Chapter 2 Microclimate

The topic of microclimatology is outlined here in some detail including its measurement, e.g. solar radiation, soil temperature, humidity, wind. The relevance of microclimate to the dynamics of plant communities and associated organisms is emphasized. The relationship between microclimate and climate is carefully defined and the very different methods used to measure microclimatic variables are described.

2.1 Introduction and definitions

The collection of weather data is standardised so that readings from different locations are directly comparable. Official weather stations must be located on a patch of level ground at least 10 x 7 m, not in a hollow and well away from buildings and trees. The thermometers must be fitted inside the familiar white-painted Stevenson screen (a ventilated box) the base of which must be 1.1 m above well-mown turf (Unwin & Corbet, 1991). Meteorologists are primarily interested in the atmosphere rather than the layer of air immediately above the ground or 'active surface', (Oke, 1987). However, this is where most plants and insects live and factors such as temperature, humidity and windspeed can differ greatly from values measured in a weather station (Cloudsley-Thompson, 1975). The influence of factors such as soil, vegetation, slope, aspect and exposure (Brunt, 1945, 1953) on this 'boundary layer' (Oke, 1987) is strongest in the lower 2 m of the atmosphere and the upper 0.5 to 1 m of the soil (Geiger, 1965). This very local climate near the ground is called 'microclimate' (Rosenberg et al., 1983) and its study is usually called 'micrometeorology' (Unwin & Corbet, 1991). Unlike conventional meteorology, it is essential that not only horizontal gradients are considered but also vertical ones (Yoshino, 1975; Stoutjesdijk & Barkman, 1992).

Naturally, vegetation has a considerable influence on the microclimate, thereby creating its own 'ecoclimate' (Stoutjesdijk & Barkman, 1992). The climate on the smallest scale is sometimes called the 'nano-' (Stoutjesdijk & Barkman, 1992) or 'epiclimate' (Monteith, 1981). This is bound directly to surfaces such as a leaf, air cavities in litter, an ant-heap, or fissures in rock (Cloudsley-Thompson, 1969). A thin boundary layer of air, characterized by its own temperature and moisture content, 'sticks' to these surfaces even in strong winds. The height above the surface, where the nanoclimate prevails, is measured in mm, whereas the microclimate is measured in cm or dm. As regards the horizontal scale:

the 'macroclimate' may extend over hundreds of km, the 'mesoclimate' over km or hm, the 'microclimate' over m or hm and the nanoclimate over cm only (Stoutjesdijk & Barkman, 1992). The microclimate is directly relevant to vegetation ecology and the distribution and population dynamics of plant and animals. The nanoclimate is linked to ecophysiology and the population ecology of very small organisms. Smith (1954) distinguished the 'plant climate' or layer of air near the ground (i.e. microclimate) from the more specific 'insect climate' (i.e. nanoclimate) or conditions under the bark of a tree, in an ants' nest, or a burrow in the soil.

2.1.1 Solar radiation

As electromagnetic radiation this forms part of a continuum of radiation types differing in wavelength. Light between 400 and 700 nm used in photosynthesis is referred to as 'photosynthetically active radiation' (PAR). This makes up about half of the energy provided by solar radiation. During the year, the radiation intensity varies with the highest value in July when the earth is nearest the sun, and its lowest value in January, when the earth is farthest away. Part of this radiation is scattered (particularly shorter wave-lengths) or absorbed, but the bulk reaches the earth's surface. The proportion of solar radiation reflected by the soil surface or vegetation or 'albedo' varies (e.g. with soil colour, Ludwig & Harper, 1958) considerably from 0.1 for a coniferous forest to 0.95 for fresh snow (Stoutjesdijk & Barkman, 1992). Agricultural grasslands and low crops with a homogeneous, closed texture and an even canopy have relatively high albedo values, up to 25% of total reflectance. More natural grasslands have lower values since openings and height differences in the vegetation lower the reflection. It also depends on the angle of incoming radiation, often and is higher at lower angles.

2.1.2 Air temperature

The above-ground temperature drops rapidly with increasing distance from the soil surface and a general profile occurs above any surface. Near the soil surface we find a thin layer of air without any air movement. Heat transfer occurs through conduction but the temperature decreases greatly in this thin layer. Above it occurs turbulence, small parcels of hot air are rising and are replaced by colder parcels from above. As a result the temperature fluctuates a great deal here. A very small organism living on the ground experiences very large temperature differences and must show behavioural adaptations to cope with this. For exmaple,, the beetle, Cicindela hybrida, obtains access to heat in the early morning by pressing itself against the warm sand, already warmed up by the sun. As soon as the temperature at the soil surface rises above 40 °C, the beetle avoids heat problems by raising itself up on its legs ('stilting') so that its body moves up to 8 mm above the surface (Dreisig, 1980).

