, sandstone, shale, clay etc.). It is thus difficult and not relevant to talk about any one vegetation type being restricted to or representative solely of sedimentary rocks. It is, however, apparent that because of the unique composition and character of some sedimentary rocks that some vegetational types are more or less taken as being distinctive of certain rock formations. This is no where more clearer than with calcareous sedimentary rocks and much of the botanical and ecological literature exploring the linkages between flora and geology has concentrated on these rock types, while research and literature on the vegetation of other rock types is comparatively scarce.

5.1 Calcareous rocks

Calcareous rocks (eg chalk and limestones) are those dominated by calcium carbonate ($CaCO_3$). Some rocks, such as chalk are almost pure $CaCO_3$, while in others the amount of $CaCO_3$ may be much reduced. The factor common to all calcareous rocks is that they are alkaline in pH, although it does not necessarily follow that calcareous rocks give rise to alkaline soils. Geology plays a significant role in defining the framework within which ecological assemblages and plant communities occur, but other factors are involved in determining whether resultant soil conditions are alkaline or acidic. This aspect is discussed later with respect to the development of so-called limestone heath vegetation.

In Britain calcareous rocks outcrop widely, but predominate in southern England. Here, the most characteristic is the Chalk, which forms the North and South Downs of Kent, Sussex and Hampshire, much of Salisbury Plain and the Chilterns. Chalk also underlies a significant part of East Anglia and forms much of east Yorkshire. Buff coloured limestones of Jurassic age outcrop as a ridge or spine that stretches from the Dorset coast, via the Cotswolds, and through to the East Midlands. These softer, young limestones contrast with the harder and older Carboniferous Limestone which largely outcrops in Derbyshire and North Yorkshire.

The flora of chalk and limestone has been well studied and documented by a large number of botanists and naturalists. The most comprehensive work is that of Lousley (1950), who describes the flora associated with all of the major limestone and chalk outcrops in Britain.

The variety of the different floras described by authors such as Lousley perhaps reflects the diversity of chalk and limestone types throughout the UK and potentially aspects such as the $CaCO_3$ content within individual rock units may play a role in determining the overall composition of a flora. However, it is also apparent that a significant component of the observed variation in plant communities is due to differences in climate and relief, as by and large the flora of the chalk and Jurassic limestones of southern England are very similar. However, there are clearer distinctions to be made between the floras of the younger Mesozoic limestones and chalk and the older Carboniferous Limestone which dominates more upland areas such as the Peak District and North Yorkshire.

It is not possible here to provide a full description of the floras (and faunas) associated with calcareous rocks in England. However, a number of key linkages are discussed below and an example provided of the complexity of relationships that occurs in some specific geological situations.

5.1.1 The chalk

Chalk is the most important of all the formations which give rise to calcareous soils in the British Isles. Of marine origin, chalk is in essence, a very pure limestone which provides it with specific characteristics (eg high porosity and softness). The ecology of chalk represents the combination of and interaction between a number of factors, but particularly climate, soil and biota. Of these the geology and chemical composition of chalk has an important role to play with respect to soil extent and characteristics.

The nature of chalk soils is greatly influenced by topography. Where slopes are steep, as it is on some of the characteristic chalk scarp slopes (eg North and South Downs), the rate of erosion is such that it prevents soil from forming at all, leading to the exposure of a fragmented layer of the bare rock at the surface. The gradient at which the characteristic chalk grassland turf forms on chalk slopes has been investigated by Adamson (1922) who found that a slope with an average gradient of 30.6^{o} had a continuous ground flora while one with a gradient of 36.5^{o} was either bare or had a very sparse vegetation. A slope of about 37-38^{o} would appear to be the greatest angle at which closely grazed chalk grassland can be sustained. Slope plays an important role in the occurrence of bare ground on chalk, which in turn is an important factor influencing the presence of certain plant species and invertebrates, particularly those requiring particular microclimatic conditions (see Box 1 on the silver spotted skipper).

Due to the porosity of chalk, water retention is of particular importance for plants on chalky slopes and outcrops. In order to reduce water loss through transpiration, many plants typical of chalk slopes are low growing and also possess other physical adaptations such as small leaves (eg fairy flax *Linum catharticum*), thick cuticles (eg autumn gentian *Gentianella amarella* and many orchids) or hairy leaves (eg hairy violet *Viola hirta*). Some species like bee orchid *Ophrys apifera* die back after flowering in order to avoid the driest summer months. The majority of plants associated with chalk are perennials with extensive and relatively deep root systems, enabling plants to maximise water uptake from the porous substrate (Lousley 1950).

Interestingly, Lousley notes that the majority of flowers that are constants in chalk grassland are not confined, or nearly confined, to this community. Species such as common birdsfoot trefoil *Lotus corniculatus* and wild thyme *Thymus praecox* are also characteristic components of many other communities across a wide area of England. However, species that are largely confined to the chalk tend to be local and there are a relatively large number of species showing a high degree of exclusiveness (eg chalk milkwort *Polygala calcarea*). The occurrence of a constant sub-community of plants (ie non-exclusive) across the chalk and other substrates indicates that it is perhaps the physical factors that are important in controlling distribution rather than any specific properties of chalk itself. It may well be that for species such as thyme and birdsfoot trefoil that factors such as high soil porosity and nutrient deficiency are important factors in determining the presence and distribution of these species. Such conditions may be associated with a number of rock types, and it is notable that both these species can occur on soils derived from non-calcareous rocks or deposits. Conversely, the occurrence of a relatively high number of species that are almost confined to the chalk also indicates that there may well be controlling factors more intimately associated with the rock type and its derived soils.

Besides chalk grassland and its component species, there are a number of shrubs and trees that are closely associated with the chalk. These include dogwood, *Cornus sanguinea*, privet *Ligustrum vulgare*, wayfaring tree *Viburnum lantana* and spindle *Euonymus europaeus*. In some areas (eg the chalk of Salisbury Plain), juniper, *Juniperus communis* is also a characteristic species, although it also grows widely in association with other rock types, suggesting a more complex relationship (see section 5.1.5).

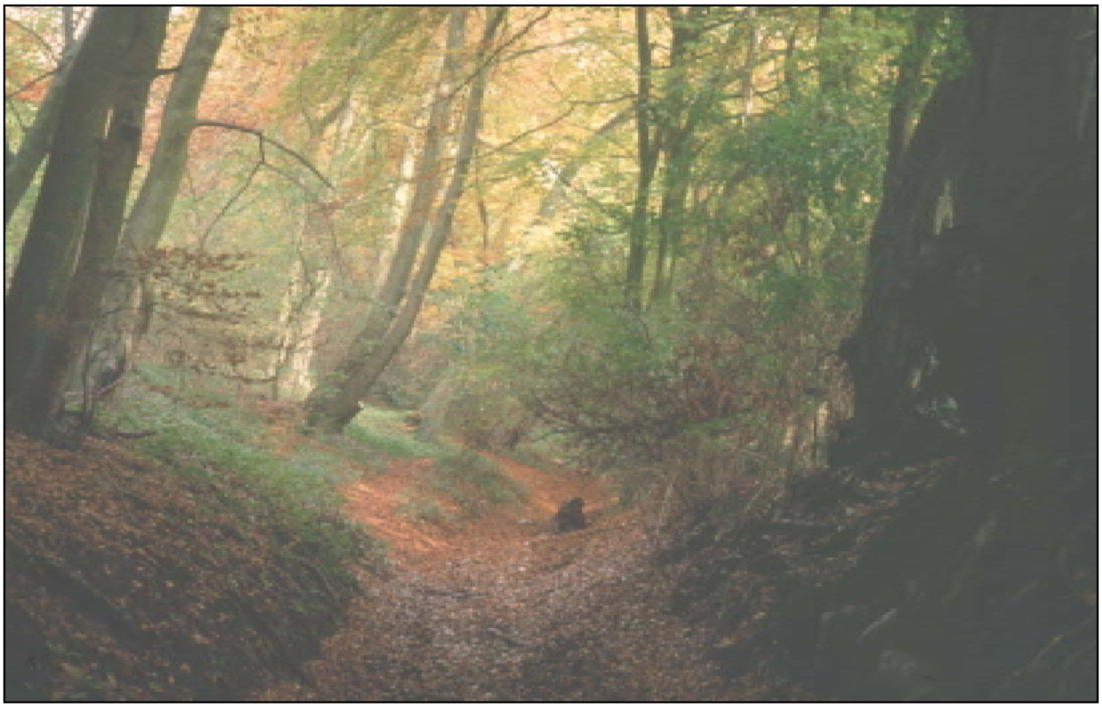

Photo 3. Beech woodland, The Chilterns
Photo English Nature

Beech *Fagus sylvatica* woodland is also intimately connected with the chalk and occurs on circumneutral to calcareous soils in England. A number of National Vegetation Communities (NVC) are recognised and each community has a different associated suite of species which change according to slope and soil type. As slopes become steeper, there is a shift from relatively deep, moist and moderately base-rich soils to thin, dry and strongly base-rich profiles. There is an associated floristic change in the woodland understorey, with bramble *Rubus fruticosus* dominating on the shallowest slopes and dog's mercury *Mercurialis perennis* becoming more prominent as the gradient increases. Beech woodland in England belongs to the central and northern European associations of the habitat, but typically lacks some of the more Continental species, but with correspondingly more Atlantic species, including holly *Ilex aquifolium* and bluebell *Hyacinthoides non-scripta* (reflecting the climatic differences between western and continental Europe). In England and Wales, beech woodland is relatively abundant within its range in southern England and Wales on circumneutral to calcareous soils along the slopes of the major hill systems of the chalk and the southern limestone outcrops.

Well known sites on the chalk of southern England include the beechwoods of the Chilterns, east Hampshire and the North Downs. Beech woodland is also found on the Jurassic limestone of the Cotswolds and interestingly the flora and mollusc fauna here is more diverse that than that of the Chilterns. Whether this reflects particular differences in soil type between the chalk and limestone or differences in other aspects such as past management or climatic (Atlantic) influence is difficult to establish. Beech woodland dies out to the west, with the most westerly sites being present on the limestones of south Wales (eg Cardiff beech woods). This change probably reflects climatic influences rather than the lack of suitable soil types and geological outcrops further to the west.

Text Box 1 – The silver spotted skipper butterfly. A calcareous restricted species ?

A classic example of a species that has been considered to show a relationship with a geological association is the silver-spotted skipper butterfly *Hesperia comma*. This butterfly breeds in open chalk grassland that contains areas of short, sparse turf typical of thin soils. Its present day distribution is entirely restricted to the Chalk in southern England although it formerly used to occur on limestone grassland in central (the Cotswolds) and northern England (Yorkshire). Significantly, it would appear that there are other factors at play in its distribution and not just the presence of its foodplant, sheep's-fescue *Festuca ovina*, which is widely distributed in England.

The silver-spotted skipper is at the north-west limit of its European range in Britain and requires some of the hottest and driest grasslands available. It is thought that the sparse vegetation and bare ground characteristic of chalk downland provides warmer conditions which may aid larval and pupal development. Grazing (eg by rabbits and/or sheep) is also very important in maintaining the short turf required. On mainland Europe the species makes use of patches of *F.ovina* on non-calcareous soils. This perhaps suggests that in Britain the species is present in those areas where the right microclimate is present and these tend to be provided for on south-facing slopes on chalk and limestone habitats. On the continent, with its warmer climate, these attributes are provided across a wider geographic area and the species is not solely restricted to areas of calcareous rock.

Another characteristic tree of the chalk is yew *Taxus baccata.* Yew woodland occurs on shallow, dry soils usually on chalk or limestone slopes, but in a few areas stands on more mesotrophic soils are found. Yew woodland is scattered, predominantly on calcareous substrates, in southern England, and to a lesser degree in northern England (eg the Morecambe Bay Pavements where this species grows on the Carboniferous Limestone). The combes of the south-east flank of Butser Hill in Hampshire support dense yew woodland in association with scrub and chalk grassland, which is typical of the occurrence of this woodland type on the chalk.

One extremely rare habitat associated with the chalk is semi-natural and natural box *Buxus sempervirens* scrub. At only one site, Box Hill in Surrey, does the scrub form a stable (ie persistent) natural or near-natural community, as it is developed on steep, chalk slopes, where other tree species are unable to grow to mature size. Here natural erosion maintains the open conditions required for the survival of this habitat type. Box is also found as scrub vegetation at other locations, notably in Buckinghamshire and on the oolitic limestone of the Cotswolds. However, in these areas box occurs as seral scrub gradually reverting to woodland where unmanaged and so does not represent a stable formation.

5.1.2 Carboniferous Limestone

In contrast to the Chalk, the Carboniferous Limestone is a hard limestone with a lower $CaC0_3$ content and a more extensive outcrop than the Chalk. This characteristic rock forms a number of prominent upland areas around the country, notably the Mendips of Somerset, the Derbyshire/Staffordshire Dales (the White Peak), West Yorkshire (eg Malham, Ingleton) and the Yorkshire Dales. The wide occurrence of this limestone type across England means that there are distinct floral differences between southern and northern outcrops. It is likely that these differences owe more to climatic variation and changes in relief rather than variations in the rock itself, although beds of sandstone and shale are more prominent in the northern Carboniferous Limestone succession.

Throughout its outcrop there are a number of characteristic plants and communities, that while not restricted to the Carboniferous Limestone, are more intimately associated with it than outcrops of the Chalk, Magnesian Limestone and Jurassic limestones at similar latitudes. One such community is upland mixed ashwood, although the term upland refers here more to the occurrence of this community type in northern England rather than its presence at altitude. Upland mixed ashwoods are found on base-rich soils in the north and west, in most of which, ash *Fraxinus excelsior* is a major species, although locally oak *Quercus robur*, birch *Betula pendens*, elm *Ulmus* spp., small-leaved lime *Tilia cordata* and even hazel *Corylus avellana* may be the most abundant species. Despite variations in canopy composition the ground flora remains broadly similar.

The largest examples of this woodland type occur on the Carboniferous Limestone, on well-drained soils, but this woodland also occurs on more acid poorly-drained soils where there is flushing of nutrients. Most upland mixed ashwoods are probably ancient, but ash is a vigorous colonist of open ground, and some important areas such as Derbyshire Dales are mosaics of ancient and recent ash woodland, while south-west examples include the Mendips. The boundaries between this woodland type and lowland mixed deciduous woodland may be unclear in places, for example in Somerset and South Wales, because the two types form an ecological continuum determined by climate.

Upland mixed ashwoods provide a habitat for a number of important UK Biodiversity Action Plan (BAP) species including the netted carpet moth *Eustromia reticulatum,* pearl bordered fritillary *Boloria euphrosyne*, high brown fritillary *Argynnis adippe*, and dormouse *Muscardinus avellanarius*.

The flora of some areas of Carboniferous Limestone outcrop is very rich and several outcrops support species of restricted or exclusive occurrence. One well known example is the Cheddar pink *Dianthus gratianopolitanus*, which is only known in Britain from the vertical cliffs of Cheddar Gorge in the Mendips. Further to the north, the Carboniferous Limestone outcrops of the Avon Gorge at Bristol are considered to support the richest limestone flora in Britain (Lousley 1950). Most of the trees, shrubs and climbers on the limestone are those found on the Chalk (eg yew, wayfaring tree, dogwood and spindle), but ash largely takes the place of Beech and small-leaved lime is also common. Two trees are endemic to the Avon Gorge (ie found nowhere else in the world) these are both species of mountain ash (*Sorbus bristoliensis* and *Sorbus wilmottiana*). Interestingly, all of Britain's ten rarest trees are species of *Sorbus* and of these seven are confined to Carboniferous Limestone outcrops in England and Wales.

Overall, 27 Nationally Scarce plants are native to the Gorge and its environs, 17 of which were recorded there from 1970 onwards and still present in 1996 and 10 which were lost from the area before 1970. Of these the most well known are the round-headed garlic or Bristol onion *Allium sphaerocephalon* and Bristol rock cress *Arabis scabra*, which occur only at this locality in Britain (although *A.sphaerocephalon* also occurs in Jersey, where it is effectively part of the French rather than the British flora). The reasons for the preponderance of scarce and rare species associated with the Carboniferous Limestone of the Bristol area are difficult to determine with any certainty. There are some suggestions that the geology of the area has a role to play in the presence of these species, notably the two species of endemic *Sorbus*, which as discussed previously is a tree genus that would appear to be clearly associated with the Carboniferous Limestone in England. It is likely that it is the coming together of a number of significant influences, namely the western oceanic climate, geological substrate, wide range of structural habitat elements and the largely inaccessible nature of the gorge outcrops that provide the basis for the unique flora of the area.

Some of the best outcrops of the Carboniferous Limestone are to be found in Derbyshire and Staffordshire where they form the Derbyshire Dales, or the White Peak. The flora of this area of dissected plateau is dominated by calcicole species and is similar to that of outcrops to the south except that a number of northern species are located here at their southernmost limit. The changes to the flora are therefore more climate influenced and in effect the geology plays no more of a controlling role than it does further to the south. Species that make an appearance here are mountain pansy *Viola lutea*, Jacob's ladder *Polemonium caeruleum* and globe flower *Trollius europeaus*. Conversely, some of the more common plants of calcareous formations of southern England are absent or rare. This is particularly so with respect to many of the orchids and species such as wayfaring tree, traveller's joy *Clematis vitalba* and stemless thistle *Cirsium acaulon.* However, many of these southern species are present further to the north, but are found on the Magnesian Limestone outcrop to the east of the main mass of the Carboniferous Limestone of Derbyshire and Yorkshire. This north-eastward extension for southern components of the chalk and limestone flora may reflect the lower altitude of the Magnesian Limestone in comparison with the Carboniferous Limestone massif or possibly soils derived from the Magnesian Limestone are more akin to those of the Chalk than the Carboniferous Limestone.

The outcrop of the Carboniferous Limestone is interrupted by the Millstone Grit of the Pennines (which forms the Dark Peak) before reappearing in West Yorkshire where it forms the cliffs, scars and pavements of the Yorkshire Dales. Further north, along the Pennines, the limestone becomes increasingly replaced by shale and sandstone units within the main succession. Lousley (1950) notes that although it is not easy to generalise about the flora of the Carboniferous Limestone of northern England, its characteristic feature is its 'upland' nature. Hills such as Ingleborough and Mickle Fell rise over 700m and much of the main plateau is at a height that would be described as upland. As such, northern plant species are far more dominant in the flora than in Derbyshire, although there are still many species common to both areas. Species which are particularly associated with the Carboniferous Limestone of northern England include bird's eye primrose *Primula farinosa*, bitter milkwort *Polygala amara* and dark-flowered helleborine *Epipactis atrorubens*, which is one orchid with a northern rather than a southern distribution.

Perhaps the most botanically interesting aspect of the northern limestone is the flora associated with limestone pavement (see Section 10.2 for a description of the geomorphology of this habitat). The vegetation of limestone pavements is unusual because of the combinations of floristic elements, including woodland and woodland edge species, such as hart's-tongue fern *Phyllitis scolopendrium* and dog's mercury. On the clint surfaces or the upper walls of the grikes there are plants of rocky habitats, such as wall-rue *Asplenium ruta-muraria* and maidenhair spleenwort *Asplenium trichomanes*. The fissures (or grikes) in the pavement provide shelter from the desiccating action of the wind and from grazing animals and hence may support an assemblage of rare and interesting plant species. Such species include a number of ferns such as rigid buckler-fern *Dryopteris submontana* (which has its main population centre on the limestone pavement of West Yorkshire) and limestone polypody *Thelypteris robertiana* and the small bird's foot sedge *Carex ornithopoda*. Where humus builds up at the bases of the grikes, plant species associated with acidic conditions may occur such as melancholy thistle *Cirsium heterophyllum*, bracken *Pteridium aquilinum* and Devil's bit *scabious Succisa pratensis*.

In areas where limestone pavement is more wooded, then species such as dark-flowered helleborine may occur along with baneberry *Actaea spicata* and angular Solomon's seal *Polygonatum odoreatum* and more common species such as Lily-of-the Valley *Convallaria majalis* and ramsons *Allium ursinum*. The limestone pavement at Malham supports a number of nationally scarce species such as hutchinsia *Hornungia petraea* and hoary whitlowgrass *Draba incana*. Also found are some of the distinctive species of limestone habitats, including downy currant *Ribes spicatum*, rigid buckler-fern, limestone fern *Gymnocarpium robertium* and spring sandwort *Minuarta verna*.

The influence of climate over geology, or perhaps more correctly the interaction between these two physical components is neatly illustrated by the composition of the floras found on the Carboniferous Limestone of the Morecambe Bay area. Here the rocky outcrop of Hutton Roof Crag, which rises to a height of 300m, supports a flora very similar to that of the dales and hills of West Yorkshire. Farther to the west, the Carboniferous Limestone outcrops around the Kent Estuary, in the area of Silverdale and Arnside, where it comes down to the coast. The main feature of the flora of this area, in comparison with Hutton Crag, is the presence of a number of plants that are much more common in southern England. These include fly orchid *Ophrys insectifera,* dropwort *Filipendula vulgaris*, western spiked speedwell *Veronica hybrida* and maidenhair fern *Adiantum capillus-veneris*. A number of coastal limestone species (eg hoary rock-rose *Helianthemum canum* and goldilocks *Crinitaria linosyris*) characteristic of more southern climates are also present.

The outcrops of Carboniferous Limestone from southern to northern England provide an excellent illustration of the influence of geological substrate on plant community composition and structure and the interaction with climate and relief. There are apparent differences between the calcicole floras of the chalk and the Carboniferous Limestone (eg predominance of beech over ash on the Chalk), which in part are probably attributable to geological differences between these two formations. It is difficult to pin down what the defining factor is that enables distinctions between the two rock types and their floras to be made. Certainly in southern England the differences between the floras is unlikely to be due to altitudinal or climatic differences as much of the Chalk outcrop is at a greater elevation (eg Salisbury Plain, Marlborough Downs) than the Carboniferous Limestone of the Bristol area or parts of the Mendips. However, it is perhaps the hardness of the Carboniferous Limestone, in comparison with the Chalk, and the fact that it produces landforms of greater prominence (eg gorges, cliffs and crags) which sets it apart from the Chalk. This hardness, in contrast to the Chalk, may affect factors such as weathering and the chemical characteristics of derived soils, water retention and availability to plants and the formation of a greater range of bare rock and structural niches (eg fissures and crag faces) that can be exploited by plants.

