

Chapter 7 Effects of microclimate on plants and animals

The previous chapters on climate, vegetation structure and types, and the relationship between microclimate and vegetation structure aimed to lay the foundation for a detailed examination of the effects of microclimate on plants and animals. The first part of the present chapter describes the effects of microclimate on established vegetation since they are more readily apparent. Then, the effects of microclimatic factors on germination and seedling establishment are considered. These early stages have a particularly important bearing on the distribution and abundance of plants. The second section covers the effects of microclimate on invertebrates. Firstly, it considers the various, inanimate and animate, microhabitats (with their specialized microclimates) in which invertebrates may live. Secondly, it covers the actual physiological effects of the microenvironment on thermal and water balance and the extent to which this is determined by invertebrate morphology and behaviour.

7.1 Plants

7.1.1 Established vegetation

The spatial pattern in the vegetation of the British Isles is often strongly correlated with climatic variables. Precise explanations for many vegetation patterns are unknown, but some progress has been made (Hendry & Grime, 1990). For example, mountain sorrel (*Oxyria digyna*) is confined to areas of the north-west where the annual rainfall exceeds 1600 mm (Perring & Walters, 1976), while in contrast the stemless thistle (*Cirsium acaule*) is restricted to regions of Britain with a mean July temperature of 16 °C (Perring & Walters, 1976). At lower temperatures, the thistle fails to release significant quantities of seed. Near its northern limit, it mainly occurs on south-facing slopes (Piggott, 1974). On a finer-scale, pronounced differences in vegetation occur between neighbouring north- and south-facing slopes (i.e. differing in aspect, Hutchings, 1983) correlated with differences in soil temperature, persistence of frost, soil moisture and solar radiation (Rorison & Sutton, 1975). For example, at Millersdale, north Derbyshire, on a south-facing, dry, open grassland, there were three times as many seedlings and a higher proportion of autumn germinating, monocarpic species compared with the closed turf of a nearby north-facing slope (Hillier, 1984).

The morphology of dominant plants often determines the ecology of associated plant communities. The undergrowth in forests is probably

affected by differences in transmitted light, throughfall and litter density, and as a consequence by differences in moisture and oxygen content of litter and humus (Barkman, 1988a). In heathlands, Calluna exerts powerful influences on the conditions under which other species must survive or establish (Gimingham, 1978). However, these influences are not constant throughout the life of individual Calluna plants and four phases have been recognized (Barclay-Estrup & Gimingham, 1969). The actual age of these stages varies considerably with habitat. In the pioneer phase young individuals are pyramidal in shape and scattered (i.e. low cover). In the building phase (ca. 6 years) when the plant is at its most vigorous, it becomes hemispherical in shape and reaches maximum height and cover. In the mature phase (ca. 15 years), the plant grows less actively and its canopy becomes less dense in the centre, since the older branches collapse sideways forming a gap. In the degenerate phase (ca. 15 years), the central frame-branches tend to collapse and die, extending the gap. Eventually, the only parts which remain alive are the outermost branches which are rooted in litter, and sustain a ring of foliage-bearing shoots surrounding a gap. As regards the ability of other plant species to co-exist the adverse microclimatic effects of Calluna, mainly reduced illumination, are greatest in the building and mature phase. However, some niches are available for associated species even during these stages.

Gimingham (1978) characterised the species which occupy the various niches available in uneven-aged stands as follows. 1) Competitors, with a general similarity in size, form, structure and development to Calluna itself, existing alongside it throughout the sequence of growth phases, e.g. Vaccinium myrtillus (bilberry). 2) Species with 'complementary strategies': i) shade tolerant subordinates forming lower strata beneath a Calluna canopy, present throughout the sequence of growth-phases, e.g. Erica cinerea (bell heather), ii) species requiring open phases for establishment, but surviving with reduced vigour in the building and mature phases, e.g. Festuca ovina (sheep's fescue), iii) species surviving throughout the whole sequence in one spot by dying back each winter to an underground perennating organ, from which climbing and straggling shoots are produced each year, bringing foliage to the periphery of the Calluna canopy, e.g. Potentilla erecta (tormentil), iv) species requiring open phases for establishment, but spreading as the Calluna canopy develops by means of rhizomes or creeping stems which extend laterally into new gaps, e.g. Pteridium aquilinum (bracken), v) small, low-growing species which appear only in the open phases, e.g. Polygala serpyllifolia (heath milkwort), certain lichens and bryophytes. There is a major difference in the sequence displayed by even-aged stands from that observed in individual bushes growing in a stand of mixed ages. During the