Hence, the air in the lowest few cm has completely different properties as far as turbulence, temperature and humidity are concerned than at a higher level. Uplifting air masses are important on a small scale for 'ballooning' spiders (Vugts & van Wingeren, 1976) and on a larger scale for soaring birds of prey (Scorer, 1954). Turbulent exchange (or thermal convection) is responsible for most of the vertical transport of air masses which carry heat and water vapour upwards and supply the CO_2 required for photosynthesis from the atmosphere above. It may also transfer heavier objects such as seeds, spores and small insects (Stoutjesdijk & Barkman, 1992).

2.1.3 Air humidity

All soils, air and organisms on earth contain water which is essential for life to exist. Water affects the albedo, heat capacity and thermal conductivity of objects. It may evaporate or condense as haze, mist, fog, dew or hoarfrost. This depends on the temperature and humidity of the air. It is difficult to separate the biological process of transpiration by plants from the purely physical process of evaporation. The joint water dissipation of soil and vegetation to the atmosphere is therefore called 'evapo-transpiration'. The most commonly used humidity parameter is 'relative humidity' (%) or the amount of water vapour in the air divided by the amount that would be contained in the same volume of saturated air at the same temperature. A related measure, 'saturation deficit', is the difference between the vapour pressure of the air and the vapour pressure of saturated air at the same temperature (in millibars).

2.1.4 Soil microclimates

Soils vary in factors such as pore space, texture and structure that influence soil water and air content and temperature. Hence, soil temperature depends on external factors such as latitude, altitude, season, time of day, weather conditions, aspect and shadow but also on the physical properties of the soil, namely, albedo, specific heat by volume and heat conductivity. The smaller last these three parameters, the more the surface temperature will rise during radiation e.g. the darker or more moist the soil (low albedo), the greater the radiant energy absorbed (Jones, 1976). Sandy soils and other coarse, loose and dry soils (high albedo) are subject to wide fluctuations in surface temperature with little penetration.

Compacted, wet soils are better conductors and exhibit more equable surface temperatures and greater penetration (Brunt, 1953). Daily variations in weather cause temperature to fluctuate regularly in the upper layers, but when one gets down to a depth of about half a metre, the exact depth depending on the type of soil and recent rainfall, then the temperature is almost constant during the day and night. Seasonal variations extend down to a depth of many metres (Unwin & Corbett, 1991). A surface layer of material of low conductivity tends to insulate the soil below from the effects of temperature variations. Thus, freshly fallen snow, moss cover or a well developed litter layer will protect against a subsequent frost.

2.1.5 Wind

This is an environmental factor that varies tremendously from point to point. At high wind speeds the most obvious effects are mechanical, while at low speeds the effects concern transport processes such as heat transfer and evaporation (Grace, 1977). Measurements have shown that wind velocity decreases exponentially with decreasing height above any surface. The effect of increasing wind on the temperature of objects is to bring them nearer to the temperature of the air. Hence, it is in the boundary layer, close to surfaces, that the more extreme temperatures can develop.

Windspeed is always much reduced within vegetation. This reduction may be gradual in more open vegetation where the wind speed decreases considerably towards the surface, or rather the amount of air movement, because the turbulence can be very great. In vegetation with a closed canopy, the amount of air movement decreases abruptly but may increase again further down where the vegetation under the canopy is more open, and decreases yet again near the ground (Stoutjesdijk & Barkman, 1992). When an object is placed in an airstream, the airflow is modified. One of the most effective ways of decreasing wind speed, by providing shelter, is to plant a hedge. Rosenberg (1966) found that shelter sharply reduced wind movement over a canopy of plants and generated a new diurnal pattern of air and soil temperature (Brown & Rosenberg, 1972). This may increase crop yields but can encourage fungal diseases (due to increased humidity) and harmful insects (Hatfield, 1982).

2.2 Measuring microclimate

The instruments used in microclimate measurement usually differ from those used by meteorologists in three ways. In the first place, they are much smaller. In a weather station, size is unimportant, and the slow response of a large thermometer may even be considered an advantage in that it averages out short-term variations in temperature. In contrast, microclimatic measurements aim to record these short-term variations which may, for example, correlate with aspects of insect behaviour. Small thermometers have the advantage that they respond rapidly and are little affected by direct solar radiation. The second difference is that microclimatic instruments are not located in a specially screened and protected environment, but are placed exactly where the measurement is required. The third difference is that readings are taken much more often than once a day, and may even be continuously monitored. Most microclimate instruments are electrical sensors connected to meters that measure voltage, current or resistance. Techniques for microclimatic measurement are discussed by Cloudsley-Thompson (1962, 1969), Unwin (1978, 1980; Unwin & Corbet, 1991) and Stoutjesdijk & Barkman (1992).