5.1.3 The Jurassic Limestones

Rocks of Jurassic age (approximately 180 million years old) extend almost 300 miles through the centre of England from the coast of Dorset in a north-easterly direction to North Yorkshire. This sequence of rocks comprises limestones, sandstones and mudstones that vary frequently in character from location to location. However, amongst them are a number of prominent limestone units that give rise to alkaline soils and calcicole floras. The most well known of the limestones are the oolitic limestones that outcrop on the Dorset coast, (eg the Portland Stone) the Cotswolds, Northamptonshire and Rutland and parts of the North Yorkshire coast. Due to its outcrop through the central part of England the Jurassic oolitic limestones provide a 'floral link' between the limestone floras of west and east and also between north and south. There is a gradual transition in species of restricted distribution from southern and western species in Dorset, to more eastern species around Stamford and finally to northern species in North Yorkshire.

Much of the flora of the southern oolites is similar to that of the Chalk, with beech woodland being prominent in parts of the Cotswolds, and areas of calcareous downland possessing many of the same herb species, although meadow cranesbill *Geranium pratense* is much commoner on the oolitic limestone than the Chalk. Lousley (1950) indicates that there are only a few plants that would appear to be associated closely with the Jurassic oolites, these being downy woundwort *Stachys germanica* and perfoliate penny-cress *Thlapsi perfoliatum*. Other species occur more commonly than on other calcareous substrates, such as wasp orchid *Ophrys trollii*, woolly-headed thistle *Cirsium eriophorum*, yellow star-of-bethlehem *Gagea lutea* and purple milk-vetch *Astragalus danicus*.

The typical Cotswold flora extends through much of Oxfordshire, Northamptonshire and Lincolnshire and it is not until Yorkshire that the flora takes on a slightly different composition. In the Scarborough area many of the species typical of southern outcrops can be found including many of the commoner orchids (eg bee orchid *Ophrys apifera* and autumn lady's tresses *Spiranthes spiralis*), but more northern species such as baneberry *Actaea spicata* and stone bramble *Rubus saxatalis* also make an appearance.

5.1.4 The Magnesian Limestone

The Magnesian Limestone is exposed in a narrow outcrop on the east side of the Pennines with its southern limit near Nottingham and its northern, some 150 miles to the north, at Tynemouth. The succession varies throughout its outcrop but the most important geological subdivision consists of a thick-bedded yellowish limestone which contains a higher proportion of carbonate of magnesium than is usual for other limestones.

The Magnesian Limestone is of Permian age and unlike the Carboniferous Limestone, which outcrops to the west, is a relatively soft rock and weathers easily to form rounded hills. Natural cliffs in the limestone are exceptional and occur in only a very few places. Due to its softness it gives rise to a good light dry soil suitable for cultivation. For this reason much of the area where the rock outcrops has been cultivated and little remains of the original vegetation. The contrast between the lowland agricultural scenery of the Magnesian Limestone and the upland rough crags and uncultivated slopes of the Carboniferous Limestone is significant. These differences are particularly evident if a comparison is made between the Derbyshire Dales (Carboniferous Limestone) and the Magnesian Limestone between Mansfield and Worksop, which occur at the same latitude.

Photo 4. Magnesian Limestone grassland and scenery, Cassop Vale, Durham
Photo English Nature

The Magnesian Limestone provides habitat for a number of calcicole species at their farthest north on the east side of England. Travellers' joy is thought to be native on the Magnesian Limestone in south-west Yorkshire, while Nottingham catchfly *Silene nutans* reaches as far north as Knaresborough. The occurrence of species typical of the southern Chalk gradually decreases northwards along the outcrop of the Magnesian Limestone so that species such as stemless thistle *Cirsium acaulon* and dark mullein *Verbascum nigrum* just peter out. However, sufficient of the characteristic plants of places like the South Downs make it far enough north to make the Magnesian Limestone of interest to botanists.

There are two rare plants that are particularly associated with the Magnesian Limestone. One is the thistle broomrape *Orobanche reticulata*, which in Britain is virtually confined to the Magnesian Limestone in Yorkshire with just a small population just to the east on the chalk. Most of its locations are in the valleys of the Ure and Wharfe where 85% of the known populations are within the influence of flood-water (JNCC 1999). The species is parasitic on creeping thistle *Cirsium arvense* but occasionally on other thistle species. The reason for its effective restriction to the Magnesian Limestone would appear to be unknown, as its hosts are common species throughout England. Potentially, there may be aspects of the chemistry of the soils derived from the Magnesian Limestone which are different to those of other calcareous rock types and which play a key physiological role in the growth of both the host and parasite. The second plant is the small sedge *Carex ericetorum* which also occurs on the chalk and on calcareous sand over the chalk in East Anglia.

One interesting distribution and potential faunal relationship with Magnesian Limestone is that of the Oak bush cricket *Meconema thalassinum* which has expanded its range northwards in recent years. In Yorkshire, which is at the edge of its northern range, the oak bush-cricket is associated with suitable habitat almost exclusively on Magnesian Limestone. It is not known whether this distribution is related to soil type or is merely a coincidence (Sutton 2003). Although, a relatively isolated example, this potential faunal-geological relationship suggests that perhaps many other similar associations exist. However, it would require significant and detailed autoecological studies to try and tease out any defining linkages amongst the many likely factors that control the habitat preferences and distribution of such species. Potentially, it may be that species at the edge of their natural ranges will only occupy sites where suitable microclimatic conditions are present, which may be due to specific plant-soil-geological relationships, and will only expand into other areas when broader climatic conditions effectively reach the same state.

5.1.5 Calcareous heathland

The previous sections have dealt with the occurrence of vegetation types typical of a range of key calcareous rock types and discussed the variety of calcicole floras associated with these rocks. However, in some instances, the relationship between some plant communities and soils derived from these calcareous rocks is more complex and gives rise to some interesting distribution patterns. One such example is that of plant communities in which juniper *Juniperus communis* forms a key component. In southern England juniper scrub may develop on a range of calcareous grassland types on thin chalk soils (eg Salisbury Plain). Where juniper is not dominant the scrub contains a rich assemblage of other shrubs, mainly of the family Rosaceae. Further north, at higher altitude on limestone, juniper scrub is often associated with limestone pavements and calcareous cliffs and screes. However, juniper is also associated with acidic substrates and the range of ecological situations in which juniper scrub is found, and transitions to other habitat types is reflected in its distribution and occurrence throughout England. In North Yorkshire, juniper occurs at high altitude on Carboniferous Limestone pavements (eg Ingleborough). Immediately to the west, juniper occurs on the Lake District High Fells in Cumbria, on upland acid substrates, where it is associated with a number of other vegetation types, notably birch, rowan and ash woodland at Birk Fell

The occurrence of juniper on both calcareous and acidic substrates suggests that a relatively complex relationship between plant growth, soil and substrate type may be at play. This complexity of relationship is not confined to this vegetation type and has been noted in relation to other calcicole and calcifuge species. Several British vegetation types have been described as limestone heath or chalk heath (Tansley and Rankin 1911) and all share the characteristic of an unusual mixture of calcifuge and calcicole species on a calcareous substrate, suggesting that the factors influencing the two groups are complex and interrelated.

Many areas identified as limestone heath are associated with superficial deposits of acidic glacial drift or loess overlying calcareous rocks and forming a mosaic of deeper acidic soils and neutral to alkaline soils (Etherington 1981). These do not form true calcareous heaths which, are formed on shallow soils in which the root systems of all species are intermingled. Etherington (1981), describes two types of calcareous heath; chalk heaths on the softer Cretaceous Chalk and limestone heaths almost confined to the hard Carboniferous Limestone of west and north-west Britain, with a few isolated occurrences on Devonian and Jurassic limestones.

Studies of soil pH and vegetation communities by Etherington (1981) of these so-called calcareous heaths reveals a number of interesting facts. All of the limestone heaths occur on loess-covered (loess is a wind blown deposit of fine-grained silt or clay associated with periods of glacial activity) surfaces which escaped the Devensian glaciation (the last glacial period, which ended approximately 12 000 years ago) and which preserve remains of highly weathered, possibly interglacial soils beneath the modern profile. Most chalk heaths occur on relatively deep and more acid soils than do the western limestone heaths. Chalk heath on loess is usually on plateaux or gentle slopes and its soils are more closely related to those found on Carboniferous Limestone plateau than to the shallow soils of limestone heaths.

Through a study of soil profiles associated with a range of so-called chalk and limestone heath plant communities, Etherington (1981) concluded that the calcifuge plant species of limestone heaths, particularly ericaceous species, are a relic of the vegetation which arose on deeper and more acid soils than those of the present day. On steep slopes on limestone and chalk, the original loess covering has been removed through soil erosion processes and hence many areas probably never supported a flora with calcifuge elements. Soil erosion has also taken place in areas where limestone-heath persists and it is likely that, despite increasing pH as acidic material was removed, some species, notably heather, have remained. Etherington suggests that heather, and other calcifuge species, in these situations reproduce vegetatively and individuals able to withstand higher pH have been preferentially selected over many years.

The possibility therefore exists that the limestone and chalk-heath vegetation of south-west England represents the remnants of communities that developed under different climatic and physical conditions to those of today. These communities are not re-creatable and their continued existence probably relies on a combination of burning and grazing in order to rejuvenate the calcifuge components of the flora.

5.2 Shales and mudstones

Shales and their metamorphic equivalents (Phyllites, slates or schists) are composed of the finest grade of clastic material, nearly pure clay, which has become compacted and indurated by pressure. The chemical composition of shale (roughly 40-50% silica, 40% aluminium oxide and water) offers very little in the way of essential nutrients for plants. Furthermore, their weathering characteristics and ability to form soils varies depending on the dip of the strata and the fissile nature of the rock itself. Given their high clastic content, it is no surprise that these rocks weather to produce soils of clay texture, with a high content of fine shaly rock fragments. They are inherently fertile, but prone to poor drainage. In areas of higher rainfall they become leached of nutrients and are mildly acidic.

In England shales (all of Palaeozoic age) outcrop and dominate in areas such as North Devon and North Cornwall (the Culm Measures) and the Lake District. Shale horizons also occur within parts of the Upper Carboniferous Coal Measures succession and outcrop throughout central and northern England.

The Culm Measures of North Devon and north-east Cornwall are named after the Carboniferous slates, shales and sandstones which underlie the area. These rocks give rise to heavy acidic soils, making farming difficult. Reflecting this and the oceanic climate, the predominant land use is grass production for livestock. Most of this is now intensive, but nevertheless the area still contains one of the greatest concentrations of species-rich grasslands remaining in the UK (known locally as Culm Grassland).

Purple moor grass and rush pastures occur on poorly drained, usually acidic soils in lowland areas of high rainfall in western Europe. In the UK, they are found in south-west England, particularly in Devon. Elsewhere in Europe they are particularly characteristic of the oceanic and sub-oceanic regions of the western seaboard, from Portugal to the Low Countries, extending eastward into central Europe.

Their vegetation, which has a distinct character, consists of various species-rich types of fen meadow and rush pasture. Purple moor grass *Molinia caerulea,* and rushes, especially sharp-flowered rush *Juncus acutiflorus*, are usually abundant. The characteristic plant communities often occur in a mosaic with one another, together with patches of wet heath, dry grassland, swamp and scrub. Key species associated with purple moor grass and rush pastures include: wavy St. Johns-wort *Hypericum undulatum,* whorled caraway *Carum verticillatum*, meadow thistle *Cirsium dissectum*, marsh hawk`s beard *Crepis paludosa*, greater butterfly orchid *Platanthera chlorantha* and marsh fritillary butterfly *Eurodryas aurinia*.

In Cumbria, heathland vegetation predominates on areas of outcrop of the acidic Borrowdale Volcanic Series and Skiddaw Slates, again reflecting the generally nutrient poor and thin nature of the soils. This vegetation is very extensive in a number of areas, notably the Buttermere Fells, Skiddaw Group, Amroth Fells and to a lesser extent Pillar and Ennerdale Fells. The principal vegetation community present comprises heather-bilberry heath, however at higher altitudes the subalpine NVC H18 community with wavy hair grass is present. Associated species include cowberry *V. vitis-idaea*, and locally bearberry *Arctostaphylos uva-ursi* and crowberry *Empetrum nigrum*.

Photo 5. An outcrop of Silurian slates in North Yorkshire, supporting acidic grassland in contrast to the surrounding vegetation of the Carboniferous Limestone.

Photo R.Cottle

A classic study of the so-called shale barrens (areas of sparse vegetation) of the mid-Appalachian Mountains in the eastern United States demonstrates an interesting link between rock type and vegetation cover (Platt 1951). Here, the fissile Barralier Shales outcrop among ridges of hard sandstone and are associated with three vegetation types: north-facing slopes with a good cover of trees, shrubs and herbs, talus slopes at the base of the barrens with a richly-wooded cover and the upper slopes and crests of the ridges dominated by the shale barrens. Analysis of physical parameters of the north or lower slopes and the barrens indicates that there are changes in soil properties, although the main difference and prime determinant in the floral differences between these areas relates to the physical nature of the barrens. In contrast to the vegetated slopes, the barrens have a thin mantle of shale rock fragments, which is unstable and can be relatively easily mobilised by weathering, human or animal activity. The steeper the slope, the more barren its appearance. Moisture and temperature are also key factors. Platt (1951) judged high insolation, and consequent rapid drying of the surface layer of the substrate, as prime conditioners of the barren habitat. Interestingly, the habitat is dominated by perennial vegetation, with only a few annuals, and notably woody plants are markedly stunted (the example is given by Platt of a 300 year old juniper that was only 4.5m high). The dominance of perennial vegetation reflects the fact that the relatively stressful conditions created by the physical nature of the substrate do not promote colonisation by annual plants. The shale barrens support eight endemic species, which have adapted to the harsh conditions (high light levels, thin soil and low competition levels), in comparison with the surrounding slopes and other substrate types. This edaphic adaptation and diversification is mirrored by species in the western United States that occur under similar conditions.

Mudstones, like shales are dominated by clay minerals and thus give rise to soils dominated by these minerals. The most widespread formation of rocks comprising mudstones in England is the Mercia Mudstone Group of rocks (Triassic), which typically comprises red mudstones, silty mudstones with local sandstone-siltstone developments. This group of rocks outcrops widely through east Devon, north Somerset, the west Midlands, North Yorkshire and Cleveland and also underlies much of northern, central and southern England and parts of Northern Ireland. Due to the diversity of the Group, a number of different soil types are associated with the outcrops, although neutral soils predominate. However, the dominance of clay minerals rock and its uncemented nature means that it weathers relatively easily to produce silty, clay-rich, often deep and generally poorly-draining soils.

In central England, pedunculate oak and ash woodland (National Vegetation Classification W8) is characteristic of the deeper soils on the Mercia Mudstone. However, in the majority of England, where this formation outcrops, the soils support arable and/or mixed farming and there is very limited evidence to suggest any influence by the rock type on vegetation.

Of particular interest is the occurrence of thick deposits of halite within the upper parts of the Mercia Mudstone succession. These deposits have been mined and exploited for many centuries in the production of salt, particularly in the west Midlands (eg Cheshire and Staffordshire). Where the salinity of soil and surface waters has been raised through anthropogenic activity and the natural seepage of brine-rich waters, vegetation more characteristic of saltmarsh communities has developed. Typically, in the UK, this vegetation corresponds to NVC types SM16 *Festuca rubra* salt-marsh community and SM23 *Spergularia marina – Puccinellia distans* saltmarsh community.

Inland salt meadows are a rare habitat type, having declined dramatically in the past 50 years in all areas where it occurs. The destruction of much of the natural habitat can be traced back to early salt-production activities. The only known remaining example in the UK of a natural salt spring with inland saltmarsh vegetation is Pasturefields Salt Marsh in the West Midlands. The vegetation consists of red fescue *Festuca rubra*, with common saltmarsh-grass *Puccinellia maritima*, lesser sea-spurrey *Spergularia marina*, saltmarsh rush *Juncus gerardii* and sea arrowgrass *Triglochin maritimum* in the most saline situations.

In southern England, notably northern Wiltshire, Oxfordshire and Buckinghamshire, extensive areas of the Oxford Clay and Kimmeridge Clay outcrop, giving rise to a variety of heavy, calcareous, clayey soils. These soils generally support pasture with some arable where soil conditions are lighter and drainage is better. Wetter areas are usually under grass ranging from ley grassland to unimproved pasture or meadows. Semi-natural grassland vegetation reflecting the generally poor-drainage and calcareous nature of the soils derived from the Oxford Clay is relatively rare, but include sites such as Otmoor in Oxfordshire. The grassland vegetation is typical of neutral to slightly calcareous soil types and corresponds to NVC communities typical of the meadow foxtail-great burnet *Alopecurus pratensis-Sanguisorba officinalis* flood plain community and the crested dog's tail-common knapweed *Cynosurus cristatus-Centaurea nigra* community. These community types are not restricted to soils derived from the Oxford and Kimmeridge clays, but are typical of clay-rich, heavy soils and are often associated with alluvial deposits in river valley floodplains.

Semi-natural woodland developed on Oxford clay is of the wet ash-maple woodland and pedunculate oak-ash-hazel (NVC: W10 and W16) types. Other tree species can include birch, hazel, hawthorn and occasionally hornbeam or holly. The ground flora often includes plants such as bluebell *Hyacinthoides non-scripta*, honeysuckle *Lonicera periclymenum*, wood anenome *Anenome nemorosa* and on ancient woodland sites, indicator species such as yellow archangel *Lamiastrum galeobdolon* and early purple-orchid *Orchis mascula*.

The other main clay outcrop in southern England belongs to that of the London Clay (Eocene, Tertiary). This formation gives rise to soil types similar to those of the Oxford Clay and, as a consequence, similar vegetation types predominate. Woodland vegetation is predominantly oak, with oak/ash on areas with more base-rich soils and a hazel and bluebell understorey/shrub layer.

In Kent and Hertfordshire, there are woodland stands of oak *Quercus* spp. with some hornbeam *Carpinus betulus* on the London Clay that are considered closer to this central European habitat type than its Atlantic counterpart (mainly mixed Atlantic bluebell-oak forests). Bluebell, which is most abundant in Atlantic parts of Europe including the UK, is unusually rare in this woodland habitat type. Typical species include great wood-rush *Luzula sylvatica*, hairy wood-rush *L. pilosa* and, locally, southern wood-rush *L. forsteri*, with greater stitchwort *Stellaria holostea*, ivy *Hedera helix* and honeysuckle *Lonicera periclymenum*. Stands fall within NVC type W10 *Quercus robur – Pteridium aquilinum – Rubus fruticosus* community.

At Blean in south-east England, hornbeam *Carpinus betulus* coppice occurs interspersed with sessile oak *Quercus petraea* (which is more commonly associated with western and northern Britain), pedunculate oak *Quercus robur* stands and introduced sweet chestnut *Castanea sativa*. The stands have traditionally been managed as coppice, and are one of the British strongholds for the heath fritillary butterfly *Mellicta athalea*. A similar type of vegetation occurs over London Clay at Wormley Hoddesdonpark Woods in Hertfordshire, where large stands of almost pure hornbeam *Carpinus betulus* (former coppice), with sessile oak. Locally, a bryophyte community more typical of continental Europe occurs, including the mosses *Dicranum montanum*, *D. flagellare* and *D. tauricum*.

This type of hornbeam woodland is predominantly a central European habitat type with its core centred on the better quality brown earth soils in the sub-Atlantic region that includes much of Germany, south Scandinavia, the low countries, and western parts of France and Austria. Its association, in England, with the London Clay is interesting and perhaps reflects some, as of yet, undescribed factors which promote the growth of both sessile oak and hornbeam in preference to pedunculate oak. It is notable that the soil conditions at Blean are described as slightly acidic and that the London Clay at Wormley-Hoddesdonpark is overlain in areas by Tertiary gravels, which may have led to leaching of nutrients from surface layers and the development of more acidic conditions.

5.3 Sandstones

Typically, the floras of sandstones are not particularly unique, their soils usually being zonal and reflecting regional climatic conditions rather than other physical parameters (Kruckeberg 2002). Only when sandstone forms prominent landforms does the flora take on any special or endemic character and it is then isolation and structure (eg sandstone inselbergs) that become the critical factors in ecological differentiation. However, chemical variation (eg $CaC0_3$ content) between sandstone formations does play part a role in influencing vegetation characteristics at a local level.

One such example, demonstrating the ecological control of sandstone geology is provided by a study of the Elbe sandstones of the Czech Republic and comparison with other sandstone regions in the area (Härtel 2002). This work established, as with other ecological studies, that the distribution of the native flora is related to a number of variables including geology, geomorphology, macroclimate and altitude. With respect to the geology, there are sharp interfaces between rich floras on calcareous sandstones and less diverse, but more specific floras on acidic sandstones. The natural vegetation of the Elbe Sandstones is dominated by acidophilous beech forests with pine and oak-pine forests. In comparison to other sandstone regions in the Bohemian Cretaceous basin, the Elbe Sandstones show the strongest oceanic influence and submontane character, while other sandstone areas are influenced by more continental and montane conditions which is reflected by their constituent vegetation.

One interesting aspect of the control of sandstones on vegetation at the landscape-level relates to their water-permeability and the effect that this has on geomorphology and plant succession. Since sandstones are generally water-permeable, rainfall water tends to soak through the rock instead of flowing horizontally on the soil surface or at the soil/bedrock transition. As a result, horizontal transport of matter by water is reduced and the resulting landscape is often a mosaic of cliffs, deep valleys or gorges and steep slopes (Herben 2002). This strong vertical differentiation accounts for the observed mesoclimatic differentiation and other features of sandstones. In addition to this, it underlies dynamic transport processes that strongly affect vegetation in sandstone regions. A number of processes are at work in this situation:

The vertical differentiation accounts for disturbance (erosion/sedimentation) dynamics that periodically rejuvenates vegetation on slopes and at the bottoms of the valleys. As a result, the sandstone vegetation may comprise a mosaic of patches of different successional stages. This acts as a strong selective force on plant species/communities, with species characteristic of disturbed ground conditions particularly dominating towards valley bottoms. Active slope processes lead to the creation of specific habitats (namely talus cones) due to the transport of rock debris from cliffs and gorge sides. Due to the relative constancy of the processes that generate them, the talus cones are recurrent structures that may bear specific biota. As a result of transport processes, organic matter (eg litter, moss carpets etc.) is often distributed over the cliff-valley base gradient; with material carried away from cliffs to the valley bottoms. This may play an important role in the support of certain vegetation types as the sandstone bedrock is often very poor in nutrients and valley bottoms are typically more nutrient-rich than the denuded areas on cliffs.

Herben (2002) makes the point that all of these processes are essential in determining the distribution and extent of the typical vegetation types within sandstone regions and that the conservation of the characteristic habitats should also include consideration of the maintenance of these processes.