period immediately following a fire, a relatively large area is for a time devoid of vegetation, and subsequently passes through a stage in which various species including Calluna are either colonising or regenerating vegetatively. The habitat in this post-burn 'phase' may differ considerably from that of the small gaps in an uneven-aged stand which may be colonized by pioneer Calluna. In particular, it permits the establishment of large numbers of tree seedlings.

a) Temperature

Temperature influences the rate of leaf expansion (Arnold & Monteith, 1974) and the frequency of leaf appearance which determines differences in seasonal production, e.g. of grass species (Peacock, 1976). However, factors which limit the vegetative growth of a plant are not necessarily those which limit the reproductive success. For example, the small-leaved lime (Tilia cordata) shows a distribution predominantly in the southern half of Britain limited by the temperature sensitivity of seed production (Piggott & Huntley, 1981). Below 15 °C, pollen germination and tube extension are largely suppressed and embryo maturation is inhibited. Plant species vary in their optimum growth temperature (Hendry & Grime, 1990): widespread grass species, like sheep's fescue (Festuca ovina) and perennial rye grass (Lolium perenne), have lower optima than species with predominantly south-eastern distribution, such as upright brome (Bromus erectus) and tor grass (Brachypodium pinnatum). In Britain, there is a strong correlation between nuclear DNA content and the time of year when a plant grows (Grime & Mowforth, 1982). High DNA content is associated with a large cell size and occurs in species which grow in late winter or early spring, e.g. native grasses and bulb plants. Conversely, plants with small cells and low DNA content tend to delay growth until early summer.

When interpreting these patterns, one must realise that the climate at plant surfaces ('epiclimate') may differ considerably from that of the air above, to an extent which depends on structural attributes of the vegetation (Grace, 1987; Grace & Unsworth, 1988). Tall vegetation (e.g. trees) is aerodynamically rough and so the air close to the plant is well mixed with the atmosphere. Here, the temperature of plant parts is correlated to air temperature. In contrast, short vegetation (e.g. dwarf shrubs) is aerodynamically smooth and so mixing with the atmosphere is much less efficient. Consequently, the climate at the plant surface differs from that of the air above, being warmer, but is highly correlated to the radiation flux. This explains the transition from forests to dwarf shrubs at the treeline (Wilson et al., 1987; Grace, 1988).

In forests, the effect of the canopy on temperatures near the ground is very important. Deciduous forests which leaf early are important habitats for some species with a predominantly mountainous distribution, e.g. mosses. This may relate to their cool microclimate and favourable light conditions in winter. In early spring, the temperature of the forest floor may rise above that in an open field. The extra heat may be important for the early development of many herbs in the forest, especially those with food reserves in rhizomes, tubers or bulbs, e.g. Ranunculus ficaria (lesser celandine), Anemone nemorosa (wood anemone). This time is favourable for these species because the forest floor receives very little photosynthetically active light later in the spring once the trees are in leaf. The time of leafing is very important for the development of a specific microclimate and the development of an understorey.

The widespread importance of microclimatic temperature differences for the development of plants is illustrated by phenological aspects, i.e. related to seasonal development. Flowers of hawthorn (Crataegus monogyna) on branches near the ground open much earlier than those on branches higher up. However, sprouting of branches on oak bushes (Quercus robur) near the ground proceeds slower than that of branches on the top of the bushes. It also occurs more slowly on heathland, where the nights are relatively cold, than on inland dunes, which remain warm at night (Stoutjesdijk & Barkman, 1992). These two examples show that both day and night temperatures may be important in triggering development.