2.2.1 Temperature

This is the most important aspect of microclimate measurement not only because it is important for the study of plants and animals, but also because it is a means of measuring other microclimate factors such as radiation, humidity and wind. An instrument that measures temperature consists of two parts: a sensor, which is a device that changes in some way with temperature, and an indicator, which provides a way of measuring this change. The familiar mercury-in-glass thermometer uses the expansion of mercury in a glass bulb as a sensor, and the indicator is provided by a mercury column in a capillary whose length is proportional to temperature. Such thermometers can indicate the temperature of the mercury-filled bulb very accurately, but this may not be the same as the temperature one is trying to measure. The measurement of air temperature is complicated by the effect of radiation which warms the sensor, and by the poor thermal coupling of the sensor to the air. The size of the sensor may affect the situation in two ways. The first is that the energy received by radiation is directly proportional to the area of the sensor exposed to it. The second is that the smaller the sensor is, the faster it can be cooled by a given wind speed. Sensors should therefore be as small as possible, and they should be well ventilated and, if possible, shielded from direct solar radiation.

For most serious microclimatic work, minature electrical sensors are used. The most versatile of these is the thermocouple, which is a junction between dissimilar metal wires. Any junction between wires made from different metals will produce a voltage that is proportional to the temperature. Another type is the thermistor, the common form of which is a device whose resistance decreases with an increase in temperature. Silicon diodes, which pass current in one direction only, can also be used. When a constant current is passed through them, they exhibit a voltage that is about 600 millivolts for each degree C rise in temperature. Of the three kinds of electrical sensor, the thermocouple is the most versatile, since it can be made to suit almost any situation. All thermocouples made from wire of the same material will have the same calibration, which is convenient when several sensors are required for an experiment. Thermistors are the most expensive of the three sensors, but are also the most sensitive. Silicon diodes are very cheap indeed which is particularly useful in situations where it is desirable to install a large number of sensors.

Finally, there is a new kind of low-cost thermometer that uses liquid crystal technology. This thermometer is usually available in the form of a strip of self-adhesive material which has a row of coloured dots or numbers that become visible at a graded series of temperatures. Similarly, there are paints that indicate temperature by means of colour change. Although not very accurate, they may be used to great effect where a non-intrusive method is required. In an attempt to obtain a temperature reading that takes account of solar radiation, thermometers are sometimes fitted into a blackened sphere, usually 15 cm in diameter. Such 'back globe thermometers' of a suitable size are particularly useful in estimating the temperature that an insect will reach when sitting on a leaf.

2.2.2 Radiation

Traditional sensors of shortwave solar radiation (solarimeters or pyranometers) use thermal techniques. In the usual design, a disk is divided up into alternate black and white segments. This is covered by a glass dome which a) prevents wind affecting the temperature of the disk and b) absorbs longwave radiation from the disk. Although the black segments absorb a much higher proportion of shortwave solar radiation, the emissivity of all segments at long wavelengths is similar. The black segments therefore get hotter, in the presence of solar radiation, than the white segments. The temperature difference between the black and white segments is indicated by thermocouple sensors.

A very much simpler approach is to use a solar silicon cell. This has the property that when connected to a low resistance, the voltage accross the resistance is proportional to the radiation received. It responds to radiation with a wavelength in the range 0.3-1.0 microns which is somewhat narrower than the range of the sun's radiation but contains most of the energy. Since the spectral composition of sunlight does not change greatly during the day, the error likely to result from this deficiency is small. Solar radiation with a wavelength in the range of about 0.4-0.7 microns is called light. Light can be measured by using a solarimeter fitted with a filter which admits only these wavelengths, but it is usually more convenient to use some kind of photocell. This is a sensor whose electrical properties are affected by light. For example, the cadmium sulphide photocell is very sensitive and easy to use.

2.2.3 Humidity

The best hygrometers are those that measure the electrical capacity of a layer of oxide on an aluminium plate. They are accurate, have a very quick response and have little effect on the air around them, but unfortunately are very expensive. Humidity can also be measured using thermal methods. The 'wet and dry bulb thermometer' or 'psychrometer' uses the difference in temperature between a sensor measuring air temperature and one measuring the temperature of a surface that is evaporating water. This difference is referred to as the 'wet bulb depression' and is independent of the rate of airflow past the sensors above a value of about 3 metres per second (m sec^{-1}). Psychrometers may be 'aspirated' where air is blown past the sensors at above 3 m sec^{-1} or 'non-aspirated', which rely on a naturally occurring air current. In practice, the former are much more accurate.

Another method of estimating humidity is to measure the 'dew point'. If a metal plate is cooled, the air in contact with it becomes saturated, and a film of dew forms. If it is then allowed to warm up, the temperature at which the dew disappears is called the dew point. The relationship of relative humidity and dew point is well established. If a small droplet of a water-based solution is exposed to the air, water molecules will move between the solution and the surrounding air until the solution is in equilibrium with the humidity of the air. This is the basis of the Corbet aqueous droplet technique (Unwin, 1980). This is a very useful technique, enabling measurements of humidity to be made on an extremely small scale. Finally, there is the simple technique for estimating humidity which is sometimes useful, particularly for the purposes of comparison. If a piece of paper is soaked in cobalt thiocyanate solution and allowed to dry, its colour will change from red to blue over range of about 50-90% relative humidity. This method is clearly inaccurate, but is useful for comparison, e.g. if one wishes to see whether one place is wetter or drier than another, even on a very small scale.