In England, there are no extensive outcrops of sandstone, but a diversity of sandstone types of differing ages ranging from the Old Red Sandstone (Devonian) of south-west England, Millstone Grit (Upper Carboniferous) of northern England, Permian-Triassic New Red Sandstone of the Midlands through to the younger, Cretaceous sandstones of southern England (eg Horsham Sandstone of Wealden age). Although dominated by silica, the chemistry of these rocks is variable, particularly with respect to $CaCO_3$ content, and these differences in chemistry may have an influence on soil attributes and, in turn, vegetation characteristics.

The permeable nature of sandstones and their tendency to weather into silica rich granular deposits leads to the production of free-draining soils. For example, in the Mendip Hills of Somerset, the Old Red Sandstone outcrops on the Carboniferous Limestone plateau support a distinct and different vegetation type due to the formation of freely-draining acidic soils which, in the higher areas, have formed podsols, largely devoid of minerals and organic matter. Similarly, outcrops of the Permo-Triassic sandstones of the West Midlands (Sherwood Sandstone) have given rise to brown earths and podzols. In some areas, these free-draining soils support heathland vegetation and coniferous plantations (eg Cannock Chase), while in others the vegetation has been cleared and arable farmland predominates.

The association of heathland, or vegetation types characteristic of acidic soil conditions, occurs in conjunction with many sandstone outcrops across England, from those described above to those forming outcrops in more upland areas eg the Millstone Grit (Upper Carboniferous) of the Peak District or the Fell Sandstone (Carboniferous) of Northumberland. This relationship is invariably related to the porous nature of the soils derived from these rocks and, through leaching, the loss of soil nutrients and calcareous material (if present). The type of semi-natural vegetation that predominates is also heavily influenced by climatic and topographic factors (eg the ravine/plateau system discussed earlier in this section). Thus, in areas of higher rainfall, such as the Dark Peak of Derbyshire, grassland dominated by purple moor-grass *Molinia caerulea* and wavy hair grass occurs on the Millstone Grit or extensive blanket bog and peat deposits may be present in areas where waterlogging occurs and these support a vegetation dominated by cotton grass *Eriophorum vaginatum* and bilberry *Vaccinium myrtillus*.

The presence of acid loving vegetation such as species of heather and the development of heathland-moorland vegetation communities and sandstone outcrop is not an exclusive linkage. These vegetation types are also representative of igneous rocks such as granite and gabbro, sands and gravels and, in certain instances, limestones and chalk. The common factor with all of these rock/vegetation interactions is that of free-draining, often thin soils which are nutrient poor and acidic in character. Thus, the presence of these vegetation communities will often provide an indication of soil properties rather than rock type.

As mentioned earlier, the differential chemistry of some sandstones may lead to the development of vegetation types which are atypical of those normally associated with these rocks. These differences can be observed in the Cretaceous sands and sandstones of south-east England. In the Wealden district of East and West Sussex, outcrops of the Lower Greensand and Upper Greensand generally lead to the production of free-draining acidic soils. As an example, the coarse-grained, uncemented and porous sands of the Folkestone Beds (Lower Cretaceous) form a broad escarpment in the area and are often associated with tracts of heath and commons and oak and birch woodland associated with former heath. However, the most elevated and steeply undulating relief of the Wealden Greensand area is formed by the more resistant and calcareous-rich sandstone of the Hythe Beds (known locally as ragstone) which forms the main part of the escarpment. The Hythe beds, in contrast to the other sandstone outcrops of the area, support lime-tolerant plant communities in areas where the $CaCO_3$ content of the soil formed from the sandstone is relatively high. Similarly, in East Hampshire, part of the Upper Greensand succession comprises a relatively hard calcareous sandstone known locally as malmstone. This hard band of rock forms a raised tract of land running north-south about 2km wide and 20km long between Woolmer and Petersfield deeply cut by many small stream valleys, falling away as an escarpment along its eastern edge. The lime-rich nature of the substrate gives rise to an unusual woodland type for this rock formation, dominated by ash with a field maple *Acer campestre* and hazel *Corylus avellana* understorey and dog's mercury forming the main component of the ground vegetation. The hardness of the malmstone has also led to the formation of natural rock exposures within the woodland which support many specialised mosses and liverworts characteristic of calcareous substrates (eg *Tortula marginata* and *Chiloscyphus pallescens* and the nationally scarce moss *Rhynchostegiella curviseta*).

5.4 Sands and gravels

Sandy dominated deposits occur widely throughout England and generally support distinctive plant and animal communities. Sands, largely of marine origin, are associated with the Mesozoic and Tertiary periods and outcrop in southern and central England. There are also significant deposits of sand covering natural bedrock derived from erosion and weathering during the advances and retreats of the Pleistocene ice sheets (eg the Breckland district of Norfolk and Suffolk).

Sandy soils generally have a high proportion of quartz grains and very low clay and silt contents. Typically they tend to be nutrient-poor due to leaching, in solution, of nutrients, as a result of their high porosity. Where soils are thin or developed over sands, this nutrient impoverishment is likely to be significant, leading to podsol formation. Sandy soils are often deficient in copper, due to low copper concentrations in quartz and other silica-rich mineral or rock fragments and the poor ability of these soils to retain any copper from other sources owing to their low sorbtive capacity. Low copper levels within the substrate may influence plant growth and its deficiency can be an issue with respect to agricultural crops grown on sandy soils.

One of the most characteristic vegetation types associated with sands and gravels is lowland heath. The occurrence of heathland vegetation in England represents the interaction between a number of influential factors. The restriction of lowland heaths to the extreme north-west of Europe gives an immediate indication that climate has a role in the development of the characteristic vegetation communities. However, it is also apparent that developmental history and, in particular, human management has played a key role in the development and maintenance of this habitat type. It is apparent though that geology does play a crucial role in controlling the physical parameters that influence the establishment of specific plant assemblages, which then may become modified through human intervention to form heathland. Many of the major heathland complexes in southern England are on geological formations such as the Bagshot Sands or the Lower Greensand, which are typically free-draining and liable to rapid leaching, with soils derived from the Lower Greensand usually being very poor in nutrients at the outset. It is also important to note that heathland vegetation also occurs on rocks that are not only poor as a source of nutrients but which also weather very slowly, as in the case of granite and gneiss.

In the Brecks, heathland vegetation (including grass heath) has developed on blown sand overlying chalk and glacial deposits. The origin of the sand has been debated but is now thought to be of ancient maritime origin from the time when the Wash was more extensive. The area is the driest in Britain (averaging as low as 55 cm per year) and has a relatively 'continental' climate, often hot in summer but cold in winter and with frosts extending into late spring and early summer. Despite the low rainfall, podsolisation occurs on the deeper sands. This leads to nutrient loss and creates the conditions suitable for the establishment of heathland vegetation. The dry acidic heath of Breckland represents the NVC H1 Heather *Calluna vulgaris* – Sheeps Fescue *Festuca ovina* heath and in some areas the presence of almost pure sand has led to the establishment of a sand sedge-dominated *Carex arenaria* sub-community, which is a very unusual feature of this location. The highly variable soils of Breckland, with underlying chalk being largely covered with wind-blown sands, have resulted in mosaics of heather-dominated heathland, acidic grassland and calcareous grassland that are unlike those of any other areas. In many places there is a linear or patterned distribution of heath and grassland, arising from fossilised soil patterns that formed under periglacial conditions. The uniqueness of the area, largely attributed to both the geological origin of the surficial deposits and climatic conditions, is also reflected by the presence of a significant number of rare plants, such as perennial knawel *Scleranthus perennis* ssp. *prostratus*, purple stemmed cat's tail grass *Phleum pheloides* and rare invertebrates.

Photo 6. Breckland heath and acid grassland vegetation, Thetford Heath
Photo English Nature

This area of heathland demonstrates the spectrum of occurrence of this vegetation type across England and clearly demonstrates that climatic differentials between east and west (ie rainfall), although playing a significant role in the development of heathland vegetation are perhaps not as important as the soil forming substrate. It would appear that it is the formation of nutrient-poor, thin soils that is the main controlling factor on the potential distribution of heath (ie it can occur across a range of rock types that produce such soils).

Gravel deposits are similar to sands in their characteristics and due to their high permeability also generally give rise to nutrient impoverished surface soils. As a consequence the vegetation associated with these deposits is similar to that of sands and sand dominated rock types. Gravel deposits on the coast support a unique vegetation and fauna adapted to the predominantly dry and saline influenced conditions. This combination of factors and the importance of dynamic processes in the formation and maintenance of these shingle deposits is discussed in Section 10.

5.5 Drift and glacially derived deposits

In many parts of England the bedrock is masked by extensive deposits of clays, sands and gravels derived from glacial activity and alluvium associated with river and estuary floodplains. Thus, in these areas, any influence that the *in situ* geology may have on plant and animal communities will have been modified or potentially absent. This is particularly the case where drift deposits are of a significant thickness. In effect, therefore, it is the general characteristics of the soils derived from these drift deposits that strongly influence vegetation type and in some situations communities have developed which do not bear a resemblance to those associated with the underlying and *in situ* rocks.

These superficial sediments include marine alluvium, which is normally clay or silty in texture and forms raw gley or stagnogley soils, river alluvium that varies enormously in texture and will form either brown soils or groundwater gleys and wind-blown sands that give rise to terrestrial raw soils or brown soils Glacial deposits are most likely to form stagnogleys due to their high clay content, but areas with coarser textured materials will form brown soils. Sands and gravels from former glacial meltwater streams are likely to produce brown soils in lower rainfall areas or podzols where the rainfall, and consequently leaching, is higher. However, the drainage patterns around glacial deposits may override this prediction.

In many respects, the types of vegetation and associated fauna found in connection with drift deposits mirror those of similar rock types from which these sediments were originally derived. Thus, the communities of the extensive boulder clays of the Midlands, East Anglia and parts of Northern England are similar to those of mudstones and clays where these outcrop naturally. The same is also true of sands and gravels of glacial origin, as the properties of these deposits are very similar to the soils derived from much older and *in situ* sandstones and gravels (eg the Tertiary sands of the Hampshire Basin and the windblown sands of the Brecks both support acid grassland and heath vegetation). Although it is the surface deposits which greatly influence the characteristic vegetation type, it is likely that the *in situ* bedrock has some influence, albeit that this may be subtle. Certainly in areas of glacial activity a significant component of the boulder clay (which largely produces soils of neutral pH) may comprise of rock fragments derived from the underlying bedrock. Soil attributes, such as pH and permeability may therefore be modified in locations where the bedrock significantly contributes to the makeup of the boulder clay or the deposit is relatively thin. This is the case over much of East Anglia, where the thick boulder clay deposits left by the

Anglian ice sheet contain a large amount of chalk derived from the underlying bedrock. Typically in areas of chalk boulder clay deposits the dominant (climax) vegetation is ash-field maple woodland (NVC 8) with a diverse understorey including hazel, dog's mercury and sweet wood ruff *Galium odorata.* In parts of Suffolk and Essex, small areas of woodland on the boulder clay are of national importance for the rare Oxlip *Primula elatior*.

The influence of glacial deposits on the landscape and vegetation communities is more prevalent in some areas and complex suites of sediments may be present reflecting the variety of depositional environments that existed during the Pleistocene.

Some areas have a more distinctive character due to the shaping of the landscape under glacial and periglacial conditions and the deposits left behind. Such an area is the Humberhead Levels, which occupies the area of the former pro-glacial Lake Humber. The character of this area is derived from this glacial impoundment and the alluvial sediments that now indicate the former position of the lake. Much of the area is extremely low-lying, with some areas lying at or below the mean high water mark and includes the broad floodplains of several major rivers, which drain to the Humber. The flat or gently undulating landscape is formed by and strongly influenced by drift deposits which overlie bedrock of Triassic Mercia Mudstones. During the last glaciation (the Devensian glaciation), a glacier extended south across this area, reaching almost as far as Doncaster. The main glacial front was, however, at Escrick, where it deposited a ridge of till, sand and gravel known as the Escrick Moraine.

The Escrick Moraine marks the northern limit of the extensive Lake Humber which was impounded by the blocking of the Humber gap by another ice front between Brough and Winterton to the east. Later, this lake was filled with sediment, predominantly in the form of laminated clays up to 20 metres thick. These create wet, gleyed soils, locally overlain by peat forming the important raised mires of the area. There are also extensive modern floodplain deposits and local deposits of wind-blown sand, which create more free-draining sandy brown earths. These latter soils are acidic in character and commonly support birch and oak woodland, heathland, or conifer plantations.

The complexity and variability of soil conditions derived from glacial deposits is also neatly illustrated by the gently rolling plain that occupies part of Shropshire, Cheshire and Staffordshire between the valley of the Mersey, the Shropshire Hills and the foothills of the Pennines to the north-east. The character of the Plain owes much to its glacial origins. Clay, sand, gravel and pebble beds all owe their occurrence and distribution to glacial activity and retreat.

Much of the Plain is gently rolling, with only gentle changes in elevation between 20 and 50m. The Plain is formed from Triassic sandstones and marls, but these are overlain by glacial deposits, largely consisting of boulder clay, with local deposits of silt, peat, sand and gravels. Glacial activity has affected the whole Plain, rounding off the hard outcrops of sandstone, creating meltwater channels, lake beds and depositing a variety of materials, from boulder clay, to marls, sands and gravels. These deposits have in places caused the formation of a number of shallow meres, some peat-filled, and mosses. Depressions within the morainic deposits form the remarkable series of meres at Ellesmere, whilst the largest mosses, at Weald Moor and Whixall Moor, are on a complex mix of sands, gravels, silts and peats. Thus, within a relatively small area (eg North Shropshire) one can move from the waterlogged peats and mire vegetation of places such as Fenn's and Whixall Moss to the heathland vegetation of sites such as Prees Heath. These relatively rapid and distinct variations in vegetation communities and habitat types have very little to do with the influence of underlying bedrock but are intimately associated with and mediated by the complex nature of the overlying glacially derived and deposited sediments.

6. Igneous rocks

By and large, igneous rock types possess discernible chemical and physical differences to sedimentary rocks, which are attributable to their formational history (see Section 3 for details). The key components that differ are their overall chemistry and hardness in comparison with the majority of sedimentary rocks. This is reflected in their lower calcareous mineral content, which in turn is a major influence on the general vegetational types (ie calcifuge) which these rocks support. The formation of igneous rocks also leads to some very specific mineralogical compositions and chemistry which in turn have specific effects upon plant communities that are adapted to the characteristic chemistry of the soils derived from these rocks. Examples of these are provided in the following section.

Igneous rocks of the quartz-feldspar mineral type weather to become more or less "normal" soils; and their physical and chemical properties do not deviate in the direction of extreme values. As such, soils derived from quartz-feldspar bearing rocks like granite or basalt tend to reflect the climate under which they were formed (known as zonal, or climate-derived soils). Any significant variations in soils formed from these rocks are therefore considered to represent the product of climatic variability (Kruckeberg 2002).

Basic igneous rocks (basalts and basic volcanic ashes) contain more minerals that act as nutrients for vegetation and weather faster and so produce more fertile soils than granites, rhyolites or acid volcanic ashes. However, volcanic rocks vary so much in terms of their chemistry (rhyolite, andesite, basalt) and texture (crystalline lava, volcanic ash, pumice etc.) that it is impossible to generalise about soil formation. Some volcanic rocks are hard and crystalline and so weather only very slowly, meaning that soil formation is extremely restricted, and in these instances soils probably owe more to superficial sediments (eg glacial or fluvioglacial deposits) than to the solid rock in many cases.

Where the effects on flora and vegetation of igneous parent material are most pronounced are with rock of mafic to ultramafic mineral content (ie those rocks containing high concentrations of magnesium and iron). Mafic rocks like gabbro and some basalts can weather to form soils which have a selective influence upon plants.

The most striking illustrations of unique floras associated with igneous rocks are those found on outcrops of dunite and peridotite, both ultramafic rocks (Brooks 1987, Kruckeberg 1985). Several authors considering the relationships between ultramafic rocks and their floras have also noted that there are strong similarities with their metamorphic counterpart, serpentinite. This is partly due to the fact that many ultramafic outcrops are partly serpentinized and igneous and metamorphic rocks are often closely associated both in space and in their soil and topographic forming properties. Thus, instances of purely igneous occurrences of ultramafic rocks tend to be relatively uncommon. One striking example, however, is Dun Mountain on South Island of New Zealand which is formed from Dunite, a rock of nearly pure olivine and chromite. The mountain supports an open scrub vegetation which contrasts with the dense southern beech *Nothofagus* forest that surrounds it, and which is present on non-ultramafic rocks. The unique vegetation type of Dun Mountain also supports several endemic species of plant (Brooks 1987).

In New Caledonia, the situation is even more extreme. Up to one third of this island is formed from ultramafic rocks, notably a form of peridotite known as harzburgite. New Caledonia is noted for its endemic flora, but what is interesting is that of the 1500 species of vascular plant, 60% of them are endemic to the island's peridotite outcrops. A notable feature of the New Caledonia flora is the high incidence of nickel hyperaccumulating species, which represents an adaptation to the high nickel levels found in the peridotite.

For the less mafic igneous rock types, such as gabbro, it is apparent that there is still some control over vegetation growth and community composition. One example is the flora of the Pine Hills, in El Dorado County, California. Here, eight rare plant species occur, three of which (the Pine Hill ceanothus *Ceanothus roderickii,* Bisbee Peak rush-rose *Helianthemum suffrutescens* and Stebbins' morning-glory *Calystegia stebbinsii*) are endemic to the Pine Hill region. Another two species are almost restricted to the area, with only a few small colonies of the plants found elsewhere. This assemblage of rare species is part of a unique plant community confined to soils known as the Rescue soils series. These soils are associated with the broader classification of gabbro soils, which have unusual properties derived from the underlying gabbro intrusion forming the Pine Hills. The soils are generally red, mildly acidic, rich in iron and magnesium, and often contain other heavy metals such as chromium.

Whittaker (1960), provides a description of the vegetational differences between vegetation on diorite and olivine gabbro in the Klamath Mountains along the Oregon-California border in the western United States. Here the term "mixed evergreen forest" can be applied to the vegetation of both rock types at low elevations. Apart from the overall general structural similarity and the sharing of some species, however, the two vegetation patterns are quite different. On the gabbro the vegetation is much more open and Whittaker found that the average densities of large stems of conifers were less than half that found on diorite. Furthermore, he also recorded that while the main canopy species were similar the composition of the shrub and herb layers differed significantly.

Other base rich igneous rock types include finely crystalline basalt and more coarsely crystalline dolerite. In the UK, these rock types support some floristically unusual communities (Hopkins 2003). For example, on the Roman Wall, Northumberland, where rock rose *Helianthemum nummularium* and wild chives *Allium schoenoprasum* can be found growing with mat grass *Nardus stricta* and tormentil *Potentilla erecta* on basalt and dolerite. At Low Force in Upper Teesdale, dolerite supports rank grassland and open scrub containing lime associated plants such as blue moor grass *Sesleria albicans,* rock rose *Helianthemum nummularium* and northern bedstraw *Gallium boreale,* as well as shrubby cinquefoil *Potentilla fruticosa* and tormentil.

There is a significant number of rare and local species which, although not confined to a single igneous rock type, can be seen to occur with surprisingly high frequency on igneous rocks. Thyme broom-rape *Orobanche rubra* is a parasite of thyme *Thymus praecox*, a widespread and relatively common host species, but its main locality in Britain is on The Lizard (on serpentine, see Section 7) and on igneous rocks of the Glens of Antrim (Hopkins 2003). Many igneous sites are remarkably rich in clovers, The Lizard hosts 23 of 25 British clovers and the Roman Wall in Northumberland is also rich in *Trifolium* species. Hopkins (2003) suggests that the reason for the distribution of these plants, and virtual restriction to igneous outcrops, may not be chemical and could be related to the fact that many of the plants are small and of low competitive ability, although tolerant of stress. As igneous rocks weather slowly to give shallow soils which are exposed to summer drought and winter frosts, it may be these physical features that are important in explaining the distribution of some species rather than the chemical characteristics of the derived soils.

The potential predominance of physical properties, rather than the specific chemistry of soils derived from igneous rocks, is also borne out from a quantitative analysis of the flora on basic igneous rocks in Scotland by Jarvis (1974). This study demonstrated the existence of three vegetation community types that could be distinguished on the basis of aspect and soil conditions (although there is considerable overlap between the communities). On rocks facing north and west is a community with goldenrod *Solidago virgaurea*, dog violet *Viola riviniana* and the moss *Dicranum scoparium*. South or west facing cliffs are characterised by wavy hair grass and the desiccation tolerant moss *Polytrichum piliferum*. In the third group, also on south-facing rock faces are sticky catchfly *Lychnis viscaria* and wall pennywort *Umbilicus rupestris*. Species such as harebell *Campanula rotundifolia* were found to occur within all three communities. This study demonstrates the complexity of relationships between aspects such as geology, soil type, relief and climate.

The granite intrusions of south-west England (eg Dartmoor, Bodmin) give rise to nutrient poor, acidic soils as a result of podsolisation. Generally podzols develop in colder wetter regions - whilst "brown earth" soils dominate the lowland areas of England and Wales for example. Leaching is greatly evident in podzols (where precipitation exceeds potential evapotranspiration). As rainwater passes downwards, clays, organic matter and calcareous material (if present) are broken down and eluviated from the surface layers to lower depths within the soil horizon. The top part of the soil profile is also made much more acidic due to 'replacement' with H^+ ions. Additionally, a thick layer of humus on the podsol surface can build up (Mor humus – formed as precipitation is greater than evapotranspiration) which is nutrient poor and acidic (pH 3.5-4.5) due to the removal of mineral ions by organic compounds percolating through the material. These surface conditions represent a combination between the distinctive geology, relief and climate of the area. The acidic substrates support heathland/moorland vegetation, which varies in its composition depending on drainage, rainfall and relief.

Wet heath predominates over much of Dartmoor and occurs over shallow peats or sandy soils (quartz-rich soils derived from the granite) where drainage is impeded. The vegetation is typically dominated by mixtures of cross-leaved heath *Erica tetralix*, heather *Calluna vulgaris*, grasses, sedges and *Sphagnum* bog-mosses. *Scirpus cespitosus – Erica* wet heath is found in areas with a moderate to high rainfall, and is the typical form of wet heath in the north and west of the UK. *E. tetralix* and *Calluna* are typically accompanied by abundant deergrass *Trichophorum cespitosum* and purple moor-grass *Molinia caerulea*.