b) Radiation

Within low vegetation, small differences in height are associated with large changes in the intensity, direction and quality of radiation, and establishment may depend on height, aspect or inclination of the first leaves produced by a seedling. Because vertical gradients are less pronounced near the forest floor, initial growth in height may be unimportant. Here, 'tolerance' rather than 'avoidance' of shade is of ecological significance (Grime & Jeffrey, 1965). Hence, radical differences in adaptation to shade are found between woodland and grassland plants. Investigators measuring the light quality under vegetation canopies (e.g. woodlands) have found a marked reduction in red: far-red (R:FR) ratio (0.2-0.4) when compared with daylight (1.3, Stoutjesdijk, 1972 a, b). The actual ratio depends on the species composition and density of the canopy. Evidence shows that low R:FR ratios may cause a marked increase in stem elongation rate (i.e. a shade-avoidance reaction (Young, 1975)). This response was much more

pronounced for species from open habitats, e.g. Chenopodium album (fat hen), than those from woodland shade, e.g. Mercurialis perennis (dog's mercury) (Smith, 1982). Deregibus et al. (1985) showed that modification of light quality by a dense grassland canopy reduced the tillering rate of grasses.

c) Humidity

In humid forests, there is a clear decrease in saturation deficit and an increase in relative humidity with vegetation height. There is often a zonation of epiphytic mosses and lichens in a forest, and in tropical forests it also includes epiphytic ferns and members of the Bromeliaceae and Orchidaceae. The higher the overall relative humidity in a forest, the higher up certain epiphytic communities will be found on the trees. Rainwater always flows to the lowest possible place. Since no tree trunk is exactly vertical, and water is guided by large branches, there is always a side of the tree to which the water moves and then descends along special tracks. Here, moss species and filamentous algae are found. The unequal distribution of rain within a forest (Anderson et al., 1969) may be accompanied by special micro-patterns in the distribution of species. Bark relief may be very important in determining differences in epiphytic vegetation (Barkman, 1988a). The biological significance of the 'open shade' (Stoutjesdijk, 1974) is found in the longevity of dew rather than in low temperatures. It is favourable for many mosses.

d) Wind

Field observation suggests that wind affects the shape and size of trees, the physiognomy of the vegetation, and the productivity of crops. Transport of heat, gases and momentum across the boundary layer depends on structural features of the vegetation. High transport rates between plant surfaces and the air occur when the leaves, stems and branches are small rather than large, and when the vegetation is tall rather than short (as explained earlier). Where overall temperatures are low and windspeeds high, tall or small-leaved plants will be colder than shorter broad-leaved plants, and so be at a disadvantage (Grace, 1983). The shaping of trees by the wind and the general effects of 'exposure' (i.e. the combination of stresses that plants suffer in cold and windy places) are likely to be caused by the effect of wind on the temperature of leaves and meristems, damage to leaf surfaces, and the direct effect of motion as an inhibitor of growth (Grace, 1981). Raunkiaer (1934) showed that cold and windy places support only a restricted spectrum of life-forms - those with buds near the ground.

Due to their immobility, plants cannot make use selectively of certain favourable microclimates. This is why certain stages of development, notably germination and seedling establishment, may be decisive for the rest of the plant's life (Grubb, 1977), including the habitat of the adult plant. To learn whether niche breadths change during the life of a plant, Parrish & Bazzaz (1985) tested the responses of three age-classes of six old-field annual plants on four environmental gradients (nutrients, water, temperature and light). They observed several ontogenetic niche shifts. Hence, the microclimatic effects on the early stages of plant development are considered separately from effects on mature plants.