2.2.4 Wind

At ground level, wind direction is seldom of great interest, since turbulence often makes it extremely variable. Wind vanes are therefore usually placed at least 1 metre above the ground. Average wind speed is usually measured by some variant of the cup anemometer. This usually has three cups that cause the shaft to rotate at a speed proportional to the wind velocity. A counter is used to count the number of turns of the rotor over a known interval of time, such as 1 hour. Wind speed is usually expressed in metres per second. If measurements are needed on a smaller scale the anemometer may take up too much space. A more suitable method is to measure the drop in temperature of a heater exposed to the air. If it is small, it will measure instantaneous wind speed, but if its thermal mass is made large, so that it changes temperature only slowly, it will average windspeed over time.

2.2.5 Recording microclimatic data

In order to build up a picture of the microclimate of a study site, measurements must be distributed within the site, and spread through time. A decision has to be made as to where and when to take measurements. Ideally, there should be a large number of measurement points, which should be read continuously. In practice, only a relatively small number of measurement points can be made, recording them at regular intervals. It is therefore important that the measurement points are relevant to the object of the experiment.

Chapter 3 Vegetation structure

Vegetation may be described in various ways, but in the present context we are concerned with its physical structure. Clearly, this structure may change markedly in both space and especially time (i.e. its dynamics). It may depend on the interaction of various factors including abiotic (e.g. climatic) and biotic (e.g. plant-soil, plant-plant and animal-plant) interactions. Climate change may influence vegetation structure through both direct effects on plant development (i.e. seedling regeneration, growth, and reproduction) and indirect effects mediated through soil processes. Management methods which are discussed in a later chapter also have an effect on the spatial and temporal patterns of vegetation structure.

3.1 Introduction and definitions

Structurally, vegetation may be described in terms of its texture, horizontal pattern, vertical pattern and co-occurence pattern (van der Maarel, 1988). 'Texture' (sensu. Barkman, 1979) is the qualitative and quantitative (i.e. relative abundance, Grubb et al., 1982) composition of the vegetation in terms of different morphological elements including species, life-forms (Raunkiaer, 1934; Dansereau, 1951), growth forms (Lovell & Lovell, 1985; Waller, 1986) and leaf sizes (Fliervoet, 1987). Horizontal pattern describes its heterogeneity due to, for example, tussock formation (Belsky, 1983), or soil heterogeneities (Lotz & Olff, 1988). Vertical pattern, which is most relevant here, is the vertical arrangement of biomass and stratification (Spenceley, 1973) and describes vegetational complexity. This can be represented as height profiles which illustrate the distribution of plant material in a vertical plane (Aber, 1979; Brown, 1991a). Co-occurrence (or sociological sensu Kershaw, 1973) patterns result from positive (mutualisms) or negative interactions (competition, allelopathy) between individuals of different species.

Most early descriptions of vegetation tended to be floristic, ignoring its structure or 'physiognomy' although recognition (by Charles Elton) of the importance of 'habitat' for organisms redressed the balance somewhat. Based mainly on the height of the perennating buds above the ground, Raunkaier (1934) described vegetation in terms of its constituent 'life-forms'. Dansereau (1951) devised a 'structural' system for the description and recording of vegetation based on life form, size, function, leaf shape and size, leaf texture and coverage. A similar system involving phytomass, leaf area index, leaf size and inclination was used by Fliervoet (1987) to characterize different grasslands. Small leaf size and horizontal inclination is characteristic of unproductive grasslands whilst larger more vertically inclined ('erect') leaves occur in highly productive grasslands. Elton and Miller (1954) recognized distinct vertical layers within terrestrial habitats, namely, the subsoil and rock, topsoil, ground zone, field layer, low canopy, high canopy and air above vegetation. 'Habitat structure', defined as "the physical arrangement of objects in space" (Bell et al., 1991) is now an expanding subject for research (McCoy & Bell, 1991). The development of suitable ecological methodology (e.g. point-frequency and harvesting, Mueller-Dombois & Ellenberg, 1974) and more recent technical advances (e.g. profile photographs, ver Hoef et al., 1989; digital picture processing, Roebertsen et al., 1988) now permit detailed analysis of vegetation structure.

3.2 Vegetation dynamics

Defined as the total changes in vegetation structure this includes five aspects: disturbance, fluctuation, periodicity, regeneration, and succession (van der Maarel, 1988). 'Disturbance' is the stochastic and patchy occurrence of environmental events, both abiotic (e.g. drought, fire) and biotic (e.g. local herbivory), leading to loss in biomass (i.e. death of leaves or individuals). 'Fluctuation' is the irregular occurrence of environmental changes on a larger temporal and spatial scale, e.g. year-to-year changes in summer precipitation. 'Periodicity' is the occurrence of regular changes, e.g. seasonal variations in biomass (Al-Mufti et al., 1977; Bobbink et al., 1989).