In areas where waterlogging occurs (eg hollows, valley sides etc.), blanket bogs are present. The vegetation of these areas is similar to that of wet heath, with heather, cross-leaved heath and deergrass dominating, along with cottongrasses *Eriophorum* spp. and bog-mosses such as *Sphagnum papillosum*, *S. tenellum* and *S. capillifolium.* Purple moor-grass and bog-myrtle *Myrica gale* are also typical of the Dartmoor and other western bogs. The blanket bogs on Dartmoor are the southernmost in Europe. The main vegetation community is *Scirpus cespitosus – Eriophorum vaginatum* blanket mire, although many of the bogs are dominated by purple moor-grass and Sphagnum spp.

In drier areas, so-called upland heath is supported by the acidic soil conditions. Dartmoor is notable as it contains extensive areas of western gorse *Ulex gallii* – bristle bent *Agrostis curtisii* heath, a type most often found in the lowlands. *Calluna – Vaccinium* heath generally occupies the steeper, better-drained slopes, with *Ulex – Agrostis* heath occurring on the lower slopes of the moor. A number of predominantly northern species occur on the southern edge of their national range. Plants found on dry heaths that are rare in south-west England include crowberry *Empetrum nigrum* and stag's-horn clubmoss *Lycopodium clavatum*.

The examples provide above tend to confirm the general picture of the influence of igneous rocks on vegetation in that it is only those rocks with a characteristic and specific chemistry that tend to support distinct communities. For rocks such as granite, the weathering and physical soil formation process along with climate probably play a much greater role in determining the nature of the vegetation rather than any specific chemical characteristic of the rock itself. In this respect, it is notable that granite and other similar quartz-feldspar igneous rocks support vegetation of a similar nature to sands and gravels and other rock formations that give rise to free-draining soils prone to podsolisation.

7. Metamorphic rocks

7.1 Introduction

Due to the fact that metamorphic rocks have been produced through the modification (via heat and pressure) of sedimentary, igneous and other metamorphic rocks their chemistry and structure is different to that of the parent rock. The difference in character between the parent rock and the resulting metamorphosed state varies depending on the nature of the temperature and pressure to which they have been subjected. Suffice to say though, that due to the huge diversity of parent material and the scale and type of metamorphism the resulting characteristics of metamorphic rocks are extremely diverse. Generally, however, the high temperatures and pressures associated with metamorphism leads to rocks becoming more crystalline, harder and therefore more resistant to weathering.

There are two main types of metamorphism; regional metamorphism and contact metamorphism. The former of these can occur over a wide area and is usually associated with episodes of mountain-building. The heat and pressure generated during the rock deformation process leads to the formation of significant tracts of particular rock types with their own crystalline and mineralogical characteristics. Contact metamorphism is much more localised and is often associated with the local emplacement of igneous bodies (eg dykes) and or the flow of lavas. In this case the influence on local landforms, habitats and vegetation may be locally significant, perhaps because of the relatively small-scale (in comparison with regional metamorphism) and abrupt nature of transitions between non-metamorphosed and metamorphosed states.

7.2 Serpentine

Serpentine is broadly used as a term to describe the rocks, minerals and soil associated with metamorphosed ultramafic rocks (eg peridotite, dunite and gabbro) that contain constituent minerals of the serpentine mineral family (lizardite, antigorite and chrysotile). A rock comprising serpentine minerals is known as serpentinite.

Soils derived from serpentine-rich rocks are widely distributed over the earth's surface and have attracted the attention of plant ecologists for many years because a distinct vegetation variant is correlated with it. Serpentines are parent materials in which: (a) iron and magnesium are high relative to silicon; (b) calcium is low relative to magnesium; (c) phosphorus, potassium and molybdenum may also be low; (d) nickel, chromium, manganese and cobalt may be present in high, even phytotoxic, amounts. A wide range of soil types arise from serpentine minerals, dependent upon detail of parent material, weathering regime, relief and biological processes. Many serpentine soils are shallow and stony, whereas others may be deep with poor internal drainage.

High levels of magnesium in the soil block a plant's ability to take in soil nutrients, especially calcium. Because they are often shallow and low in organic material and clay, serpentine soils also cannot hold water or nutrients particularly well. To live in dry, magnesium-rich, nutrient-poor, and, in some cases, toxic soils, most serpentine plants have developed special adaptations in form or internal chemistry. Some plants are extra-efficient at absorbing calcium, which offsets the negative effects of magnesium. In addition, the mineralogical and equilibrium conditions have made serpentine rocks highly erodible under normal atmospheric conditions. The montmorillonite clays formed by the minerals adsorb more water than many other clay surfaces, thus reducing available water to plants. All of these factors reduce the ability of plants to adapt to serpentine soil habitats and has led to the development of a highly specialised flora that is able to tolerate the unusual chemical and physical conditions.

Kruckeberg (2002) suggests that the vegetational contrast between serpentine and non-serpentine landscapes can be viewed as a consequence of difference in landform and community structure, morphological terms and species composition. Variations in morphology, including foliage adapted to arid conditions, reduction in stature, increase in root systems, are known as serpentinomorphoses. Serpentine floras also tend to have a greater diversity than non serpentine floras. The taxonomic attributes of serpentine floras include narrowly endemic species wholly restricted to a local or regional outcrop, ranges of non serpentine taxa extending as disjuncts or outliers on serpentine soils, indifferent taxa which range widely on and off serpentine, and excluded taxa – those species adjacent to non-serpentine substrates that faithfully avoid serpentine.

As mentioned previously, serpentines and other ultrabasic rocks occur widely around the world, most often near the edge of tectonic plates, as for example in California and in the rift valley of Africa. In the United States, serpentine soil habitats occur in areas that have been geologically active, particularly where plate tectonics has occurred and uplifting of altered peridotites has exposed these formations (Brooks 1987; Coleman and Jove 1992). In western North America, serpentine soil habitats occur along fault zones in the Central and North Coast and Cascade ranges near the subduction contact of the Pacific plate with the North American plate. Western Sierra Nevadan serpentine habitats are associated with the uplifting of the Sierran batholith and regions of vulcanism. Serpentine habitats in western North America occur from sea-level to an elevation of 2900 m. In eastern North America, serpentine habitats occur in the states of Alabama, Georgia, South and North Carolina, Virginia, Maryland, New Jersey, Pennsylvania, New York, Massachusetts and Vermont and in Quebec and Newfoundland in Canada (Roberts 1992).

Vegetation types occurring in serpentine soil habitats include grasslands, chaparral, woodlands and forest. Also, in some areas there are extensive serpentine habitats referred to as serpentine barrens, which are sparsely vegetated by annual and perennial herbaceous plant species. Serpentine chaparral vegetation is restricted to the western U.S.A., primarily in California. The dominant plant species include *Quercus durata* and *Arctostaphylos viscida*. These two species often occur in nearly pure stands; however, mixtures of these and other species occur in habitat gradients where other *Arctostaphylos* species may occur with *Garrya congdonii*, *Rhamnus californica* and several species of *Ceanothus* (McCarten and Rogers 1991).

In the U.S.A., forests on serpentine soils are extremely uncommon due to the low nutrient levels in the soil. However, some areas do have higher density vegetation particularly montane areas with higher rainfall such as the Cascade Mountains in northern California and southern Oregon. In these areas *Pinus jeffreyi* and *P. sabiniana* form patchy forested areas. These forests are often interrupted by open areas of serpentine barrens. These barrens are recognised as a major habitat in serpentine areas throughout the world (Kruckeberg 1984, Brooks 1987). The areas are often exposed areas with dramatic changes in topography such as steep, high erodible slopes. The serpentine barrens are often areas where high concentrations of toxic heavy metals occur in the serpentine minerals. Extensive studies have been conducted on plants adapted to these serpentine barrens (Kruckeberg 1985; Brooks 1987; Baker, Proctor and Reeves 1992).

The occurrence of serpentinized rocks in the UK is quite restricted, with the main and most well known outcrop being the serpentinized peridotite of the Lizard ophiolite complex of south-western Cornwall. This group of rocks represents part of the oceanic crust of mid-late Devonian age. Not only is the geology of the area particularly complex, but its associated ecology, through the development of characteristic soils, is also variable and complicated.

Much of the Lizard plateau is underlain by serpentine and where semi-natural habitats predominate the vegetation of the area is described as heathland, although an unusual mixture of species occurs (Hopkins 1983). Well-drained serpentine soils support *Erica vagans - Ulex europaeus* heath (Rodwell 1991b), in which the rare Cornish heath *Erica vagans* is the most abundant heather. Associated species include a range of plants typical of dry acid heath, such as common heather, bell heather *Erica cinerea*, tormentil, western gorse *Ulex gallii* and common gorse *U. europaeus*. However, what makes the vegetation communities unusual is the presence of typical calcicole species such as abundant common dropwort *Filipendula vulgaris*, bloody crane's bill *Geranium sanguineum* and ploughman's spikenard *Serratula tinctoria (*Hopkins 2003). On the main part of the Lizard plateau there are extensive seasonally flooded areas within the heathland. Here cornish heath dominates with abundant black bog rush *Schoenus nigricans*. A range of acid, wet heath species are found in these heathland areas including common heather and cross leaved heath *Erica tetralix*, but as with the dry heath there are also a number of associated species more typical of calcareous or neutral soils including great burnet *Sanguisorba officinalis,* fragrant orchid *Gymnadenia conopsea* and dyer's greenweed *Genista tinctoria.*

Photo 7. Heathland vegetation with gorse and heather. The Lizard, Cornwall.

Photo English Nature

The ecological basis of these unusual species mixtures has not been explored in detail, but it is possible that some of the species found on the Lizard may have evolved local genetic adaptations to the unusual conditions. Hopkins (1983) shows that the acid loving species found on serpentine are capable of growing on base rich soils but postulates that they are absent from calcium rich soils because of intolerance of calcium, not pH level.

Hopkins (2003) also notes that there are other plants which show abnormal ecological relationships on The Lizard. These include a number of coastal specialists such as Sea rush *Juncus maritimus,* which is almost universally a plant of the upper saltmarsh, which grows in the wettest areas of inland serpentine heath. Other maritime species such as spring squill *Scilla verna*, thrift *Armeria maritima* and sea campion *Silene uniflora* occur well away from the influence of salt spray on serpentine outcrops in the central parts of The Lizard. The presence of these species away from the immediate coast could reflect the chemical similarities between seawater and serpentine soil, both of which have a high magnesium content (Hopkins 1983).

7.3 Other metamorphic rocks

It would appear that there has been very limited study of the vegetation and fauna associated with other metamorphic rock types, although it is likely that associations and linkages occur. As the magnitude of difference between source rock and its metamorphosed counterpart varies quite considerably, so do differences in aspects such as weathering and soil formation. Thus, there may be little detectable differences in soil and vegetation between granite and its metamorphic counterpart gneiss, but there are distinct differences in soils and vegetation between hydrothermally altered andesite and unaltered andesite. Billings (1950) provides the example of local hydrothermal areas in the Great Basin of western North America where altered areas support stands of Jeffrey pine *Pinus jeffreyi* and ponderosa pine *Pinus ponderosa*, wholly surrounded by sagebrush *Artemisia tridentata* on nearby normal andesite rock. These areas thus represent "conifer islands" in a "sea" of sagebrush. The difference between the areas is probably due to the rapid weathering of the hydrothermally altered andesite in the presence of sulphuric acid and the production of an acid soil.

The characteristics of slates and phyllites (metamorphosed mudstones) have been considered in Section 5.2. The vegetation associated with schists and gneiss (high grade metamorphic slates and mudstones) although often rich tends to be more influenced by climate. The diversity of some of the floras probably reflects the fact that these rocks are generally quite resistant to weathering (particularly gneiss) and often form areas of high relief thus increasing the potential for geographic isolation and leading to the formation of a diverse range of microclimatic conditions. The influence of the majority of other metamorphic rocks is similar, with climate probably having a greater influence than any soil derived properties. This probably reflects the situation that for the majority of igneous and sedimentary rocks there may be very limited chemical change between the original and metamorphosed states. Kruckeberg (2002) states the example of marble (metamorphosed limestone) which he cites as supporting a flora similar to that of limestone.

Perhaps the greatest difference between a source rock and its metamorphic counterpart is that the physical properties of metamorphic rocks may vary significantly in comparison. Thus, many metamorphic rock types are generally harder and more crystalline than their source rocks, although in some cases the imposition of foliate structure (eg the fissile bedding of slates) may make them more prone to weathering.

One classic example of the influence of a change in the physical properties of a rock, rather than its chemical composition, due to metamorphism is the so called "sugar limestone" of Upper Teesdale, County Durham (Hopkins 2003). Here the intrusion of the Whin Sill dolerite has caused a thin bed of limestone (the Robinson Limestone) to metamorphose into a coarsely crystalline marble. This rock weathers extremely slowly into a thin, drought prone soil with grain size and colour similar to granulated sugar (Clapham 1978). Small outcrops of this rock occur on Cronkley Fell and Widdybank Fell and support a short species rich grassland in which blue moor grass *Sesleria albicans* is a significant component, the so called Sesleria *albicans–Galium sterneri* grassland of Rodwell (1992), which includes two distinct sub-communities found only in Upper Teesdale. These grasslands support one of the richest assemblages of rare species in Britain, including spring gentian *Gentiana verna* and Teesdale pansy *Viola rupestris*. In places the grassland grades into flushes with a range of small sedges (eg *Carex pulicaris, C. hostiana, Kobresia simplisiusculata*), butterwort *Pinguicula vulgaris* and bird's-eye primrose *Primula farinosa*. Some of the more unusual communities occur where a series of streams or "sikes" occur. These water courses have weathered the limestone to hard crusts and unstable gravels, over which, in places, prominent hummocks of the mosses *Gymnostomum recurvirostrum* and C*atascopium nigritum* occur; this is the only British locality of Teesdale sandwort *Minuartia stricta*. These sugar limestones are rare but not unique and can also be found in Perthshire, although in Scotland it lacks such rich assemblages of rare species as are found in Upper Teesdale (Rodwell 1992).

The way in which such more local metamorphism has influenced biodiversity is little understood, but may be of widespread significance. For example at The Lizard some of the richest concentrations of rare species occur not on serpentine but in coastal valleys and sea cliffs on metamorphic schists (Hopkins 2003).

Moderately base-rich metamorphic (and igneous) rocks with a relatively high siliceous content may support species-rich grassland vegetation typified by the occurrence of matt grass *Nardus stricta*. The soils developed over these rocks have an acidic pH (<7.0 and mainly <6.0) and are derived from bedrock with at least some silica. The altitudinal range varies from near sea level to an upper limit of between 800m and 900 m. These grasslands are important because they support a wide range of species, including Atlantic, sub-Atlantic and arctic-alpine plants and invertebrates. Swards are closely grazed and consist of a complex mosaic of grasses, small herbs and bryophytes.

The vegetation is characterised by a mix of grasses, typically sheep's-fescue *Festuca ovina*, common bent *Agrostis capillaris*, sweet vernal-grass *Anthoxanthum odoratum*, mat-grass, red fescue *Festuca rubra*, heath grass *Danthonia decumbens* and wavy-hair grass. A wide range of small herbs, including heath bedstraw *Galium saxatile*, tormentil, common dog-violet *Viola riviniana*, wild thyme *Thymus polytrichus* and harebell occur. Herbs such as white clover *Trifolium repens*, field wood-rush *Luzula campestris*, heath speedwell *Veronica officinalis*, yarrow *Achillea millefolium*, mountain everlasting *Antennaria dioica*, bitter-vetch *Lathyrus linifolius*, field gentian *Gentianella campestris*, pill sedge *Carex pilulifera* and spring sedge *Carex caryophyllea* are characteristic of drier swards. At high altitudes, where the swards may be more flushed, the arctic-alpines yellow saxifrage *Saxifraga aizoides*, purple saxifrage *S. oppositifolia*, alpine meadow-rue *Thalictrum alpinum* and alpine bistort *Persicaria vivipara* may be frequent. Other arctic-alpines or northern species that are represented include lady's-mantle *Alchemilla filicaulis*, hair sedge *Carex capillaris*, rock sedge *C. rupestris*, alpine mouse-ear, globeflower and mountain pansy *Viola lutea*.

Another type of grassland vegetation, typical of the high mountain zone, and associated generally with metamorphic and volcanic rock sequences is siliceous alpine and boreal grassland, which represents one of the few predominantly near-natural habitats remaining in the UK. The habitat is the most extensive type of vegetation in the high mountain zone, ie above an altitude of about 750 m and characteristically forms large continuous tracts, covering summit plateaux and the tops of the higher summits and ridges. The habitat comprises a range of grassland types whose composition is influenced by contrasting extremes of exposure and snow-lie. The flora is characterised by a strong montane element which includes several uncommon vascular plants, mosses and liverworts. It is also the most important habitat for Eurasian dotterel *Charadrius morinellus*, Britain's only montane wading bird.

The most common grassland sub-type, stiff sedge *Carex bigelowii* – woolly fringe moss *Racomitrium languinosum* -heath, varies in species composition depending on the base-richness and instability of the substrate. On relatively stable and acid siliceous rocks, such as the Borrowdale Volcanics and Skiddaw Slates of the Lake District, the flora is typically species-poor, though a few cushion herbs occur locally, such as moss campion and thrift *Armeria maritima*. In the Lake District wavy hair-grass and sheep's fescue dominate the sward, with bilberry, woolly fringe-moss, stiff sedge, fir clubmoss *Huperzia selago* and lichens of the genus *Cladonia.*

Localised bands of base-rich rocks support a more varied flora, and a species-rich sub-community develops, supporting a number of rare or local montane plants. The flora of this species-rich moss-heath includes dwarf willow *Salix herbacea*, alpine lady's-mantle, moss campion, alpine bistort *Persicaria vivipara*, and the rare montane calcicole mosses *Aulacomnium turgidum* and *Hypnum hamulosum*.

7.3.1 Calcareous mica-schist

In the Scottish Highlands, outcrops of mica schist that are locally rich in calcium support a diverse and very important flora. Here, short, often grazed, species-rich mixtures of mountain avens *Dryas octopetala*, arctic-alpine cushion herbs, grasses and sedges occur on lime-rich soils. This is one of the most important upland habitats in the UK for rare arctic-alpine plants and other rare montane or northern plants and animals, including the endemic Scottish primrose *Primula scotica*. Arctic-alpines that are characteristic of this habitat include moss campion *Silene acaulis*, alpine lady's-mantle *Alchemilla alpina*, sibbaldia *Sibbaldia procumbens*, spiked wood-rush *Luzula spicata*, cyphel *Minuartia sedoides* and purple saxifrage *Saxifraga oppositifolia*, dwarf willow *Salix herbacea*, alpine bistort *Persicaria vivipara*, hair sedge *Carex capillaris.* The habitat also supports populations of nationally rare species, such as alpine mouse-ear *Cerastium alpinum*, rock sedge *Carex rupestris,* hoary whitlowgrass *Draba incana*, alpine cinquefoil *Potentilla crantzii* and alpine speedwell. There are also rare or uncommon calcicolous bryophytes, including *Aulacomnium turgidum*, *Amblystegium compactum*, *Seligeria trifaria* and *Lescuraea incurvata*.

Key localities for this type of habitat include Ben Lawers, which has the most extensive development of alpine and subalpine calcareous grassland in the UK. The main dwarf-herb community, is found on the open hill, and is dominated by moss campion and sheep's fescue. Mountain avens also occurs but is largely confined to crags because of heavy grazing pressure. The site has an exceptional arctic-alpine flora, including a wide range of characteristic species and many rarities. Pearsall (1950) considers that in the case of Ben Lawers, it is probable that the location of the mountain contributes towards the diversity of the flora. This is because the area lies towards the eastern margins of the Highlands and thus Ben Lawers receives considerably less rainfall than that of the Western Highlands. This probably significantly reduces the effects of leaching and is also less favourable towards the formation of peat.

Fryday (1999) considers that the mountains of the Western Highlands of Scotland support a lichen vegetation that is apparently unique in Europe, and probably in the world. He considers that Ben Lawers to be "arguably, the most important lichen site in the British Isles; and without question, the most important montane site" (Fryday, 1999). The reason for this extraordinary richness lies in a combination of factors, but notably the geology (calcareous mica-schist), geographical position, climate and altitudinal range. Over 20 lichen species are known in the British Isles only from Ben Lawers, and several also appear to be British endemics.

8. Mineralisation and mining

Rocks rich in some specific minerals, which have often been exploited by man (eg tin, lead) may provide some very specific chemical conditions and physical attributes which, as the previous sections have demonstrated, provide a control on nature of the vegetation. Studies of specific adaptations to the often unique chemistry of the soils derived from such deposits demonstrate the specific adaptations of some of the associated plant species.

Land which has been subject to mining often presents special problems for plants and wildlife, but also unique opportunities. Some of the factors special to these sites include:

1. Compacted and often contaminated soils, leading to long-standing bare ground, affected by wind and water erosion and prone to extremes of temperature;
2. Lack of topsoil, soil structure, nutrients and micro-organisms;
3. Steep slopes;
4. Toxicity due to mineral content – for example residual, fine particulate copper, zinc, lead and arsenic;
5. Unstable substrates; and
6. A mosaic of hummocks and hollows

As a general rule, the longer sites have been abandoned, the more diverse the vegetation development and the greater the nature conservation interest, though mere vegetation cover is not a guarantee of importance, since species requiring 'pioneer' conditions are often a key feature of such sites. Variation in abandonment of different areas of a site can also play its part in maintaining biodiversity.

Compacted, contaminated soils on such sites may provide suitable growing conditions for a wide range of species, which may not be able to grow in more fertile areas where they are likely to be ousted by more competitive species. Typical of these are grasses and other plants adapted to contaminated soils such as common bent *Agrostis capillaris*, some varieties of thrift *Armeria* and heathers *Calluna* sp. Rushes may grow in metal contaminated water and silts, whilst stream beds may be coated with the metal tolerant algae *Microthamnion* species.

Soils rich in copper are globally scarce and over 25% of the total number of mosses and liverworts found in Cornwall have been recorded on abandoned metalliferous mine sites. Several of these species are nationally rare and many are restricted to metal-contaminated conditions. Cornish mining sites also support nine 'Nationally Rare' species, including all of the national population of *Cephaloziella integerrima* and most of *Cephaloziella massalongi* and *Scopelophilia cataractae*.

Lichens are the born survivors of extreme environments, and are often important colonisers, occurring on spoil heaps, mine buildings and adit walls. It has recently been established that mineralisation type is a key factor in determining the composition of assemblages on mine spoil, some species favouring low pH iron-rich substrates, others high pH copper-rich sites.

Ore mines often remain undisturbed and are seldom completely grassed over. Many of them have two species of plants that are specially associated with places where lead has been mined. Spring sandwort occurs where no lead has been mined, but it does not follow that the ore is not present. A much rarer plant is alpine penny-cress *Thlapsi caerulescens* and known in Britain only from Derbyshire and Rhum. The same association occurs in the Mendips where lead has been previously mined. Here though it is alpine penny-cress *Thlaspi alpestre* which occurs.

Grasslands occurring on soils that have levels of heavy metals, such as lead, zinc, chromium and copper that are toxic to most plant species are known as calaminarian grasslands (after calamine, the name for zinc oxide, which is in itself a corruption of the latin *cadmia* for zinc ore) and are of nature conservation interest in their own right. The greatest extent of the habitat occurs on artificial sites associated with past mining activities. There are three main situations where calaminarian grasslands habitat type has developed:

1. Near-natural, open vegetation of serpentine rock and mineral vein outcrops with skeletal soils;
2. Stable river gravels rich in lead and zinc and that are near-natural, although the heavy metal content may be partly an artefact of past mining activity in the river catchment; and
3. Artificial mine workings and spoil heaps, mainly on limestone; these are numerous (several thousand UK localities) and extensive, although few sites have a high species-richness.

Heavy metal toxicity of the soils, perhaps combined with a low nutrient status, is believed to maintain the open vegetation, retarding succession. Calaminarian grasslands and associated rock outcrops provide a habitat for several scarce plants, including northern rock-cress *Arabis petraea*, forked spleenwort *Asplenium septentrionale* and Young's helleborine *Epipactis youngiana*.

In the Moor House-Upper Teesdale area of Cumbria and Durham, calaminarian grassland occurs on lead-mine spoil associated with the Carboniferous limestone at high altitude in the Pennines of northern England. Much of the spoil is unvegetated and has a variety of particle sizes ranging from coarse rubble to fine sediment, and several steep, unstable slopes. Metallophytic plants such as spring sandwort, alpine penny-cress and Pyrenean scurvygrass *Cochlearia pyrenaica* occur along with lichens such as *Cladonia rangiformis*, *C. chlorophaea* and *Coelocaulon aculeatum*.

Photo 8. *Viola calaminaria*, a metallophytic species typical of old lead mining areas, Gang mine, Swaledale

Photo English Nature

Similar communities are also recorded from former mining areas in Belgium, France and Germany where the violet *Viola calaminaria* is particularly abundant. Both this species and *Thlaspi caerulescens* were the first plant species documented to accumulate high levels of metals in their leaves, notably Nickel, Cadmium and Zinc.

In the south, the extraction of copper and tin from deposits associated with the emplacement of the Bodmin granite has led to the formation of a number of mine spoil sites which support calaminarian grassland metallophyte communities. One such site is Phoenix United Mine and Crow's Nest on the south-eastern edge of Bodmin Moor. Here a long legacy of copper and tin extraction survives as mine spoil which has been colonised by a number of metallophytic bryophytes. In particular, the site supports the only known site in the world for the endangered Cornish path-moss *Ditrichum cornubicum*. Other notable metallophytes include the Red Data Book liverworts *Cephaloziella massalongi* and the endemic *C. nicholsonii*, both associated with copper-rich substrates, and the mosses *Pohlia andalusica* and *Scopelophila cataractae*, the latter possibly an introduction into this country on imported ore. Many other notable bryophytes have colonised the spoil, including the liverworts *Cephaloziella integerrima*, *C. stellulifera*, *Lophozia sudetica*, *Gymnomitrion obtusum* and *Marsupella funckii*, and the moss *Ditrichum lineare*.

In Northumberland, the Tyne and Allen River gravels encompasses the most extensive, structurally varied and species-rich examples of riverine calaminarian grasslands in the UK. The river gravels contain a range of structural types, ranging from a highly toxic, sparsely vegetated area with abundant lichens through to closed willow/alder *Salix*/*Alnus* woodland. In addition, the site is of considerable functional interest for the series of fossilised river channel features. Spring sandwort and thrift *Armeria maritima* are particularly abundant, and there are several rare species, including Young's helleborine, which has its main UK population at this site. The site is also of great importance for its lichen communities. A number of rare and scarce species are present, including the Red Data Book-listed *Peltigera venosa*.

Mining as an activity may also lead to the creation of ground conditions that favours particular plant assemblages and communities that, in part, may reflect the particular soil chemistry of these sites. A representative example is provided by the characteristic vegetation of the Stiperstones in Shropshire in comparison with areas where mining has occurred. The Stiperstones ridge is formed by quartzite rocks of Cambrian age which give rise to acidic and extremely nutrient-poor soils resulting in species-poor heathland vegetation. The slopes of the Stiperstones ridge lie mainly on Mytton Flags which are generally acidic in nature, with some slight base enrichment where springs percolate through to the surface producing flushes of wetland vegetation. Therefore, the typical Stiperstones semi-natural vegetation is heathland and acidic grassland. Following mining in the area, the spoil mounds that are left are relatively nutrient poor and verging on toxic with heavy metals and salts. Colonisation is slow and usually follows a sequence of algae, then lichens, bryophytes, and finally higher plant species such as sheep's fescue, which shows a degree of lead tolerance. Eventually woody species such as heather, which can fix phosphorus and gorse *Ulex* sp. and broom *Cytisus scoparius* which can fix nitrogen, result finally in a heathy woodland vegetation dominated by birch. Oak replaces birch where deeper soils have formed.

9. The influence and role of geomorphological processes

Geomorphology is the study of the evolution and configuration of landforms and the processes that shape them. The geology of an area and aspects such as rock type and structure are central to the formation of particular landforms and may influence the way in which key processes operate. This section deals primarily with the role that particular landforms, either associated with specific rock types or of a ubiquitous nature across the majority of rock types, may influence biodiversity. Additionally it also considers the role that some of the key geomorphological processes may have in influencing ecology, flora and fauna. An exhaustive consideration of the myriad of landforms and processes is not provided, but instead some of the key aspects of linkages between geomorphology and biology are discussed.

9.1 The influence of cliffs and cliff processes

As highlighted in previous sections, rock type, soil formation, relief and weathering play an important role in habitat development and plant presence and distribution. On shallow slopes or relatively level land the processes of soil formation are probably more critical that underlying geology in influencing and determining the biota. However, this is not the case for cliffs where soil formation is either absent or very restricted in its occurrence and there may be direct contact between the rock face and the biota.

The presence of cliffs in the landscape is dependent on both the mechanical strength and the variability in the strength of the bedrock. These differences lead, through the expression and action of geomorphological processes, to variability in the type and nature of the cliff produced. The inherent strength of a rock can be important in its ability to form cliffs and the way in which they weather. As an example, relatively recent (Tertiary <65 million years old) sedimentary rocks and lavas are weaker than the majority of igneous rocks and older (Mesozoic-Palaeozoic) sedimentary rocks. As a consequence, these latter rock types tend to form more prominent and longer term cliff features (the vast majority of cliffs in England are formed from the latter rocks, eg the Carboniferous Limestone bluffs and crags of Derbyshire). Cliffs and bare exposures do occur in some of the softer rock formations, but these are often associated with human activity (ie quarrying), or are of an ephemeral nature (eg eroding shoreline cliffs, exposures on active slopes).

Aspects such as sedimentation patterns, seismic activity and rates of cooling (for igneous rocks) also contribute to the style and form of cliff formation. Igneous rocks formed in single massive events with few internal joints or cracks tend to weather slowly and as homogenous units. As such these types of rock may provide very few microhabitats for colonisation by flora and fauna as exemplified by the granite inselbergs of parts of Africa (Porembski et. al. 1994). Where multiple events in time have occurred (eg the intrusion of dykes) then a greater number of heterogeneities may be produced which are then available for exploitation by plants and animals. For sedimentary rocks, differences in the types of rock present within a sequence and rates and types of weathering will often lead to the formation of differing slope angles, overhangs and pronounced cliffs or escarpments.

Bunce (1968) investigated the restriction of certain plant species to dolerite, rhyolite and rhyolite tuff on Mount Snowdon and the factors controlling the distribution of these species. Bunce concluded that the cliff community is essentially closed and that there is no floristic continuity between cliff and surrounding habitats. Notably, the cliffs that he studied include a rare arctic-alpine component (eg moss campion *Silene acaulis* and purple saxifrage *Saxifraga oppositifolia*).

Larson et. al. (2000) provide a summary of the literature relating to the influence of cliff geology on flora. Interestingly, their key conclusion is that there is not a clear relationship between geology, soil chemistry and species composition on vertical cliffs. They suggest that this is not surprising given that the normal process of soil formation is absent on cliffs.

Although rock chemistry may not be a predominant factor in controlling the distribution and presence of plant species it is apparent that one aspect of cliff geology and geomorphology that is important to ecological communities is the degree to which cracks, crevices and ledges are present and their spatial scale. As a general rule cliffs formed of unconsolidated materials provide few-large scale heterogeneities compared with cliffs formed of solid rock, due largely to their relatively rapid erosion (Larson et. al. (2000)). Cliffs composed of igneous rocks, such as basalt and andesite, tend to provide more habitat (ie niches) than softer sedimentary rocks. The number, size and spacing or crevices, ledges and fractures etc. can strongly influence the density and diversity of flora of cliffs. Coates and Kirkpatrick (1992) document that on sandstone cliffs in Tasmania, colonies of higher plants are found concentrated along joint crevices while sheer faces are covered only by mosses and lichens. Such distribution patterns can be observed on any cliff sections, although scant attention is usually paid to the factors that may be influencing distribution at this scale.

Photo 9. Low cliffs formed in the Ardingly Sandstone (Wealden), Wakehurst, West Sussex
Photo R Cottle

Krippel (2003) provides information on a study of outcrops of Jurassic sandstone in the eastern part of the Grand-Duchy of Luxembourg, an area known under the name of 'Petite Suisse luxembourgeoise'. This area is characterised by a mosaic of plateaus, cliffs, steep scree-covered slopes and wet valleys. The sandstone cliff formations and the dense canopy cover of the climax beech forests are responsible for a special microclimate with high humidity and buffered temperatures. These conditions, as well as the diversity of habitats contribute to an extraordinary biodiversity (in comparison to nearby areas). The vertical rock faces of deep and often narrow crevices are even characterised by exceptional microclimatic conditions which tend to mimic the oceanic climate of the European Atlantic fringe and therefore provide conditions for a number of species which are not typical of this more continental area. The 'Petite Suisse' sandstone area is particularly well known for the relictual populations of Tunbridge filmy-fern *Hymenophyllum tunbrigense* and in 1993 the Killarney fern *Trichomanes speciosum* was discovered for the first time in continental Europe in the same region. The cliffs and sandstone pillars, together with the woodland vegetation, also make the area important for mosses and liverworts.

There are few relationships noted in available literature between cliff fauna and the geological composition of cliffs, although clearly cliffs offer the same physical attributes for fauna as they do plants. Cliffs are often the preferred nesting sites for a wide range of bird species, but in particular raptors, corvids and hirundines, although cliffs of a suitable nature formed from any rock formation will provide suitable habitat for this faunal group. One interesting association concerns the bearded vulture *Gyptaeus barbatus* which, in South Africa, preferentially nests on basalt and sandstone cliffs. At these locations, the vultures come in contact with filmy concentrations of iron in caves and on ledges and then spread the iron oxide through their feathers by preening. The resultant rufous discoloration of lighter feathers on underparts camouflages the birds on the cliff face. Analysis of the feathers shows that the iron oxide acts as a protective coating which reduces wear, thus acting as a repair mechanism and it may also help in controlling ectoparasites (Brown and Bruton1991).

Another example of the influence of cliffs and rock faces in the landscape comes from a study of spider populations and diversity on sandstone rocks in the Ļeské Švýcarsko National Park, Czech Republic (RŢžiļka 2002). Here, a total of 39 species of spider were collected, half of which were found exclusively on sun-exposed rocks, a second half exclusively on shaded rocks. The assemblage obtained from sun-exposed rocks is characterised by species, as would be expected, with preferences for warm temperatures and very dry habitats (eg the jumping spiders *Zelotes puritanus* and *Zelotes petrensis*). The assemblage of shaded rocks is characterised by the presence of species characteristic of cooler temperatures and more humid conditions. What this study demonstrates is that outcrops of rocks, particularly cliff and ravine systems, increase the structural diversity of an area which in turn leads to the formation a wider range of conditions available for exploitation by fauna. This structural diversity operates at a wide range of scales, but can be particularly important at the micro-scale where abrupt changes in conditions can occur within a very small area.

Thus, the physical attributes of a rock type and its ability to form cliffs and relatively stable features within the landscape can have a very important role to play in determining the nature and diversity of niche space within a given area. Not only do rock faces themselves provide a direct and exploitable substrate for plants and animals, but the structural diversity that they introduce also leads to local modifications in climate, which in turn increases the diversity of environmental conditions and the ability of an area to support a range of species. This aspect of geology operates at all scales, from the smallest cliff ledge or bare rock outcrop to entire mountain ranges and has a corresponding influence at the biological level from the presence or absence of individual species to the distribution and extent of entire ecosystems.

9.2 Slope processes

Due to the diversity of rock types and their physical structure, the erosional and weathering processes that act upon them result in the formation of varying physical ground conditions that are exploited by plants and animals. This aspect is particularly evident with respect to the processes that operate on the variable geology of slopes and cliffs. It is perhaps in situations where the rate of weathering and the movement of material is on a relatively rapid timescale that effects on biological systems can be most readily observed and appreciated. This particularly applies to cliffs and slopes formed in soft, unconsolidated rocks (eg clays and sands) and sequences of rocks that are prone to slippage or fracture due to inherent weaknesses of structure or the action of water permeating through the succession. However, the weathering of 'hard' rocks and the transport of material away from areas of outcrop is also important in forming habitats with specific characteristics, notably scree slopes.

Scree habitats consist of rock fragments covering the frost-shattered summits of mountains or accumulating on slopes below cliffs. Siliceous screes are made up of siliceous rocks such as quartzite, granite and sandstone. Scree may be colonised by a range of pioneer species and also provides shelter for many species sensitive to frost, such as parsley fern *Cryptogramma crispa*, species requiring a humid microclimate such as Wilson's filmy-fern *Hymenophyllum wilsonii*, and species sensitive to grazing such as stone bramble *Rubus saxatilis*.

At high levels and in the mountains, both scree formed from silica-rich and calcium-rich (eg calcschist) rocks are important for their rich fern flora and act as refugia for a number of rare species. As an example, the Lakeland Fells in Cumbria demonstrate the most extensive development of screes with parsley fern. The main rock, the Borrowdale Volcanic Series (but more locally Skiddaw Slates), varies much in base-status, but the screes are chiefly base-poor. Siliceous screes are one of the most extensive habitats within the Lake District High Fells, covering large areas on moderately steep ground, always interspersed with other habitats. The screes vary from recently formed loose scree in lower sections of gullies and below cliffs to stable areas colonised by grasses, bryophytes and ferns. Major scree areas occur in the Wasdale Screes, Helvellyn and Fairfield, Buttermere Fells, Scafell Pikes, Pillar and Ennerdale Fells and Skiddaw Group. The communities are well developed and diverse with a wide range of characteristic species, including an abundance of parsley fern with associated species such as alpine lady's mantle, stone bramble, heath bedstraw and sheep's fescue. Lemon-scented fern *Oreopteris limbosperma* is also found on the screes within Pillar and Ennerdale Fells. The screes also provide a suitable microclimate for many oceanic moss and liverwort species such as *Scapania ornithopiodes* and *Kiaeria starkei*, found in Helvellyn and Fairfield.

Calcareous and calcschist screes develop from base-rich rocks including limestone, calcareous-schists and the more basic igneous rocks, such as serpentine and basalt. The vegetation of these screes normally consists of assemblages of calcicole and basiphilous species, the composition of which is heavily influenced by altitude. Characteristic species at high altitude include purple saxifrage, holly-fern *Polystichum lonchitis* and alpine meadow-grass *Poa alpina*, while at lower altitude limestone fern *Gymnocarpium robertianum*, herb-robert *Geranium robertianum* and wall lettuce *Mycelis muralis* are more usual.

Areas around Teesdale are representative of this type of habitat where extensive screes have developed from weathering of the Carboniferous Limestone outcrops. Plant communities are diverse and there is a mix of northern and southern floristic elements, including holly-fern, rigid buckler-fern *Dryopteris submontana*, limestone fern, musk thistle *Carduus nutans* and mossy saxifrage *Saxifraga hypnoides*. Hairy stonecrop *Sedum villosum* occurs where scree is flushed by springs.

Slope habitats are particularly prevalent on the coast where sloping to vertical faces develop where a break in slope is formed by slippage and/or coastal erosion. Cliff profiles at the coast vary with the nature of the rocks forming them and with the geomorphology of the area. Broadly, maritime cliffs can be classified as ‘hard’ or ‘soft’, although in practice there is a continuum of types. Cliffs formed in hard rock types such as granite or Carboniferous Limestone tend to be vertical or very steeply sloping and support few vascular plants other than on ledges and in crevices or where a break in slope allows organic material to accumulate. Vertical cliff faces which support only limited vegetation also form in rock types such as sandstone and chalk which erode to a vertical profile, although erosion in some cases can be relatively rapid.

Soft cliffs are formed of less resistant sediments such as clays and sands and, being unstable, often form less steep slopes. Important sites for this type of habitat includes the cliffs of north-east Isle of Wight formed in the Tertiary sands and muds of the Headon and Bouldnor Formations and the extensive landslip systems of the West Dorset coast formed in the Lower Jurassic mudstones and limestones of the Lias. These cliffs are subject to frequent slumping and landslips, particularly where water percolates through the rock and reduces its sheer strength. The relative mobility of cliffs formed in unconsolidated sediments or ‘soft’ rocks (invariably of sedimentary origin) leads to the constant formation of newly exposed faces and bare slopes. This means that these cliff types can often support a wide range of vegetation from pioneer communities on freshly exposed sediments through ruderal and grasslands communities to scrub and woodland. Wet flush vegetation commonly occurs on soft cliffs where groundwater issues as seepage. An example of this type of cliff system is provided by Overstrand cliffs on the North Sea coast of Norfolk. The cliffs here are up to 70 m high and are composed of Pleistocene sands and clays with freshwater seepages in places and are subject to moderately frequent cliff-falls and landslips. Much of the length is unprotected by sea defences and is therefore natural in character. The vegetation exhibits cycles of succession with ruderal communities developing on the newly exposed sands and mud followed by partially stabilised grasslands and scrub. Seepage areas support wet fen communities and in places perched reedbeds occur.

In some locations the complex geology of a site may lead to the formation of cliff slope habitats that vary considerably along a section although the processes acting upon the succession are similar. Such an example is provided by the Cretaceous and Tertiary sediments exposed on the south coast of the Isle of Wight. Here, the western and eastern extremities of the Island consist of high chalk cliffs with species-rich calcareous grassland vegetation, the former exposed to maritime influence and the latter comparatively sheltered. At the western end, the site adjoins the Isle of Wight Downs, providing an unusual combination of maritime and chalk grassland. The most exposed chalk cliff tops support important assemblages of nationally rare lichens, including *Fulgensia fulgens*. Between these two areas, the coastal section is composed of slumping acidic sandstones and neutral clays with an exposed south-westerly aspect. The vegetation communities are a mixture of acidic and mesotrophic grasslands with some scrub and a greater element of maritime species, such as thrift *Armeria maritima*, than is usual on soft cliffs. This section supports the Glanville fritillary butterfly *Melitaea cinxia* in its main English stronghold.

Soft cliffs are particularly important for some groups of invertebrates, notably beetles, flies and ants, wasps and bees as they provide a suite of conditions which are rarely found together in other habitat areas, the most comparable being man-made quarries. The combination of friable soils, hot substrates (particularly south-facing slopes) and open aspect maintained by successional slope failure processes provides a continuity of conditions that are of a very restricted nature. These microhabitats support many rare invertebrates that are confined to such sites. A study for the Countryside Council of Wales by Howe (2002) found that periglacial head deposits on the south Gower coast and Quaternary deposits of glacial till and sand on the Lleyn peninsula supported important invertebrate assemblages. As an example, sites on the Lleyn peninsula support the only UK populations of the mason bee *Osmia xanthomelana* and the only Welsh populations of the ground beetle *Tachys micros*, the weevil *Sitona gemellatus* and the cranefly *Symplecta novaezemblae* (Howe 2002).

MigoŒ(2002) in a review of the slope processes of sandstone outcrops notes that punctuated rock slope evolution, with long periods of relative stability interrupted by episodes of massive failure and scarp retreat, appears to be a characteristic sandstone landscape phenomenon, that would appear to be unparalleled in other rock types, although similarities can be sought in the development of marine cliffs. Importantly he notes that with respect to biological interests, the consequences of these processes include repeated exposure of fresh rock surfaces for colonisation by organisms, interruption of biological succession within both rock face and talus, and occasional destruction of habitats in the lower slope. Interestingly the question is also posed as to what extent plants and animals themselves contribute to increasing slope instability and eventually, failure.

One interesting example of the influence of slope processes comes from the high plateaus of the Scottish Highlands. Here, open and unstable substrates can lead to an enrichment of the flora, particularly on solifluction terracing. Alternate freezing and thawing of soil water on slopes at high altitude forms the terracing. Many plants benefit from the instability, which stirs up the soils, releases nutrients and counteracts the effects of leaching. A special feature in the UK is that strong winds at high altitude can keep the more exposed risers of the stair-like terraces open, resulting in distinctive bands of vegetation. Norwegian mugwort *Artemisia norvegica*, which is known from only two mountains in the north-west Highlands, is present in open moss-heath on solifluction terracing and on open basal rock surfaces.

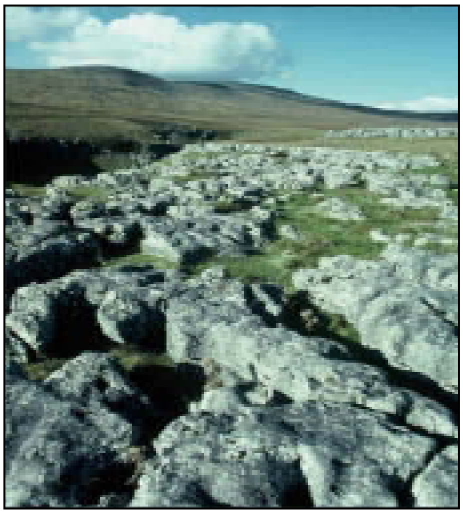

Photo 10. Limestone pavement, Ingleborough, North Yorkshire.
Photo R.Cottle

9.3 Karst systems

Karst is the name given to the terrain created by limestone solution and characterised by a virtual absence of surface drainage. Previous sections have dealt with the vegetation associated with limestones and calcareous rocks. However, typical limestone landforms such as solution hollows and limestone pavement, associated with rock outcrops such as the Carboniferous Limestone, can be considered to represent the product of geomorphological and weathering processes with respect to a specific rock type. Although the flora and fauna of karst areas is dominated by species and communities favouring calcareous substrates, the unique nature of the landforms and the landscape itself can provide markedly different conditions for the development of specific habitat types, notably limestone pavement and caves.