'Regeneration' includes the associated development of new organs and individuals from seed or vegetative reproduction in relation to disturbance, fluctuation and periodicity. A central concept in the dynamics of structure is the 'gap' (Grubb, 1976; Peart, 1989; Hillier, 1990), i.e. any opening in the vegetation canopy. Despite their extremely small size, (Harper et al., 1965) attempts have been made to quantitatively measure such germination microsites in grasslands (Silvertown & Smith, 1988, 1989) and heathlands (Williams, 1992). 'Succession' concerns long-term directional changes in ecological patterns and strategies (e.g. plant species composition, Mellinger & McNaughton, 1975; Nicholson & Monk, 1975; Tramer, 1975) as a result of major changes in the environment (Odum, 1969; Brown and Southwood, 1987). The processes of regeneration and succession bring about changes in structure, which can be described as changes in horizontal and vertical pattern. Changes during succession lead to 1) changes in texture and increase in average size of the plant unit area, plant height diversity, leaf size diversity, growth form diversity and biochemical diversity, 2) increase in the vertical differentiation, 3) increasing complexity of interaction patterns, with a tendency towards increasing local patch dominance and 4) increase in gap size and gap age diversity, both important for species diversity (van der Maarel, 1988).

A number of ecological patterns are associated with the change from variable, unpredictable 'pioneer' to more stable 'climax' communities (Odum, 1969; Bazzaz, 1979). Most studies have found that plant species diversity increases rapidly in early succession, then levels off before declining at climax (Odum, 1969; Nicholson & Monk, 1974; Brown & Southwood, 1987). Despite the decline in plant taxonomic diversity in late succession, insect diversity is maintained by the higher 'architectural' (Lawton, 1986) diversity of climax vegetation (Southwood et al., 1979). Studies have found that both niche breadth and overlap (Bazzaz, 1987), seed size (Fenner, 1987) and plant defence (Brown & Southwood, 1987) are greater and reproductive effort (Newell & Tramer, 1978; Stewart & Thompson, 1982) and seed bank formation (Donelan & Thompson, 1980) less in earlier compared to later successional species.

3.3 Factors affecting vegetation structure

Both abiotic (e.g. fire, drought, nutrient stress) and biotic conditions (e.g. competition, herbivory, mycorrhizal infection; the latter discussed by Newman, 1988) affect plant performance and thereby determine vegetational composition and structure.

3.3.1 Abiotic factors

a) Fire

The influence of fire on vegetation structure (size, age, spatial distribution) depends on its periodicity (Hobbs, 1984; Gibson & Hulbert, 1987; Mushinsky & Gibson, 1991). The manner in which a habitat burns depends not only on ambient temperature, wind speed, and humidity, but also on the spatial distribution of fuel loads and structural variation. Specific plant structures have higher flammability.

Hobbs and Gimingham (1984) found that variation in fire temperatures between stands of Scottish heathlands was related to vegetation structure (type and height of plants), amount, and distribution of fuel. Heterogeneity of fire temperatures within a stand of vegetation appears to be related to moisture content of the litter layer (Hobbs et al., 1984). Also, they found higher, and more variable temperatures in older stands, reflecting the patchy nature of old, undisturbed heathlands. This patchiness coupled with the creation of gaps for seedling regeneration and increased flowering and seed dispersal of certain species can increase heterogeneity (Shafi & Yarranton, 1973).

b) Drought

Availability of soil water is a prime determinant of plant community structure largely mediated through differential patterns of seedling regeneration. Communities where water is in short supply tend to be dominated by plants showing some type of drought tolerance or annuals which escape the drought as dormant seeds (Crawley, 1986). Because such species show different germination patterns, unpredictable rainfall patterns or drought stress may be an important factor causing year-to-year fluctuations in species composition and relative abundance (Hopkins, 1978; Tilman & El Haddi, 1992; Espigares & Peco, 1993). Hopkins (1978) found that the exceptional drought in 1976 (the severest for 250 years) resulted in almost 40% bare ground compared with ca. 5% in normal summers. This was associated with an increase in annual and a decrease in perennial species.

c) Nutrient availability

In low nutrient environments (e.g. calcareous soils) plants are slow-growing, small in size and, have small, leathery, long-lived leaves and high root: shoot ratios (Chapin, 1980). Plant communities tend to be open with bare gaps between the plants due to slow rates of vegetative spread (Grime, 1990). This permits seedling establishment of subordinate species thereby promoting coexistence (Hillier, 1990). Experimental addition of nutrients to chalk grasslands affects the vertical structure of the vegetation favouring dominant grasses, e.g. Brachypodium pinnatum (tor grass), thereby reducing light penetration in the canopy and decreasing species richness (Bobbink et al., 1988; Bobbink, 1991; Willems et al., 1993). The nature and rate of succession in calcareous grasslands also depends on soil fertility (Green, 1972; Gibson & Brown, 1991a).

d) Topography

Evans and Dahl (1955) found that the topographic variability of an abandoned field was primarily responsible for the major vegetational subdivisions. Similarly, Sterling et al. (1984) found that microrelief proved to be a key factor responsible for vegetation structure in the early stages of succession, where the ridges and furrows created by the plough created fine-grained patterns. Similar, 'hummock-hollow' microtopography with associated soil and floristic heterogeneity is found in dune grasslands (Gibson, 1988a, b). On skeletal soils, a mosaic of crevices and rocks may produce heterogeneity in rooting depth and soil moisture status which may increase species richness (Grime *et al.*, 1987; Glenn-Lewin & ver Hoef, 1988). In limestone pavements, the species composition of 'grikes' which vary in depth and width is determined by both the microclimate and the intensity of sheep grazing (Silvertown, 1983).

e) Aspect

In northern latitudes warm, dry south-facing slopes are the most suitable habitat for plants with a southern distribution whilst cool, moist north-facing slopes favour plants with a northern distribution. This is mainly related to differences in solar radiation (Pope & Lloyd, 1975). The plant geographer, S. A. Cain, remarked that a plant species at the edge of its range finds itself on the slope with an aspect facing towards the centre of its distribution. As an example, wild strawberry (*Fragaria vesca*) is found in the Mediterranean lowlands where it occurs mainly on north-facing slopes, in temperate Europe it occurs on level ground and gentle slopes, whereas in N. Norway the species is restricted to south-facing slopes (Stoutjesdijk & Barkman, 1992). The Mediterranean plant *Frankenia laevis* shows a clear preference for the south side of sandy ant hills of *Lasius flavus* in Norfolk salt marshes (Woodell, 1974). When a plant grows on both slopes, the development is usually faster on the south-facing slope. Stoutjesdijk and Barkman (1992) showed that the flowering of dandelions (*Taraxacum officinale*) on the south-facing slope of a dike was almost completed before that on the north-facing slope.

On the 800 m high Lagern, a limestone mountain range running east-west near Baden in the Swiss Jura, Stoutjesdijk and Barkman (1992) observed a very sharp transition separated by a mountain ridge 50 cm wide. On the south-facing slope was a *Quercus pubescens* woodland with southern species such as *Orchis pallens*, *Viola mirabilis* and *Melittis melissophyllum*. The north slope supported a beech forest containing subalpine species such as *Thalspi alpestre* and *Asplenium viride*. This is like comparing an altitudinal difference of 1000 m or a latitudinal difference of 1000 km. Marked differences also occur in temperate coastal dunes. South-facing slopes have an open plant cover with *Corynephorus canescens* and lichens whilst north-facing slopes have a dense dwarf shrub cover with the boreal species *Empetrum nigrum*. In the moss layer, several liverworts and *Leucobryum glaucum* are typical of the north-facing slope (Stoutjesdijk, 1959). Differences can be found also on a very small scale. The vegetation on north and south exposed sides of ant-hills is often very different in both total cover and species composition.

3.3.2 Biotic factors

a) The seed rain

The spatial distribution of seedlings of a species is determined by the distribution of parent plants, the pattern of seed rain around them (or 'seed shadow', Janzen, 1971) and the availability of suitable gaps for germination. Seeds are dispersed by a number of agents including wind, water, and animals (van der Pijl, 1982). Large herbivores may transport seeds both internally (Welch, 1985) and externally (Edwards and Gillman, 1987). But for many species most seed comes to rest close to the parent plant (Salisbury, 1942; Rabinowitz & Rapp, 1981) and seed density falls off exponentially with distance from the parent (Harper, 1977). Verkaar et al. (1983) studied wind dispersal of short-lived species of chalk grassland and found rather limited dispersal of seeds (0.3 to 3.5 m) affected by the interaction of stem height and wind profile. This produces a close qualitative correlation between the species composition of the seed rain and existing flowering plant community (Jefferson & Usher, 1989).

b) Soil seed banks

Only an estimated 10-30% of the seeds released by a chalk grassland plant emerge in the spring of the following year (Keizer et al., 1985). Predation by voles, ants and beetles may reduce potential germination by 30-70% (Verkaar et al., 1986). Seed burial may also occur and a reserve of seeds, the seed bank, may remain 'dormant' in the soil delaying germination to a later, more favourable season (Fenner, 1985; Silvertown, 1988). Weedy or ruderal species that produce many small seeds are a major component of grassland seed banks (Rice, 1989). Hence, seed longevity is greater in annuals than perennials and in forbs (especially legumes) than grasses (Roberts, 1981). In addition, smaller seeds have increased chances of burial and reduced seed predation (Grime, 1989). Differences between species in estimated seed bank size reflect variations in the extent to which species form seed banks as well as their established abundance and seed production. Seed banks may be markedly patchy (Chauvel et al., 1989) as a result of the dispersal process, since seeds being generally aggregated around the mother plant. The spatial distribution of seeds depends on the size and shape of the seed 'shadow' and the seeds themselves, the dispersal agents and the spatial heterogeneity of parent plants (Dessaint et al., 1991).