The main process involved in the formation of many of the characteristic landforms is the widening of fissures, joints and faults by solution for which the water table must be well below the surface in order to allow water to percolate continually downwards through the rock.

The surfaces of many limestones are minutely sculptured. In the Ingleborough district of North Yorkshire the joint planes of the Carboniferous Limestone become enlarged to form grikes, while the joint blocks remain as clints. Limestone pavements, such as those of North Yorkshire, are confined to glaciated massive limestones and are absent in unglaciated areas of similar lithology, for example the Mendips. The postulated reason for this is that the beds have to be strong enough (ie massive) to resist general glacial destruction and yet fissile enough along the major bedding planes to be stripped off. The formation of clints and grikes has been attributed to a post-glacial phase after drift deposits have been stripped from the limestone surface, when the joints are enlarged by weathering as the first phase in the destruction of the surface into rubble and ultimately soil. Thus, in this view, clints and grikes are essentially transient features.

A range of calcareous rock, heath, grassland, scrub and woodland NVC types can occur on limestone pavement (see Section 5.1.2). The vegetation of limestone pavements is unusual because of the combinations of floristic elements, including woodland and woodland edge species, such as hart's-tongue and dog's mercury. On the clint surfaces or the upper walls of the grikes there are plants of rocky habitats, such as wall-rue *Asplenium ruta-muraria* and maidenhair spleenwort *Asplenium trichomanes*. The grikes provide a shady, humid environment favouring woodland plants. Grazing pressure is a key factor in determining ecological variation in limestone pavements. Where grazing pressure is low, woodland may cover the pavement and woodland vegetation may mask the limestone surface. Here only the massive areas of pavement may be exposed as clearings. Where there is heavy grazing pressure, vegetation may be found only in the grikes, but, where grazing is lighter, dwarf trees, herbs and ferns may protrude from the grikes. Grikes that are about 60 cm deep provide shelter without unduly limiting light and are usually the best floristically.

Unlike massive limestones, chalk does not usually possess a neat series of joints, but a multitude of irregular cracks. There is usually no joint control of the relief comparable with that of Carboniferous Limestone districts, not is the rock hard enough to be fretted at the surface by solution, or strong enough to allow a great development of caves. The general form of chalk landscapes, dominated by smooth convexo-concave curves is probably due to the permeability of the rock and its waste mantle. Whether the form of chalk slopes is unique, as is sometimes maintained, is doubtful, as some other rocks such as the softer Jurassic limestones and some permeable sandstones, if stripped of their vegetation (eg woodland) appear to be very similar in form. The typical rolling downland of chalk regions probably owes as much of its quality to its vegetation and land use as to its slope forms. Where the chalk is mantled by superficial deposits, such as Clay-with-flints or boulder clay, its vegetation and land use change and it appears to lose many of its typical landscape qualities.

Provided the water table is below the surface, rain will percolate downwards along the joints and at certain locations, notably the intersections between joints, naturally larger channels may be present. These will be slowly enlarged by solution into holes which may be funnel-shaped (eg dolines and swallow holes) or shaftlike (eg avens). Continued solution and the movement of water through the limestone at various levels leads to the formation of caverns.

9.3.1 Caves

The unique environmental conditions provided by caves, particularly the lack of natural illumination, has led to the evolution of a specialist flora and fauna. Microclimatic conditions vary widely within and between caves, and this determines the composition of the fauna and flora. Many species feed on detritus derived from the surface; others are carnivorous. Cave-dwelling species (cavernicoles) can be divided into three categories:

- Troglobites – obligate cave-dwellers which typically display morphological adaptations, such as reduced pigmentation and regressed eyes.
- Troglophiles – facultative cave-dwellers which may have permanent populations in caves but which are also found in other suitable habitats.
- Trogloxenes – species which are found in caves but only for part of their life cycle.

The cavernicolous flora and fauna of the UK and other parts of northern Europe is highly impoverished compared to southern Europe. The reason for this is that most karst areas in the UK (except for parts of southern England) were glaciated during the Pleistocene, and many species are therefore recent colonists. Southern Europe escaped glaciation and consequently has a richer fauna of highly specialised relict troglobites.

Cavernicoles in the UK include bacteria, algae, fungi and various groups of invertebrates (eg insects, spiders and crustaceans). Characteristic troglobites and troglophiles include the blind cave spider *Porrhoma rosenhaueri,* a ground beetle *Trechus micros*, the amphipod *Niphargus glennei*, only known from Devon, and *Arrhopalites pygmaeus* (a springtail). Some caves are important hibernation sites for bat species. For instance the limestone caves of the Mendips provide a range of important hibernation sites for lesser horseshoe bat *Rhinolophus hipposideros* and greater horseshoe bat *Rhinolophus ferrumequinum*.

9.4 The Influence of geology on fluvial habitats

In recent years there has been an increasing interest in the interaction between the physical and biological environments of rivers, lakes and estuaries (ie the interactions between hydraulics, sediment transport, morphology and flora & fauna). The development of ideas relating to these interactions have come together through the combined discipline of "biogeomorphology". Geomorphological processes within fluvial systems may affect biota, which may in turn affect the geomorphological processes themselves. It is clear that the influence of geomorphological processes operates over a range of time and spatial scales and involves aspects such as sediment transport, channel hydraulics and slope evolution. The geological evolution of an area may have played, or be playing, an important role in the geomorphological processes, particularly with respect to sediment supply and the morphological control of drainage systems. These aspects, in turn, may influence the form and function of fluvial systems and interactions with their associated biota. These interactions are complex and, as mentioned, operate over a variety of scales. A full discussion of the way in which geology may influence these geomorphological processes and in turn the response and interaction with biota is largely beyond this study.

However, there are perhaps, more direct ways in which geology has an influence upon fluvial habitats and this is through its influence upon water chemistry. The chemistry of surface water and groundwater is influenced by the local geology. Reactions between rainwater and bedrock, over a matter of days or months as infiltration and percolation occur, are responsible for the mineral (solute) content of groundwater. The extent to which the reaction with the host rock proceeds is governed by the residence time of the water, which may be influenced by the type of flow movement and the geology of the aquifer. A rock system with a high number of fissures and joints has high water mobility and low solute concentration due to short residence time. By contrast, a rock system with a microscopic pore system has a long residence time and high solute concentration because the water stays in contact with the rock for long time. This natural baseline in chemistry varies from one rock type to another and is seen at its simplest in the distribution of different areas of hard and soft water. Water chemistry also evolves with time as the water moves along flow lines. A number of geochemical processes — for example oxidation and reduction (controlling natural levels of Fe, Mn, As and Cr), mineral solubility (controlling F and Ba concentrations), and sorption and exchange with mineral surfaces (affecting the concentrations of many metals and ionic constituents) — may help shape the unique natural characteristics of surface waters and groundwater.

The alkalinity of water (controlled by the content of anions of carbonates, bicarbonates, and hydroxides) is one of the key aspects influencing fluvial biology. The geology and geochemistry of a watershed can be used to predict alkalinity. While watersheds with a granitic bedrock have a low alkalinity and a low buffering capability, areas with calcareous sedimentary bedrocks have waters with high alkalinity and high buffering capability.

9.4.1 Rivers

An example, of the influence of variation in bedrock geology on riverine habitat is provided by the River tweed in Northern England and Scotland. Here, the upper stretches of the Tweed and its tributaries drain rocks with a relatively low content of base minerals, mainly Ordovician and Silurian greywackes and shales. The catchment at this stage is characterised by low-intensity extensive land uses dominated by sheep, heather moorland and significant coniferous forestry. From little more than an upland stream the Tweed rapidly gains in size but retains the characteristics of an upland stream of predominantly fast current and shallow depth. Consequently these physical factors are reflected in the types of vegetation that it can support. In the upper reaches, Mosses and Liverworts are the dominant plant types both within the channel and growing on rocks, and also the adjacent bank sides. Over 90% of the Moss species occurring in the river are restricted to this section. Larger plants also occur but are scarce as most species, with the exception of water crowfoot (*Ranunculus* species), are confined to areas of slower water downstream. The number of groups of invertebrate species is restricted compared with lower sections of the river with mayflies and stoneflies amongst the most abundant.

The underlying geology of the middle reaches of the River is subject to change, with a transition from the base poor Ordovician and Silurian shales to richer, less acid sandstones and volcanic rocks below St Boswells. This shift in geology along with more intensive pastoral land use results in comparatively richer water chemistry within the river. Together with a reduction in flow rate and increase in water depth these changes are reflected by the plant and animal communities, which are dominant in this stretch of the river. Emergent vegetation on the river banks is now more apparent, characteristic species include Reed Canary Grass and Bur-reed. Milfoil and Water Crowfoot which are rooted in the riverbed become more abundant. The invertebrate fauna is increasingly diverse with leeches, molluscs, aquatic beetles and crustaceans becoming more significant. Stoneflies and mayflies are still plentiful whilst blackflies and caseless caddis flies are also relatively abundant.

The composition of fluvial vegetation, particularly species of water crowfoot *Ranunculus* spp., varies depending on geology and river type. In each, *Ranunculus* species are associated with a different assemblage of other aquatic plants, such as water-cress *Rorippa nasturtium-aquaticum*, water-starworts *Callitriche* spp., water-parsnips *Sium latifolium* and *Berula erecta*, water-milfoils *Myriophyllum* spp. and water forget-me-not *Myosotis scorpioides*. Three main sub-types are defined by substrate and the dominant species within the *Ranunculus* community. The habitat type is widespread in rivers in the UK, especially on softer and more mineral-rich substrates. It is largely absent from areas underlain by acid rock types (principally in the north and west). The main variants have very different distributions and have different significance for conservation in a European context.

Sub-type 1: This variant is found on rivers on chalk substrates and is therefore restricted to southern and eastern England. The community is characterised by pond water-crowfoot *Ranunculus peltatus* in spring-fed headwater streams (winterbournes), stream water-crowfoot *R. penicillatus* ssp. *pseudofluitans* in the middle reaches, and river water-crowfoot *R. fluitans* in the downstream sections. *Ranunculus* is typically associated in the upper and middle reaches with *Callitriche obtusangula* and *C. platycarpa*. A typical example of this type of community is provided by the River Itchen in Hampshire, a classic chalk river dominated throughout by aquatic *Ranunculus* spp. The headwaters contain pond water-crowfoot *Ranunculus peltatus*, while two *Ranunculus* species occur further downstream: stream water-crowfoot *R. penicillatus* ssp. *pseudofluitans*, a species especially characteristic of calcium-rich rivers, and river water-crowfoot *R. fluitans*.

Sub-type 2: This variant is found on other substrates, ranging from lime-rich substrates such as oolite, through soft sandstone and clay to more mesotrophic and oligotrophic rocks. There is considerable geographic and ecological variation in this sub-type. Faster-flowing western rivers on harder rocks, for example in Wales and south-west England, support stream water-crowfoot, while western and northern rivers on sandstone or alluvial substrates often support both *R. penicillatus* ssp. *penicillatus* and river water-crowfoot. The River Axe is a south-western example of this sub-type 2, where the mixed catchment geology of Jurassic and Cretaceous sandstones and limestones gives rise to calcareous waters where *R. penicillatus* ssp. *pseudofluitans* dominates, giving way to *R. fluitans* further downstream. Short-leaved water-starwort *Callitriche truncata* is an unusual addition to the *Ranunculus* community and gives additional interest.

Sub-type 3: This variant is a mesotrophic to oligotrophic community found on hard rocks in the north and west. Rivers in Wales, Northern Ireland and south-west England are significant for the occurrence of stream water-crowfoot. Other typical species include the aquatic moss *Fontinalis squamosa*, alternate water-milfoil *Myriophyllum alterniflorum* and intermediate water-starwort *Callitriche hamulata*. More oligotrophic examples of this community lack *Ranunculus* spp. and are dominated by *M. alterniflorum*, *C. hamulata* and bog pondweed *Potamogeton polygonifolius*.

Two particular invertebrate species associated with chalk rivers and associated calcareous wetlands are Desmoulin's whorl snail *Vertigo moulinsiana* and the southern damselfly *Coenagrion mercuriale. V. moulinsiana* is restricted to calcareous wetlands, usually bordering lakes or rivers, or in fens (eg alkaline fens; see below). High humidity appears to be important in determining local distribution within sites. It normally lives on reed-grasses and sedges, such as reed sweet-grass *Glyceria maxima* and tussocks of greater pond-sedge *Carex riparia* and lesser pond-sedge *C. acutiformis*, where it feeds on the microflora. Sites where good populations of this species occur include chalk stream habitat in the Kennet and Lambourn valleys and along the margins and associated wetlands of the Rivers Avon, Bourne and Wylye. The southern damselfly has very specialised habitat requirements, being confined to shallow, well-vegetated, base-rich runnels and flushes in open areas or small side-channels of chalk rivers.

9.4.2 Lakes and ponds

Lakes and waterbodies characterised by water with a high base content (hard oligo-mesotrphic waters), most often calcium but very rarely magnesium, are usually confined to areas of limestone and other base-rich substrates, from which the dissolved minerals are derived. In part the rarity of the habitat type is due to the fact that since calcareous rocks are free-draining, waterbodies occur on the surface of these rocks only very rarely. In addition, such waterbodies are characterised by very clear water and low nutrient status. Abundant charophytes (stoneworts) are typically the most prominent component of the vegetation; they can occur as dense beds that cover a significant part of the lake bottom over muddy marl deposits. This type of lacustrine habitat occurs in three main situations within the UK; lakes on a predominantly limestone substrate, coastal sites based on calcium-rich shell-sands and lakes with nutrient inputs from other base-rich influences, eg serpentine and boulder clays.

The first type is the most common in the UK. A typical example is provided by Malham Tarn in North Yorkshire, which is considered to be the best example of an upland stonewort *Chara*-dominated lake in England. The water drains from the surrounding Carboniferous limestone and is calcareous and low in plant nutrients. Another lake associated with the Carboniferous Limestone is Hawes Water situated within the limestone pavements of the Morecambe Bay area. The water feeding the lake is highly calcareous and is fed by springs within it. This site is considered to be the best example of a lowland hard oligo-mesotrophic lake with *Chara* spp. in England, owing to the clarity, low nutrient status and high calcium content of its water. The rare rugged stonewort *Chara rudis* and scarce species *C. aspera*, *C. hispida* and *C. pedunculata* occur here.

An interesting example of this type of the influence of geology on this type of lake habitat is provided by Orton Pit, Peterborough. Here, an extensive pond system occupies the disused ridge-and-furrow created as a result of the extraction of Oxford Clay for the brick-making industry. The Oxford Clay is relatively calcareous and this results in the formation of alkaline surface water which is also low in nutrients. The site supports a total of ten species of charophyte including the main English population of bearded stonewort *Chara canescens. C. canescens* is an early coloniser of ponds at the site and is rarely found in ponds over 20 years old. It favours brackish conditions, which at Orton Pit are thought to be produced by the release of salts contained in the Oxford Clay which become oxidised over time. Other nationally scarce stonewort species present include *Chara aspera*, *C. contraria*, *C. pedunculata* and *Tolypella glomerata*. The distribution of *Chara* species across the site varies according to the age and stage of succession of the ponds, with few being found in ponds greater than 25 years old.

A unique series of oligo-mesotrophic waterbodies in which high base-status is not due to limestone or shell-sand occur on the Lizard peninsula in south-west England. The outcrops of serpentinite (see Section 7.2) give rise to calcium-deficient ground waters that are rich in magnesium. Groundwater drains from adjoining wet and dry serpentine heaths to feed the oligo-mesotrophic waterbodies in which another unusual feature is the occurrence of stonewort species typical of calcareous lakes, together with species normally associated with acid conditions, such as bog pondweed *Potamogeton polygonifolius*. Stoneworts present include three Red Data Book species – *Chara baltica*, *C. curta* and *C. fragifera*.

In the more mountainous areas of north-west Britain, where hard, acidic rocks tend to dominate, lakes and ponds characterised by clear soft water and low to moderate levels of plant nutrients occur and support a characteristic assemblage of plant species. The vegetation community is largely comprises amphibious short perennial vegetation, with shoreweed *Littorella uniflora* being considered as the defining component. This species often occurs in association with water lobelia *Lobelia dortmanna*, bog pondweed *Potamogeton polygonifolius*, quillwort *Isoetes lacustris*, needle spike-rush *Eleocharis acicularis*, and floating water bur-reed *Sparganium angustifolium*. Species such as yellow water-lily *Nuphar lutea*, amphibious bistort *Persicaria amphibia,* stoneworts and other pondweeds *Potamogeton* spp. may be present in more mesotrophic conditions. Floating water-plantain *Luronium natans* and pillwort *Pilularia globulifera* are two nationally scarce plants that occur in this plant assemblage.

Oligotrophic lakes, characterised by acidic waters are relatively rare and in England appear to be confined to areas of sand and gravel outcrops or where rocks result in the formation of acidic free-draining soils (eg some volcanics, granites, gabbros etc). The water is typically very clear and moderately acid and low in nutrients. The catchment area for these waterbodies at many sites in England and the UK comprises large tracts of lowland heathland which reflects the acidic substrate upon which they are located. Destruction of lowland heaths, land drainage and nutrient enrichment have contributed to the scarcity of the habitat type. The waterbodies are characterised by the presence of water lobelia, shoreweed, or quillwort *Isoetes lacustris* and typically the vegetation consists of zones in which the individual species form submerged, monospecific lawns.

Examples of these waterbodies include Hatchet Pond in the New Forest which are located amidst wet and dry lowland heath developed over fluvial deposits. It contains shoreweed *Littorella uniflora* and isolated populations of northern species such as bog orchid *Hammarbya paludosa* and floating bur-reed *Sparganium angustifolium*, alongside rare southern species such as Hampshire-purslane *Ludwigia palustris*. Hatchet Pond is therefore important as a southern example of this lake type where northern species, more common in the uplands of the UK, co-exist with southern species. Another example is Oak Mere, in the

West Midlands of England. This is a large waterbody that has formed in a kettle hole in the fluvio-glacial sands of the Cheshire Plain. The site has clear water of low nutrient status characteristic of oligotrophic waters and a marginal zone of shoreweed *Littorella uniflora*. The site supports an assemblage of plants that are now rare in the lowlands of England, including floating mats of bog-moss *Sphagnum* spp. and the scarce narrow small-reed *Calamagrostis stricta*.

9.4.3 Tufa and spring-fed alkaline fens

One particular fluvial habitat with a strong geological relationship is tufa. Tufa is associated with hard-water springs, and forms where groundwater rich in calcium bicarbonate comes to the surface. On contact with the air, carbon dioxide is lost from the water and a hard deposit of calcium carbonate (tufa) is formed. These conditions occur most often in areas underlain by limestone or other calcareous rocks, particularly in the uplands of northern England and the Scottish Highlands.

Tufa-forming spring-heads are characterised by the swelling yellow-orange mats of the mosses *Cratoneuron commutatum* and *C. filicinum*. Many rare, calcicole species live in the moss carpet, particularly arctic-alpine species, such as bird's-eye primrose, Scottish asphodel *Tofieldia pusilla*, alpine bartsia *Bartsia alpina* and false sedge *Kobresia simpliciuscula*.

Tufa-forming springs are also often associated with calcareous lowland alkaline fens where they may form prominent upwelling masses of short open vegetation around the springheads that feed the fen system. There may also be transitions to a wide range of other habitats, particularly calcareous grassland, acid grassland, heath, limestone pavements and calcareous cliff and scree.

Alkaline fens consist of a complex assemblage of vegetation types characteristic of sites where there is tufa and/or peat formation with a high water table and a calcareous base-rich water supply. The core vegetation is short sedge mire (mire with low-growing sedge vegetation). This type of fen may also occur with various types of swamp (such as species-poor stands of great fen-sedge *Cladium mariscus*), wet grasslands (particularly various types of purple moor-grass *Molinia caerulea* grassland) and areas rich in rush *Juncus* species, as well as fen carr and, especially in the uplands, wet heath and acid bogs. There may also be considerable variation between sites in the associated communities and the transitions that may occur. This variation relates to the geomorphological situation in which the fen occurs, namely: flood plain mire, valley mire, basin mire, hydroseral fen (ie as zones around open waterbodies) and spring fen. Another important source of ecological variation is altitude, with significant differences between lowland fens, which are rich in southern and continental species, and upland fens, which are rich in northern species.

A typical example of this type of habitat are spring-fed flush fens of NVC type M10 *Carex dioica – Pinguicula vulgaris* mire, which are extensive across Ingleborough, and commonly associated with calcareous grassland types, but also found amidst acid grasslands and heathland communities. They are often species-rich communities, in which rare or locally distributed species such as bird's-eye primrose, black bog-rush *Schoenus nigricans*, few-flowered spike-rush *Eleocharis quinqueflora* and flat-sedge *Blysmus compressus* are frequent. A lowland example is represented by valley fens in Norfolk, where the calcareous-rich waters are derived from spring water issuing from the Chalk aquifer. Such spring-fed flush fens at the heads of lowland valleys are very rare in the lowlands. Most of the vegetation here is of the small sedge fen type, but there are transitions to reedswamp and other fen and wet grassland types. There is a rich flora associated with these fens, including species such as grass-of-Parnassus *Parnassia palustris*, common butterwort *Pinguicula vulgaris*, marsh helleborine *Epipactis palustris* and narrow-leaved marsh-orchid *Dactylorhiza traunsteineri*. These valley alkaline fens also support good populations of Desmoulin's whorl snail and other rare and scarce invertebrates.

9.5 Coastal processes

The sustainability, resilience and carrying capacity of coastal systems is determined to a large extent by ecological and morphological processes. Usually, these processes have been treated separately, but it is now recognised that there is a strong mutual interaction and the ecology and morphology of coastal areas form an eco-morphological continuum.