The species composition and abundance in the seed bank often reflects that in the above-ground vegetation. This has been postulated to occur under frequent and unpredictable disturbance (Henderson, et al., 1988) which tends to favour the annual and short-lived perennials (i.e. ruderals) that readily form seed banks. This contrasts with chalk grasslands where the two differ markedly (Schenkeveld & Verkaar, 1984; Jefferson & Usher, 1987). In these cases, the vegetation may be more closely related to the seed rain (Jefferson & Usher, 1987).

c) Grazing

The actual impact of herbivory may be unrelated to quantitative consumption and differences in the type and timing of tissue removal are often critical (Edwards & Gillman, 1987). The specific effects of grazing depend on its intensity (Putman, 1986), timing (Jones, 1933) and selectivity (Spedding, 1971). Preference occurs for greener, more digestible foods which are higher in energy and nutrients (Crawley, 1983). Sheep prefer leaf to stem and green to dry matter as both are higher in nitrogen and phosphorus and lower in fibre (Arnold, 1964). Satiated animals are more choosy, greater selectivity occurs with higher forage availability and in more patchy swards and seasonal switching occurs with changes in availability and quality (Putman et al., 1987). Preferences may result in very uneven habitat use. Oosterveld (1983) showed that ponies grazing a 100 ha grassland used 3% heavily, 70% moderately to highly and 27% at a very low level. Furthermore, grazers not only defoliate, but also have an impact from producing dung and urine (Marsh & Campling, 1970; Lotero et al., 1966), trampling (Bates, 1935; Edmond, 1968; Liddle & Moore, 1974; Thomas, 1960a) and dispersing seeds (Janzen, 1971; Welch, 1985).

Grazers may profoundly influence the physical structure of vegetation. Native grazers as diverse as ungulates (McNaughton, 1984), geese (Cargill & Jefferies, 1984) and tortoises (Merton, et al., 1976) may modify vertical structure by reducing canopy height and creating 'grazing lawns'. Sims et al. (1978) studied the structure and function of ten western North American grasslands and found that mean live biomass and dead plant material averaged 98 and 160 g m^{-2} in ungrazed grasslands and 89 and 70 g m^{-2} in grazed grasslands respectively. In the subhumid grasslands of Argentina, Sala et al. (1986) found that in grazed areas most of the green material was concentrated in the 0-5 cm layer while in the ungrazed treatments the largest portion of the leaf area was in the 10-30 cm layer.

Gibson et al. (1987a, b) found that a short-period of spring grazing by sheep produced major changes in sward characters, such as height and density, which persisted throughout the season. In the New Forest, grazed areas are less structurally diverse than those in enclosures (Putman et al., 1991).

In contrast, grazing often increases horizontal structural diversity. Bakker et al. (1983) found that preferential grazing of an initially uniform sward created both a macro-pattern of different plant communities and a stable 'micro-pattern' of short, heavily grazed and tall, lightly grazed patches. Similar patterns have been found in grasslands grazed by cattle (van den Bos & Bakker, 1990) and horses (Edwards & Hollis, 1982) but the latter are the result of selective eliminatory behaviour rather than grazing per se (Odberg & Francis-Smith, 1976). In contrast, where underlying soil heterogeneities exist, e.g. hummock-hollow systems in dune grassland (Gibson, 1988a, b), grazing may reduce patchiness in the vegetation.

Grazers may act directly as 'mutualists' by adding species or as 'predators' driving them to local extinction. However, most of the effects of grazing on plant communities occur indirectly by modifying relative competitive abilities. Effects on vegetation structure are also often compositional. By creating a short turf, grazers may create suitable gaps for seedling establishment. Compared to grazed turf with patches of bare ground, a tall ungrazed sward restricts germination of perennial herbs (Rusch, 1988; Watt & Gibson, 1988). Defoliation tends to eliminate graze-sensitive species favouring those tolerant or resistant by virtue of low palatability, physical defence, toxins or prostrate growth form (Putman, 1986). Jones (1933) found that the composition of grass-clover swards was determined by the timing of sheep grazing. Hard spring grazing favoured the dominance of Trifolium repens (white clover), but later grazing tipped the balance in favour of Lolium perenne (perennial ryegrass). Clear evidence comes from long-term exclosure studies. In the Serengeti, 13-14 year protection from grazing led to the removal of the grazophile, Andropogon greenwayi, due to competition from the productive, grazing sensitive Pennisetum (McNaughton, 1976).

Further evidence on the effects of grazing is provided by the changes resulting from the decline in the rabbit population due to myxomatosis (Thomas, 1960b, 1963; Sumpton & Flowerdew, 1985). On chalk grasslands, rabbits (and sheep) grazed down the aggressive perennial grasses, Brachypodium pinnatum (tor grass) and Bromus erectus (upright brome), permitting avoided species to co-exist (Tansley & Adamson, 1925). Elimination of rabbits by myxomatosis caused competitive exclusion to reduce species richness (Thomas, 1963). Hence, grazing may increase diversity by preventing dominant species from competitively excluding sub-ordinates (Willems, 1983; Bakker, 1985). However, where the dominant species are unpalatable grazing may reduce diversity (Milton, 1970; Rawes, 1981).

d) Insect herbivory

The potential of insect herbivores to affect plant communities is shown by pest outbreaks and biological weed control (Crawley, 1989). However, most natural insect populations remain at low densities so their effects are more subtle. Experiments on 'weed' communities on sandy, acidic soil conducted by Dr V. K. Brown and workers at Imperial College, Silwood Park, Berkshire using chemical exclusion techniques have provided evidence of the effects of natural levels of foliar insect herbivory on 1) plant populations in terms of growth, size variability (Brown & Gange, 1989a; Gange et al., 1989) and reproduction (Gange, 1990) and 2) community characteristics such as vegetation structure (Brown et al., 1988a), species richness (Brown & Gange 1989a, b) and succession (Brown, 1982; Brown et al., 1988b). Parallel studies on early successional limestone grassland communities at Wytham, Oxon. have shown that above-ground insect herbivory may affect both the direction and rate of succession with effects of similar magnitude to a short-burst of spring grazing (Gibson et al., 1987b). The growth of perennial grasses was enhanced in foliar insecticide-treated plots and the net result was a taller, denser sward with lower plant diversity (Brown et al., 1988b).

Recent work on the weed communities at Silwood Park has examined the role of below-ground herbivory using soil insecticides (Brown & Gange, 1991). Brown and Gange (1989a, b) found that soil-insecticide application increased perennial herb growth at the expense of perennial grasses. Depression of species richness in controls was attributed to the effect of soil insects on seed banks and seedlings (Brown & Gange, 1989b). This is in contrast to foliar-feeding insects which suppressed the performance of above-ground vegetation to increase diversity (Brown, 1982). However, recent studies on 'pasture' communities at Silwood Park have shown that application of both foliar and soil insecticides has the same effect of increasing perennial grasses and depressing diversity (Gange & Brown, 1991).

e) Litter

Herbivory and other 'disturbances' (sensu Grime, 1979) that destroy biomass or reduce productivity may reduce litter production. Litter accumulation, which undergoes seasonal (Facelli & Pickett, 1991; ter Heerdt et al., 1991) and successional variations (Cormack & Gimingham, 1964; Facelli & Carson, 1991), may inhibit plant growth and seedling emergence by intercepting light, reducing thermal amplitude (Thompson et al., 1977) and releasing phytotoxins (Rice, 1974; de Jong & Klinkhammer, 1985). It can also increase microbial attack (Goldberg & Werner, 1983) and desiccation of emerged seedlings (Grubb, 1977), affect nutrient and water availability (Knapp & Seastedt, 1986) and act as a physical barrier (Facelli & Pickett, 1991). The experimental creation of open patches in a dense sward or litter layer increased establishment of Rhinanthus augustifolius (de Hullu, 1985), Solidago spp. (Goldberg & Werner, 1983) and several biennial species (Gross & Werner, 1982) as well as total species richness (Carson & Peterson, 1990). Seedling emergence is usually negatively related with litter coverage (Werner, 1975). Collins and Good (1987) found that tree seedling densities were highest in areas with more light and least litter. Similarly, the ground flora varies markedly within woodlands according to the amount of litter accumulation (Frankland et al., 1963; Sydes & Grime, 1981).

f) Bryophytes

Grasslands are often rich in bryophyte species (During & Willems, 1986; and lichens: Titlyanova et al., 1988) though their biomass is relatively low. Seasonally highest from autumn to spring, when other vegetation is reduced, bryophyte biomass is strongly related to aspect and management (Quene & Bakker, 1988). Biomass is higher on north-facing slopes, with a higher moisture content, than south-facing slopes (van Tooren et al., 1987) and increases in the sequence abandoned -> annually burned -> autumn mowed -> sheep grazed grassland. The emergence and performance of seedlings are affected as a result of the microclimatic conditions, retention of seeds and seed predation within the bryophyte layer (van Tooren, 1988). The low red/far-red ratio reduces the emergence of some species, e.g. Linum catharticum (Keizer et al., 1985). Allelopathic effects of bryophytes may reduce germination (van Tooren, 1990) and droughting of roots may kill seedlings trapped in the bryophyte layer and unable to reach the soil. However, the establishment of some some species may be positively affected by the bryopyte layer due to elevated soil moisture or nutrient levels.