Geomorphological processes may affect biota, which may in turn affect the geomorphological processes themselves. It is clear that the influence of these processes operates over a range of time and spatial scales and involve aspects such as sea-level change, plate tectonics, cliff erosion and accretion. Within this context geology may have an important role to play, both in the long term (eg plate tectonic movement) and short-term (eg availability of sediment). This influence is explored briefly in the following sections with particular emphasis on the products of geological and geomorphological interaction (ie the habitat forming substrates)

The geophysical setting and geological history of an area determine the materials that are available to be shaped by coastal processes, which can in turn strongly influence the distribution and extent of specific coastal habitat types. The rate of landform development depends on the strength or resistance of rocks or on the material strength of sediments which determines how susceptible they are to reshaping by the processes operating along a coastal section.

The type of rock forming the coast is an important influence and constraint on coastal geomorphology. Igneous and metamorphic rocks are generally more resistant than sedimentary rock. The differing density and structure of rock types give gives rise to differing resistance to the physical forces operating on the coast. Unconsolidated, or soft rocky, coastlines (eg sands, gravels) are the least resistant and may not have sufficient rock strength to maintain vertical cliff faces in response to erosion. The structural characteristics of rocks are also important. Rock mass, strength and resistance to shearing depend on the strength of the intact rock and its state of weathering, and the nature of the joints or weaknesses in the rock. These are reflected in the spacing, dip, width, continuity and infill of joints and fissures together with the movement of water into or out of the rock. On this basis, the strongest rocks, and those least prone to erosive coastal processes, are quartzite, dolerite and gabbro, followed by marble, granite, slate, schist and finally chalk and lignite. Rock mass can be weakened (or strengthened) by intrusions or by jointing and bedding patterns.

Lithology is a fundamental constraint on coastal geomorphology, where bedrock forms the shoreline. There are distinctive landforms associated with some lithologies (eg karst landforms on coasts formed from limestone, reflecting the solubility and rock strength of limestone). Granite, to a lesser extent is also characterised by a suite of distinctive landforms.

The extent to which the geology of an area is expressed on the coast depends on whether the underlying rocks are veneered with more recent sediments, which in turn influences the types of habitat likely to be present. The direct expression of harder rocks on the coast gives rise to very particular ecological conditions which are exploited by specific groupings and assemblages of species. Similarly, softer, more mobile sediments, which may be present over hard bedrock on the shore, provide a range of differing conditions which give rise to different habitats.

Along much of the world's coastline, muds, sand and gravel derived primarily from river discharge predominate. The range of grain size and mineral composition depend on physical and chemical weathering processes in the source area which are determined by climate and tectonic factors. In these cases the lithology of the hinterland may be more important than the immediate underlying rock in influencing the composition of sediments. World-wide, it is estimated that rivers supply 90% of coastal sediments whereas cliff erosion accounts for only about 5%.

The rocks of a catchment are broken down by weathering processes and are then more amenable to erosion and reworking. The supply of coastal sediment will often reflect local source; the coloured Eocene sands of Alum Bay on the Isle of Wight give rise to the sandy beach at the base of the cliffs. Most beaches in temperate areas are composed of quartz and feldspar grains, derived ultimately from the weathering of granitic rocks, gneisses and schists (ie typical of continental landmasses). Coastal sediments are important in relation to geomorphology as these are the materials from which landforms are constructed and by which the coastal system adjusts. This is most clearly demonstrated on sandy beaches and dune systems where the waves and wind expend energy redistributing sediments so that the beach (including backshore dunes) is reshaped towards equilibrium. It is perhaps this constant re-adjustment of the geological/physical (ie substrate resistance and sediments) environment to the forcing processes that is of greatest significance to the species assemblages and overall characteristics of many coastal habitats. The resistance offered by geologically stable and 'hard' rock types (eg granite) may provide stable substrate conditions which allow complex, diverse communities with long-lived individuals, to develop. At the other extreme, mobile sediments, particularly in high energy environments (eg sand beaches) offer very stressful environmental conditions that support relatively impoverished and specialist communities. These broad habitat types are discussed in more detail in the following sections. Low-energy, fine sediment sinks, as typified by estuaries are not discussed as, although large-scale geological form may play an important role in the overall morphology of estuarine systems, geology has a very limited role to play and in effect fine sediments are almost ubiquitous and will accrete wherever the physical conditions are conducive to deposition.

9.5.1 Sand dunes

The instability of these aeolian deposits is their most characteristic feature and when combined with their general deficiency in mineral nutrients they would appear to be unlikely habitats for flora and fauna. With their variety of shape, size and horizontal and vertical extent, dune deposits also provide landform heterogeneity, albeit at a relatively small-scale in the UK. In turn, vegetation, though often sparse, does accommodate to the variations in dune morphology. Vegetational characteristics, particularly through the successional and stabilising process also provide variation in the niche availability for fauna, particularly invertebrates.

Sand dune deposits in the UK are largely restricted to coastal areas although similar features are present in the Breckland district of Norfolk and Suffolk where glacially deposited sands have formed dune fields (now largely stabilised). Coastal dunes often show pronounced surface heterogeneity (eg foredunes, ridges, lee slopes and slacks) where wind, hydrology and salinity combine to create a distinctive and diverse habitat for a range of plants and animals.

Coastal dunes only develop on certain coasts, being most extensive where there are suitably strong onshore winds, sufficient sediment supply of medium to well-sorted sand and vegetation to assist in the trapping of the sand. In active dune systems, the foredunes directly overlooking the beach play an important role in storing sediment and protecting the land from extreme wave and tidal conditions.

The vegetation on dunes usually shows a zonation of species, with sand binding grasses such as marram *Ammophila arenaria* and sand sedge *Carex arenaria* and herbs on the foredune and shrubs and trees at greater distance from the beach. Whether sand dune vegetation shows an orderly successional change needs to be viewed in the context of the nature of the dune system. One single dune ridge is more likely to show a stable zonation reflecting environmental gradients in factors that vary with distance from the sea, such as salt content in the sand, exposure to wind and humic content of the soil. Where there are a series of foredune ridges that have prograded, then distance may equate to time and a temporal sequence of vegetation may result. The same applies to any structure where sediment is deposited as part of a prograding system (eg shingle spits and nesses). Dune succession is likely to be episodic as geomorphological change is episodic. Some dunes such as the grass-covered machair dunes of western Scotland become arrested in their development due to repeated disturbance.

9.5.2 Coastal shingle

The ecology and geomorphology of shingle has been well described by a number of studies and authors, particularly that for Dungeness (eg Ferry 2001).

Shingle structures that support vegetation develop when a sequence of foreshore beaches are deposited at the limit of high tide. More permanent ridges are formed as storm waves throw pebbles higher up the beach where backswash cannot remove them. Several beaches may be piled against each other and extensive structures can form. Clearly, an adequate supply of shingle is required in order to build these structures. On the east coast of England much of this material has been derived from glacial deposits in the North Sea basin which have been transported landwards under sea-level rise following the cessation of the last glacial. Many of the larger shingle deposits are now of relict nature and reflect formation under physical conditions different to those operating today. Much shingle on the south coast has been derived from erosion of the Chalk and the release and subsequent marine weathering of this material.

The ecological variation in this habitat type depends on stability, the amount of fine material accumulating between pebbles, climatic conditions, width of the foreshore and previous management practice. Narrow, less stable structures (spits and bars or the fringing beach associated with older, fossil beaches) are more exposed to waves or salt spray. Where wave energy causes movement of the shingle, the plant communities have affinities with the annual vegetation of driftlines. The presence of yellow horned poppy *Glaucium flavum*, sea kale

Crambe maritima and sea pea *Lathyrus japonicus*, all species that can tolerate periodic movement, is significant. In more stable areas above this zone, where sea-spray is blown over the shingle, plant communities with a high frequency of salt-tolerant species such as thrift *Armeria maritima* and sea campion *Silene uniflora* occur. These may exist in a matrix with abundant lichens.

Photo 12. Lichen heath vegetation on shingle ridges, Dungeness.
Photo English Nature

On the largest and most stable structures (eg Dungeness, Orfordness) the sequence of vegetation includes scrub, notably broom *Cytisus scoparius*, blackthorn *Prunus spinosa* and holly *Ilex aquifolium*. Acid grassland vegetation may occur on older areas of shingle with the associated development of lichen heath. This sequence of plant communities is also influenced by natural cycles of degeneration and regeneration of the shrub vegetation that occurs on some of the oldest ridges.

The ecological development of vegetation on shingle is subject to a number of significant controlling factors, chief of which would appear to be the porous nature of the shingle substrate. This means that little organic matter and nutrients are available to plants (even on stable ridges humus may only be found down to 2cm), and additionally, drainage of rainfall through the shingle is fast and periodically leads to a high degree of desiccation.

9.5.3 Rocky shorelines and reefs

Rocky marine habitats tend to develop in areas where geological outcrops formed of resistant rock occur in the intertidal and subtidal zones. Intertidal rock platforms may extend in an unbroken transition into the subtidal to form reefs.

Rocky reefs are extremely variable, both in structure and in the communities they support. They range from vertical rock walls to horizontal ledges, sloping or flat bedrock, broken rock, boulder fields, and aggregations of cobbles. Reefs are characterised by communities of attached algae (where there is sufficient light – on the shore and in the shallow subtidal) and invertebrates, usually associated with a range of mobile animals, including invertebrates and fish. The specific communities that occur vary according to a number of factors. For example, rock type is important, with particularly distinct communities associated with chalk and limestone. There may be further variety associated with topographical features such as vertical rock walls, gully and canyon systems, outcrops from sediment, and rockpools on the shore. The greatest variety of communities is typically found where coastal topography is highly varied, with a wide range of exposures to wave action and tidal streams. Exposure to wave action has a major effect on community structure, with extremely exposed habitats dominated by a robust turf of sponges, anemones and foliose red seaweed, while reefs in the most sheltered sea lochs and rias support delicate or silt-tolerant filamentous algae, fan-worms, ascidians and brachiopods. Other factors that may significantly affect species composition include water temperature, the presence or absence of tidal streams, water turbidity and salinity. A strong vertical zonation is also apparent. In the intertidal zone, lichens occur at the top of the shore, with littoral biotopes characterised by barnacles, mussels or species of fucoid (wrack) seaweeds. Vertical zonation extends subtidally into the circalittoral (below the photic zone).

A prime example of a rocky reef system where geology is of importance in providing both the overall structural framework to the habitat and also the presence or absence of specific species is Flamborough Head in Yorkshire. Here a number of species associated with the chalk are found and the site is also of importance as it lies close to the biogeographic boundary between two North Sea waterbodies and encompasses a large area of hard and soft chalk on the east coast of England. The reefs and cliffs on the north side of the headland are very hard, resulting in, for example, the presence of many overhangs and vertical faces, a feature uncommon in sublittoral chalk. The clarity of the relatively unpolluted seawater and the hard nature of the chalk have enabled kelp *Laminaria hyperborea* forests to become established in the shallow sublittoral. The reefs to the north support a different range of species from those on the slightly softer and more sheltered south side of the headland.

The Upper Cretaceous chalk exposed on the Thanet Coast of Kent demonstrate the diversity of reef type provided by this one rock type. Here, the longest continuous stretch of coastal chalk in the UK, has sublittoral chalk platforms that extend into the littoral and form chalk cliffs. The sublittoral chalk reefs within the site are comparatively impoverished, owing to the harsh environmental conditions present in the southern area of the North Sea, but are an unusual feature because of the scarcity of hard substrates in the area. The subtidal chalk platforms extend offshore in a series of steps dissected by gullies. Species present include an unusually rich littoral algal flora, essentially of chalk-boring algae, which may extend above high water mark into the splash zone in wave-exposed areas. Thanet remains the sole known location for some algal species.

At a number of sites around the UK, the influence of varying geology is apparent in the form and structure of the reefs and rocky shoreline habitat present and in the types of communities associated with them. In Pembrokeshire, the outcropping rocks mainly comprise igneous rock but also include areas of more friable Old Red Sandstone and some limestone. Extensive areas of sublittoral rocky reef stretch offshore from the west Pembrokeshire coast and between the Pembrokeshire islands and small rocky islets. Limestone reefs occur in the south of the site. Reefs also extend through Milford Haven and into the variable salinity conditions of the Daugleddau estuary. The wide variation in exposure to water movement, the range of rock type, slope, aspect and topography, and the high water quality, together with local exposure to abrasion from adjacent sediments and reduced salinity in the Daugleddau, are reflected in the wide diversity and species abundance of biological communities.

Staying in Wales, one particular reef type is represented by the Sarnau of Cardigan Bay (Sarn Badrig, Sarn-y-Bwch and Cynfelyn Patches). These are very unusual shallow subtidal reefs, which extend many kilometres from the coast into Cardigan Bay. The Sarnau are glacial moraines (resulting from the last glaciation) and are composed entirely of boulders, cobbles and pebbles mixed with various grades of sediments. Fast tidal streams and strong wave action have a profound influence on the marine communities present, and the reefs are characterised by a large number of species resistant to scour and sand cover.

At Strangford Lough in Northern Ireland, glaciated or sea-worn bedrock outcrops are found at many locations. Massive boulders (glacial erratics or the cores of eroded drumlins) occur on the shore and form rocky islands known as ‘pladdies’. Whilst Silurian rocks predominate, sandstones and limestone also outcrop and it is apparent that the fauna and flora associated with these outcrops are dependent on the rock type, the angle of bedding-plane and degree of weathering, the position on the shore, and the degree of exposure to currents and waves.

9.6 Bare ground

Although not strictly a feature of geomorphology processes, bare ground has an important ecological function and can be linked to both geomorphological processes and rock type (eg slope processes in soft sediments). Areas of bare ground, wherever located, often provide valuable habitat space, particularly for invertebrates which are able to exploit relatively small areas. This feature is more important where it occurs naturally such as heathland, calcareous grassland, maritime cliffs, dunes and shingle deposits on the coast, scree slopes, mountain tops and rivers with exposed areas of mud, shingle and sand. From a geological perspective, naturally occurring open and bare ground can be associated with any rock type and in any location as it forms through the action of physical processes rather than as a direct result of the geology itself. There are, however, certain instances in which the local geology plays an important role in the creation of bare ground and the ecological associations that result.

The most useful processes are those that continually inhibit plant succession and maintain firm bare ground over relatively long periods, such as the effects of thin, drought-prone or salt influenced soils, bare rock or scree. Periodic disturbance of soil and vegetation such as that caused by land-slipping or blows in sand dunes and heaths and that caused by animal burrows all have similar effects. It therefore comes as no surprise that areas of open ground and associated fauna and flora therefore tend to be more prevalent in areas where the local geology leads to the production of thin, permeable soils such as those that derive from sands and gravels and calcareous bedrock and in areas where slope instability is a function of the local geology.

As an example of the importance of bare ground to invertebrate assemblages, Key (2000) highlights the fact that of the scarce invertebrates found on the Dorset heathlands (formed largely on Tertiary aged sands and gravels) the majority are associated with bare sand rather than heathland vegetation (117 vs 48 species, respectively).

The ruderal plants that initially colonise bare ground, of interest in their own right, also support many plant-eating invertebrate species that are restricted to particular plants. Some species require plants that are stressed by drought or low nutrient levels, or the warm microclimate generated by the plant growing adjacent to warm, bare soil. Key (2000) suggests that this certainly the case with the UK BAP-listed weevil *Pachythchius haematocepahlus*, which feeds on *Lotus corniculatus*, but only in conditions of extreme heat stress on very dry, south-facing banks exposed to saltwater sea spray on the south coast of England. Clearly, this is a very specific association produced through the interaction of a diverse range of parameters. However, the role that the local geology plays in leading to the derivation of suitable baseline conditions (ie thin, permeable soils on which *L. corniculatus* can survive) is important to note.

10. Comparative studies and links at the landscape level

10.1 Introduction

The discussion and examples provided in the previous sections demonstrate the existence and nature of the influence of geology on plant life. While these provide an illustration of the specific characteristics and influences of rock types, it is perhaps difficult to demonstrate and understand their influence and role in determining plant distribution and extent in isolation. It is, as shown by the paucity of examples provided in the available literature, even more difficult to illustrate the influence of geological factors on fauna, although the indirect, physical influence of rock type can be important. There are, however, a number of studies which provide a clearer indication of the distinctiveness of vegetation and habitat changes associated with geology, that can be observed at the landscape level. These studies, although few and far between, pull together information on the chemical, physical and biological attributes of the study areas in order to provide a scientific basis for changes that are observable and discernible to the human eye.

10.2 Comparative studies

Wentworth (1981), describes the vegetation characteristics of a small isolated mountain range from south-eastern Arizona (the Mule Mountains) and describes the environmental variation produced through the combination of elevation, and rock and soil types. The vegetation response to the variation is an array of plant communities from desert scrub and grassland at lower elevations to arborescent scrub, oak woodland and coniferous forest at higher altitude. The Mule Mountains contain large, accessible areas of limestone and granite outcrops located over similar ranges of elevation and topographic position and thus provide an excellent opportunity to determine the key factors in the presence and distribution of vegetation communities. Studies of the vegetation patterns by Wentworth (1981) show that within the Mule Mountains, limestone and granite areas existing under similar climatic regimes support markedly different plant communities. The differences are the result of modifications of species distributions by soil and physical and chemical properties acting through the physiological requirements of individual species and the competitive interactions between them.

In the arid conditions of the Mule Mountains the calcareous soils represent a more xeric habitat. This is largely due to the fact that soils on limestone are finer textured than those developed on granite and tend to hold water in their upper layers where it is more readily lost through evaporation, whereas the coarser soils developed on granite allow water to penetrate to greater depths where evaporation is reduced.

Differences in the availability of mineral nutrient elements between soils of granite and limestone may also contribute to contrasting vegetation, and soil pH is certainly one of the key controlling factors. The granitic derived soils of the Mule Mountains are not particularly acidic (pH 6.1) and thus potential problems associated with acid soils such as aluminium toxicity or calcium deficiency are unlikely to be an issue. The soils on limestone are relatively basic (mean pH of 7.8) and therefore certain deficiencies of some cations (Fe, Mn, Zn, Cu and Co) may occur. Of these, the actual or physiological unavailability of iron on limestone has received significant attention.

Wentworth notes several contrasting community properties between the granite and limestone outcrops. He notes, in particular, the predominance of shrubby vegetation forms at lower elevations on limestone. Arborescent and herbaceous vegetation (especially perennial grasses) tends to be more prevalent on granite. These differences can be observed in the absence of any known climatic differences, hence soil properties must determine vegetation structure. Soil aridity could be a contributing factor to reduced stature and the greater importance of partially woody (suffrutescent) species in the limestone vegetation. A more favourable moisture regime on granite could promote grassland and open oak woodland under the same climate.

The species richness of plant communities on granite is significantly greater than that on limestone. Wentworth suggests that the physical and chemical properties of the calcareous soils may act as barriers against successful colonisation of the limestone by some species of the prevalent flora. Because of the location of the Mule Mountains on the edge of the Chihuahuan desert the net result is an attenuated flora on limestone, representative neither of the rich regional flora nor that of the Chihuahuan Desert. This does not mean to say that the flora on the limestone is depleted, rather that species richness is low only in comparison with that of the species-rich communities on granite.

The field studies undertaken by Wentworth (1981) lead him to conclude that although soil properties controlled by differences in parent material must be the primary causes of vegetation contrast between limestone and granite, differences in community composition, structure and physiognomy create secondary environmental effects. As an example he quotes that the scattered tree canopies of the open oak woodland on granite result in a heterogeneous understorey microenvironment in terms of litter quantity, solar radiation soil temperature and other soil and chemical factors modified by the biota. On limestone, the low, mixed shrub canopy creates an understorey that probably differs in many significant ways from that of open oak woodland. These secondary factors in the environments of limestone and granite must contribute further to differences in species composition and community characteristics between the two rock types.

The properties of the limestone communities described by Wentworth are also paralleled by similar communities in other parts of the World. Xeromorphism and reduction in community structure are commonly found on soils developed from special parent materials including dolomites, limestones, zinc and copper-rich rocks and serpentines.

The White Mountains, a desert range just to the east of the Sierra Nevada of California, provide another example of the way in which rock lithology has a significant bearing on vegetation. Here, Kruckeberg (2002), describes the situation where the quartzitic sandstone of the Campito Formation abuts the Reed dolomite (a calcium-magnesium carbonate rock) there is an abrupt contrast in vegetation. On the sandstone, a dense, low stand of sagebrush

Artemisia tridentata borders subalpine forests of bristlecone pine *Pinus longaeva* at the lithological contact with the dolomite. This striking contrast between the woody vegetation is also evident in the herbaceous flora. Mooney (1966), recorded a neat edaphic difference for two species of fleabane *Erigeron*. On the sharp contacts between the two lithologies, with *Erigeron clokeyi* being restricted to the sandstone while *E. pygmaeus* is restricted to the dolomite. The causes of this edaphic partitioning are likely to be related to differences in substrate colour (light on dolomite and dark on sandstone) which in turn affects temperature and moisture retention and substrate chemistry.

A detailed phytosociological study by Gigon (1971) (quoted in Kruckeberg 2002) admirably demonstrates the ecological contrasts between carbonate and siliceous substrates. In his study area, the Davos region of Switzerland, the acid glacial till and dolomite limestone of the area were considered the main variables, with climate, topography and time (since glaciation) held constant. Well-defined substrate specificity occurs, with a community on limestone supporting seven calcicole species and a *Nardus strictus* dominated community on siliceous rocks with twenty-three calciphobe species which are absent from the adjoining limestones.

10.3 Natural Areas

A fundamental characteristic of England is the great variety of geology, soils and climate that occur in such a small area. This is reflected, in part, by the subdivision of the country into 97 Natural Areas, which in themselves often provide a reflection of the underlying geology or its modification through weathering and geomorphological processes (see Section 1).

Although, connections and influences can be noted at all scales of observation it is perhaps at the landscape and Natural Area level that any associations between dominant vegetation type and geology can be more readily made. Although sometimes complex and masked by other influences, relationships at this level can be discerned throughout England. However, it is perhaps in those locations where specific assemblages occur, or there are disjunct and clear changes in distribution that the influence of geology may become more apparent and defined. While it may be possible to demonstrate changes in key semi-natural habitat types and vegetation communities for virtually all transitions from one Natural Area or geological outcrop to the next, it is, perhaps more appropriate to use select examples to demonstrate the type of association that exists at this level and the nature of transitions. These are discussed below, but in effect, similar types of distributions and influences exist across the country, in line with the processes discussed in previous sections.

10.3.1 Isle of Wight

The Isle of Wight provides an excellent example of the role that geology plays in the development of characteristic landscape form and the distribution of vegetation communities related to underlying geology. In many respects the ability to demonstrate this comes form the extremely diverse nature of the geological makeup of the Island and the often very clear and apparent changes from one rock formation to the next.

Many examples of the influence of geology on plant life could be gained from a consideration of the various rock formations that form and outcrop on the Island. However, one of the best illustrations is that provided by the narrow ridge of chalk that runs across the Island, between the prominent landform of Culver cliff at the eastern end to the Needles in the west. At Culver Cliff there is an abrupt change from the short, dense characteristic downland turf at the point where the chalk outcrops to the longer, coarse grasses that occur on the Gault Clay and Ferruginous Sands that form the cliff section running towards Sandown. All the common chalk plants, such as yellow-wort *Blackstonia perfoliata*, squinancywort, salad burnet, common rock rose, small scabious and marjoram *Origanum vulgare* can be found in the downland turf at Culver Cliff.

At the western end of the Island it is easy to mark almost to a metre the point at which the Tertiary sands and clays of Alum Bay give way to the white chalk forming Tennyson Down and the Needles, not by looking at the geology, but by walking along the cliff top and noting the change in the vegetation. The chalk downland of Tennyson Down supports many species typical of this habitat in other parts of southern England. The more acidic soil conditions present on the adjacent Tertiary sands of Alum Bay and Headon Warren support plants typical of lowland heathland communities including heather, dwarf gorse *Ulex minor* and common gorse *Ulex europaeus*. Here then, under similar climatic and altitudinal conditions, the basic factor of variability between the observable vegetation communities must relate to the change in bedrock geology. It is likely that the physical and chemical properties of the soils derived from the two rock types differ significantly enough to influence the ability of plant species to become established, resulting in differing plant communities. The key differences are likely to be in pH (more alkaline soil on the chalk), water retention and possibly surface temperature, all of which are important factors in determining plant distribution. One interesting aspect of the chalk downland flora at Tennyson Down and Freshwater is the dwarfed nature of the flora. Many of the common downland species, such as slender-headed thistle *Carduus tenuiflorus*, black knapweed, small scabious and hairy rock cress *Arabis hirsuta* are significantly reduced in stature, probably as a result of the wind and dry conditions (Lousley 1950).

10.3.2 The East Thames corridor

The East Thames Corridor, stretching from London along either bank of the Thames to the open coast, epitomises the way in which a combination of factors come together to produce a unique set of ecological conditions. The geology of the area has played a significant role in the development of these conditions, but its influence on the overall makeup and structure of the communities present cannot be simply isolated or explained.

Geologically, the East Thames Corridor sits at the eastern end of the London Basin. The anticlinal structure of the London Basin brings the Chalk of the North Downs to the surface in north Kent and across the Thames in south Essex (eg at Grays). The Thanet sands and London Clay, which lie above the Chalk, are exposed in areas such as Grays and throughout the area there are sands and gravels deposited during the Quaternary period in the former floodplain of the Medway and Thames rivers. Extensive quarrying of the chalk, sands and gravels for building and construction has led to the formation of numerous pits and quarries which have supplemented any natural exposures that occur in the area. Importantly, the combination of chalk, sands and gravels has given rise to a diverse range of soil characteristics. Generally the sands and gravels give rise to acidic conditions (due to leaching of calcareous material) and the chalk to alkaline, although the acidity of the soils derived from the gravels and sands varies across the area according to the amount of chalk incorporated into them. The London Clay is neutral to alkaline and silts and clays within the complexes of the river terrace sequences are neutral to alkaline. The vegetation of the area varies greatly in response to the range of geological textures and acidities in their various combinations, in line with the characteristics and associations described for these rock types in previous sections.

In recent years, attention has focused on the ecological groups of species found together in the East Thames Corridor. One such grouping is the invertebrate assemblage of the Thames Terrace sands and gravels in this region. The importance of this fauna has been known for some time, but it is only in recent years that the significance of this fauna has been recognised, in part driven by the threats of development. The East Thames Corridor posses a remarkable concentration of rare and scarce invertebrate species, holding, for example, 96% of the Essex aculeate Hymenoptera fauna and 74% of the national fauna. Rare and characteristic species are not confined to this group and a significant number of other species from other groups such as beetles (Coleoptera), flies (Diptera), spiders (Araneae) and bugs (Heteroptera) also occur.

There is some suggestion that the extensive metapopulations of many Red Data Book and Nationally Scarce species have come to more prominence due to longer, warmer summers, which have encouraged an increase in population size and favoured expansion range. The unique characteristics of the invertebrate fauna are summarised by Plant and Harvey (1997) and Harvey (2000), who conclude that it is a combination of the geological, climatic and ecological characteristics of the area which has led to the development of such an interesting and diverse fauna.

The region has a unique climate in Britain, which is more continental than that of the rest of the country. There is a frequent soil-water deficit in the months of May-August in south Essex, which is the driest part of the UK, and in the summer the area is one of the warmest parts of the country. The climate is undoubtedly one of the key factors in the importance of the region to invertebrates. The low rainfall and frequent summer droughts, when combined with the generally nutrient-poor substrates formed on the terrace gravel and sands, generally prevents the development of extensive scrub. This enables the relatively bare and open areas favoured by warmth-loving invertebrates to be maintained for long periods, which in turn allows populations and communities to become established.

The overall management of the area (whether planned or accidental) also makes a very important contribution to the diversity of the rare invertebrate species recorded from the area. Harvey (2000) indicates that it is the presence of unmanaged flower-rich grassland with sparsely vegetated areas which is of crucial importance. Older habitats maintained through low-level grazing or occasional local disturbance, which maintains the open nature of the ground conditions, prevents the loss of the flower-rich grasslands which provide a nectar source for many of the aculeate hymenoptera species. Activities, which in many other habitats would be viewed as of an adverse nature, such as motorbike scrambling and unmanaged fires, are beneficial in that they maintain areas of open and bare ground and prevent succession of the grasslands to scrub.

The role that the geological attributes of the area have played in the development of this assemblage cannot be fully isolated. However, it is apparent that the ecological communities present are reliant, to a large extent on the basic framework of ground conditions that the geological strata of the area provide. As an example, Harvey (2000), quotes that approximately 47% of the aculeate fauna recorded from the region are ground nesting species and a significant proportion of the rest of the fauna are parasitic or kleptoparasitic on these species. For ground-nesting aculeates, nesting requires bare ground, usually sandy, but sometimes firm and in various aspects ranging from flat ground to vertical banks and cliffs. Harvey (2000), suggests that the most important communities are found in areas where there are extensive areas of relatively unmanaged, undisturbed and flower-rich grassland for foraging and hunting, combined with open sandy ground and south-facing banks and slopes for nesting.

The East Thames Corridor therefore shows, in a microcosm, the way in which the various factors influencing the ecology and biodiversity of an area interact. Take away any one of these influencing factors and the resulting fauna and flora, and in particular in this case the unique invertebrate assemblage of the area, would be different to that present today. This is not to suggest that an alteration in any one of the factors would necessarily have a detrimental influence on the ecological assemblages present, as the ecology of the area that developed under the differing conditions, while altered, would have its own value (as viewed from the human perspective). However, management (ie human intervention) is the one factor which we are able to control and therefore to a certain extent the ecological outcomes are contained within certain boundaries by the overriding physical parameters (ie geology, soil and climate).

11. Conclusions

The United Kingdom, for its size, is probably one of the most geologically diverse countries in the World and exhibits a staggering array and diversity of rock types spanning all of the main geological periods from the Precambrian through to the Holocene. This rich geological heritage has played a significant role in the shaping of the English countryside, from the direct influence that geology has on the form of the landscape through to the exploitation of geological resources by man. In many respects, the diversity of the English landscape is a reflection of its geological diversity. Places such as the Malverns, the North Downs, the Breckland district of East Anglia, the Dark Peak and Dartmoor, would not possess their distinct character, feel and inherent ecological interest were it not for their underlying geology (Precambrian volcanics, Chalk, glacial sands, Carboniferous sandstone and granite respectively).

Although the influence of geology on landscape character is one which can be readily appreciated, its relationship with the biological interest of an area is less clear or apparent. The previous sections have set out an overview of some of the information and evidence available on the potential influence of geology and geomorphology on biodiversity, particularly with respect to plant life.

The influence of geology and geomorphological processes may be manifested through a number of factors, both direct and indirect. The direct influence of rock type can be related to both its chemistry and its physical structure. There are numerous examples of how bare rock or rocky slopes act as a habitat for a wide variety of species and community types (eg talus slope communities) and at this level it can be said that rock exposure provides an important function within ecosystems and the biosphere. However, many of the species/assemblages which utilise rock as a habitat do so regardless of its composition (ie sedimentary, igneous or metamorphic), although general characteristics such as hardness vs softness are important factors in determining the suitability of rock types for specific ecological functions (eg as nesting habitat for birds or insects). If, however, we delve beyond the general statement that rock provides a habitat, it is apparent that certain rock types do support recognisable and distinct communities and that these associations must, in some way, be related to the particular properties of the rock itself.

The immediate and direct influence of rock type can be seen in the distribution of lichens, with many species favouring either calcareous (basic) or acidic substrates on which to grow. However, other factors, such as climate and aspect are also very important in defining the boundary conditions (ie the niche space) that support species populations. Significant variations may therefore exist in the distribution of species from one place to another depending on the interaction between these physical variables. Thus an outcrop of Carboniferous Limestone in southern England may well support a different, but broadly similar, plant assemblage to an outcrop of the same rock in northern England. The differences between the two assemblages, in this case, are likely to be more attributable to climatic factors and potentially relief, rather than the geology. A good naturalist can almost determine the likely presence or absence of certain species by the physical conditions around them. For many Victorian and Edwardian naturalists a geological map was often the main instrument used in determining suitable areas to discover new localities for plant rarities and planning botanical tours.

In situations and locations where the variability in the main controlling parameters (ie climate, relief, human management) is reduced to one of near constancy and the variability is provided by the geology it is apparent that vegetation distribution and community composition can be strongly influenced by rock type. The way in which a rock weathers and acts as parent material for soil formation is perhaps the most direct and obvious mechanism for influencing plant species and their growth. The main parameters that rock type influence are soil chemistry, texture, grain size and, as a consequence, porosity. These aspects are all of importance in setting the boundary conditions for plant growth. Numerous studies, show that there is a distinct difference between calcicole and calcifuge plants, largely attributable to differences in pH and its role in controlling the uptake of specific minerals by plants, and this perhaps is the key factor that differentiates the floras of calcareous and non-calcareous rocks. Specific plant-rock associations do occur, but these are restricted to particular rock types with a very distinct chemistry (eg serpentines, dolomites, gabbros etc.) where the presence or absence of certain elements or compounds effectively confines the chemical parameters to a relatively narrow horizon to which, over the millennia, plant populations have adapted and speciated. Rock type may also play an important role in influencing water chemistry, which at the simplest and probably most profound level, leads to the formation of surface and ground waters of alkaline to acidic character. The aquatic communities of lakes and rivers reflect, to one degree or another, the derived water chemistry, with species being adapted to differing pH regimes.

At a physical level, some rocks because of their structural properties and relative resistance to erosion, produce features of relief within the landscape (eg cliffs, hills etc.). These features, in turn, provide heterogeneity with respect to the physical conditions that support plant and animal communities. This acts at all scales, from the smallest cliff or bluff through to hill and mountain ranges. At this larger scale the geological influence is manifested through processes of tectonic uplift (mountain building) and major events (eg the emplacement of intrusive rocks). The relief created by these processes may then have a marked influence on regional and local climate regimes which in turn have a strong control on biota. This also works at a much smaller scale, as evidenced by the often dramatic changes in temperature between ravines and bluffs in areas of sandstone relief and between cliff tops and bases.

Geomorphological processes are the natural modifiers of the structural framework provided by rocks. The action of these processes produce dynamic change within the landscape at a range of spatial and temporal scales. The physical variability introduced by processes such as slope failure promotes ecological succession and cyclicity and increases niche diversity within an area. The influence and character of the physical spaces created by these processes can vary tremendously depending on rock type. Again, this is another example of the almost infinite combination of situations that may arise through the interaction between processes and the physical and biological environment.

The literature and information reviewed for this study demonstrates that geology and geomorphology have a significant influence on biological communities and biodiversity. It is not possible to define this influence with any certainty, but it is apparent that at the simplest level it exists as a direct relationship between chemical supply and biological demand. However, even at this scale the chemistry of rock outcrops and their potential for direct influence on biota may be mediated through soil forming processes. Thus, direct linkages are rare and may be confined to rock surface dwelling organisms such as lichens. Indirect and often complex relationships between geology and geomorphology and biota therefore represent the normal situation. Perhaps the most obvious and least indirect expression of influence is between the weathering of rock, the formation of soil and influence of this on plant growth. But introduce into this relatively straightforward relationship the intricacies of interaction with all of the other physical parameters that have an influence upon and control floral and faunal dynamics and the situation becomes extremely complex. Discerning the potential and actual influence of geological and geomorphological factors at this ecosystem level is more difficult. However, ecological studies demonstrate that geology does have an influence on soil chemistry and the physical structure of the landscape and therefore it can be stated that both geology and geomorphological processes are fundamental building blocks to ecosystems. At this level, given the complexity of linkages, the geological influence diminishes along any line of interaction until it may be difficult to establish or discern any connection between individual species and communities with the geology upon which their habitat is founded. Similarly, because of the multitude of interactions and processes operating in the formation of habitat types, teasing out the geological and geomorphological influences is a difficult task.

Perhaps the most important point to make with respect to the issue of geological influence on biodiversity is that geology (ie rock type) and geomorphological processes are diverse in themselves. This diversity creates and leads to diversity, both in terms of interaction with other processes and by virtue of any direct or soil mediated influence. Without this diversity of rock type and physical form created by rocks, the conditions available to organic life, however subtle or non-descript to us, would be significantly reduced and in this respect the biodiversity that we observe is a direct function of and consequence of geological form and process.

In the UK, it is thanks significantly to our geological diversity that we have a rich and complex mosaic of landscapes, habitats and species. If the country were composed of one dominant rock type then, without doubt, the diversity that we see and appreciate would be quite different and in all likelihood impoverished in comparison with the existing situation.

12. References

ADAMSON, R.S. 1922. Studies of the vegetation of the English Chalk – I. The woodlands of Ditcham Park, Hampshire. *J. Ecology*, 9, 113-219.

BAKER, A., PROCTOR, J., & REEVES, R., eds. 1992. *Vegetation of ultramafic (serpentine) soils: proceedings of the first international conference on serpentine ecology*. Intercept Limited, UK.

BEER, V. 2002. The microclimatic conditions in a part of Saxon Switzerland and its influence on vegetation. An example in the region of "Grosser Zschand". *In*: Abstract proceedings for Sandstone Landscapes: Diversity, Ecology and Conservation; 14 - 20 September, 2002, Doubice in Saxonian-Bohemian Switzerland, Czech Republic.

BIRKELAND, P. 1984. *Soils and Geomorphology*. Oxford.

BILLINGS W.D. 1950. Vegetation and plant growth as affected by chemically altered rocks in the western Great Basin. *Ecology*, 31, 62-74.

BOYLE, A.P., MCCARTHY, P.M., & STEWART, D. 1987. Geochemical control of saxicolous lichen communities on the Creggaun Gabbro, Letterfrack, Co. Galway, Western Ireland. *Lichenologist*, 19, 307-317.

BROOKS, R. 1987. *Serpentine and its vegetation*. Dioscorides Press, Portland.

BROWN, C.J., & BRUTON, A.G. 1991. Plumage colour and feather structure of the bearded vulture (*Gyptaeus barbatus*). London: *Journal of Zoology*, 223, 627-640.

BUNCE, R.G.H. 1968. An ecological study of Ysgolion Duon, a mountain cliff in Snowdonia. *Journal of Ecology*, 56, 59-75.

COATES, F., & KIRKPATRICK, J.B. 1992. Environmental relations and ecological responses of some higher plant species on rock cliffs in Northern Tasmania. *Australian Journal of Ecology*, 17, 441-449.

COLEMAN, R.G., & JOVE, C. 1992. Geological origin of serpentinites. *In*: A.J.M. BAKER, J. PROCTOR & R.D. REEVES, ED. *The Vegetation of Ultramafic (Serpentine) Soils,* 1-17. Andover, UK: Intercept.

COX, E.H.M. 1945. *Plant Hunting in China*. London: William Collins and Sons.

COX, J.E., & LARSON, D.W. 1993. Spatial heterogeneity of vegetation and environmental factors on talus slopes of the Niagara Escarpment. *Canadian Journal of Botany*, 71, 323-332.

ETHERINGTON, J.R. 1981. Limestone heaths in south-west Britain: their soils and the maintenance of their calcicole-calcifuge mixtures. *Journal of Ecology*, 69, 277-294.

FITZPATRICK, E.A. 1986. *An Introduction to Soil Science*. Longman.

FRYDAY, A.M. 1999. *Location of rare lichens on the Ben Lawers NNR, Perthshire*. Unpublished report for Scottish Natural Heritage

GRIME, J.P., & HODGSON, J.G. 1969. An investigation of the ecological significance of lime-chlorosis by means of large scale comparative experiments, 67-99. *In*: I. H. RORISON, ed. *Ecological aspects of the mineral nutrition of plants.* Oxford: Blackwell.

HARVEY, P. 2000. The East Thames Corridor: a nationally important invertebrate fauna under threat. *British Wildlife*, 12(2), 91-98.

HERBEN, T. 2002. Denudation/accumulation dynamics and vegetation patterns in sandstone regions. *In*: Abstract proceedings for Sandstone Landscapes: Diversity, Ecology and Conservation; 14 - 20 September, 2002, Doubice in Saxonian-Bohemian Switzerland, Czech Republic

HOPKINS, J. 2003. Geology and wildlife. *British Wildlife*, 14(3).

HORA, F.B. 1947. The pH range of some cliff plants on rocks of different geological origin in the Cader Idris area of north Wales. *Journal of Ecology*, 35, 158-165.

HOWE, M.A. 2002. A review of the coastal soft cliff resource in Wales, with particular reference to its importance for invertebrates. *CCW Natural Science Report*, No. 02/5/1.

JARVIS, S.C. 1974. Soil factors affecting the distribution of plant communities on the cliffs of Craig Breidden, Montgomeryshire. *Journal of Ecology*, 62, 721-733.

JARVIS, S.C., & PIGOTT, C.D. 1973. Mineral nutrition of *Lychnis viscaria*. *New Phytologist*, 72, 1047-1055.

JOINT NATURE CONSERVATION COMMITTEE. 1999. *British Red Data Books 1. Vascular plants*; 3rd Edition. Compiled and edited by M.J. EDDINGTON.

KERNER VON MARILAUN. 1903. *The Natural History of Plants*. Vols 1 and 2. London: Blackie and Son, Ltd.

KEY, R. 2000. Bare ground and the conservation of invertebrates. *British Wildlife*, 11(3), 183-191.

KRUCKEBERG, A. 1985. California Serpentines: Flora, Vegetation, Geology, Soils and Management Problems. *University of California Publications in Botany*, 78. Berkeley: University of California Press.

KRUCKEBERG, A. 1992. Plant life of western North American ultramafics. *In:* B. ROBERTS, & J. PROCTOR, eds. *The ecology of areas with serpentinized rocks: a world view,* 31-74. Kluwer, Dordrecht.

KRUCKEBERG, A. 2002. *Geology and plant life*. University of Washington Press. Seattle and London.

LARSON, D.W., MATTHES, U., & KELLY, P.E. 2000. *Cliff ecology. Patterns and process in cliff ecosystems*.

LOUSLEY, J.E. 1950. *Wild flowers of the chalk and limestone*. London: Collins New Naturalist Library.

LUNDQVIST, J. 1968. Plant cover and environment of steep hillsides in Pite Lappmark. *Acta Phyogeographica Suecica*, 53, 1-153.

MCCARTEN, N., & ROGERS, C. 1991. *Habitat management study of rare plants and communities associated with serpentine soil habitats in the Mendocino National Forest*. Colusa: U.S. Department of Agriculture, Mendocino National Forest.

MOONEY, H.A. 1966. Influence of soil type on the distribution of two closely related species of Erigeron. *Ecology*, 47, 950-958.

PLANT, C.W., & HARVEY, P. 1997. *Biodiversity Action Plan. Invertebrates of the South Essex Thames Terrace Gravels – Phase I: Characterisation of the existing resource*. Report Number BS/055/96. Peterborough: English Nature.

PLATT, R.B. 1951. An ecological study of the mid-Appalachian shale barrens and of the plants endemic to them. *Ecological Monographs*, 21, 269-300.

POREMBSKI, S. and others. 1994. Vegetation of rock outcrops in Guinea: granite inselbergs, sandstone table mountains and ferricretes – remarks on species numbers and endemism. *Flora*, 189, 315-326.

REINERS, W. 2002. Geological control of plant species distribution in Wyoming. Abstracts from: *Geology, Biogeochemistry, and Ecology: A New Synthesis for Arid Landscape Processes*. Geological Society of America, Annual Conference, Denver, 2002.

ROBERTS, B. 1992. The serpentinized areas of Newfoundland, Canada: a brief review of their soils and vegetation. *In*: A. BAKER, J. PROCTOR, & Reeves, R. eds. *The Vegetation of ultramafic (serpentine) soils: proceedings of the first international conference on serpentine ecology*. UK: Intercept Limited.

RODWELL, J.S. 1992. *British Plant Communities. Grasslands and Montane Communities*, Vol. 3. Cambridge: Cambridge University Press.

ROHRER, J.R. 1983. Vegetation pattern and rock type in the flora of the Hanging Rock area, North Carolina. *Castanea*, 48, 189-205.

RUNE, O. 1953. Plant life on serpentines and related rocks in the north of Sweden. *Acta Phytogeographica Suecica*, 31, 1-39.

SNAYDON, R.W. 1962. The growth and competitive ability of contrasting natural populations of *Trifolium repens* on calcareous and acid soils. *Journal of Ecology* 50, 439-447.

SUTTON, P. 2003. Grasshoppers and relatives. *In*: Wildlife Reports, *British Wildlife*, 14, 208.

TANSLEY, A.G. 1917. On competition between *Galium saxatile* and *Galium sylvestre* on different types of soil. *Journal of Ecology*, 5, 173-179.

TANSLEY, A.G. 1949. *The British Isles and their vegetation* (2 volumes). Cambridge: Cambridge University Press.

TANSLEY, A.G., & RANKIN, W.M. 1911. The vegetation of calcareous soils. B. The sub-formation of the chalk. In: A. G. TANSLEY, ED. *Types of British Vegetation*, 161-186. Cambridge: Cambridge University Press.

WENTWORTH, T.R. 1981. Vegetation on limestone and granite in the Mule Mountains, Arizona. *Journal of Ecology,* 62(2), 469-482.

WHITTAKER, R.H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, 30, 279-338.

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