7.1.2 Germination

The small proportion of the seed bank or seed rain which germinates to give seedlings is a function of the number of 'safe sites' available (Harper, 1977), providing the seed with a) dormancy-breaking stimuli, b) conditions for germination and c) resources for germination. Seed regeneration in most plant communities is dependent on the presence of competition-free 'gaps' (or microsites) created by physical or biological disturbances (Grubb, 1976). Experimentally-created gaps generally have higher seedling numbers (Goldberg & Werner, 1983; Goldberg, 1987; McConnaughay & Bazzaz, 1987; Hillier, 1990). More seedlings appear in pioneer than mature *Calluna* stands (de Hullu & Gimingham, 1984). Gap micro-environments differ from closed vegetation in terms of light, temperature, water supply, litter, predators and diseases (Evans & Young, 1982; Naylor, 1985). The size (Miles, 1974; Goldberg & Werner, 1983; McConnaughay & Bazzaz, 1987), shape, slope, aspect (Hillier, 1990), soil microtopography (Harper *et al.*, 1965; Sheldon, 1974; Blom, 1978), timing and persistence of gaps are important. Species vary in their germination characteristics such as responses to dry storage, chilling, scarification, temperature and light flux (Bostock, 1978; Grime *et al.*, 1981). Many of the responses which seeds make to specific germination cues can be readily interpreted as adaptations for 'gap detection.'

a) Temperature fluctuations

In species whose seeds have a requirement for fluctuating temperatures to break dormancy (Thompson, 1969, 1974a, b; Rice, 1985) germination is limited to gaps in the vegetation. A covering of vegetation acts as a very effective temperature buffer, insulating the soil surface against large diurnal fluctuations. Thompson *et al.* (1977) found that over a 23-day period in early autumn, daily fluctuations at 1 cm soil depth were

generally in the range 5-10 °C in a 20 cm gap, but only in the range 0-4 °C beneath a closed grassland canopy. Since the soil itself acts as an insulator, the deeper a seed is buried the less affected it will be by daily temperature fluctuations. A response to fluctuations will therefore also provide the seed with a depth-sensing mechanism, since only seeds near the surface will experience a fluctuation of sufficient amplitude to be able to germinate (Fenner, 1985).

Thompson and Grime (1983) carried out a survey of 112 herbaceous species from a wide range of habitats to determine their response to diurnal temperature changes. Each species was subjected to a regime of 18 h at 22 °C in the light, alternating with 6 h at a lower temperature range in the dark. These regimes simulated conditions on an exposed soil surface. In order to simulate conditions experienced by buried seeds, a number of species were subjected to similar temperature regimes, but in continuous darkness. In all cases, the amplitude of fluctuation required to attain 50% germination was determined. In the light, 46 species showed increased germination in fluctuating temperatures. This response was most characteristic of wetland species, and to some extent disturbed ground plants. Many of the species, without a strict light requirement for germination (Cresswell & Grime, 1981), which responded to temperature fluctuations in darkness are disturbed ground and grassland plants.

b) Light quality

This is also used by seeds for gap-detection. The light transmitted through leaves is much reduced in the red end of the spectrum, so that the ratio of red to far-red radiation is markedly reduced beneath a natural canopy (Stoutjesdijk, 1972a, b). The germination of many seeds is inhibited by light with a low red: far-red ratio, because it transforms the phytochrome to an inactive form which prevents germination (Borthwick et al., 1954; Grime & Jarvis, 1966). In a survey of 139 species, Gorski et al. (1977) found that all the species which required light for germination (i.e. were inhibited by darkness) were also inhibited by leaf-transmitted light. These generalisations are broadly confirmed by the subsequent work of Silvertown (1980) on 27 chalk grassland species and Fenner (1979) on 18 East African weeds. Nearly all the species whose seeds have been shown to be sensitive to canopy shade are plants of disturbed ground, e.g. Arenaria serpyllifolia (thyme-leaved sandwort), Veronica arvensis (wall speedwell) and Cerastium holosteoides (field mouse-ear)(King, 1975), Bidens pilosa (bur-marigold)(Valio et al., 1972; Fenner, 1980), Plantago major (greater plantain)(Pons, 1986; Pons & van der Toorn, 1988).

c) Microtopography and water relations

The effect of microrelief on germination is largely controlled by the amount of contact between the seed and the soil surface which depends on seed size, shape and orientation. White (1968) sowed different sized seeds of rape (Brassica napus) and radish (Raphanus sativus) on surface textures of four different degrees of coarseness. He found that the microsite requirements of the smaller seeds were more easily satisfied. Oomes and Elberse (1976) found that small, flat seeds (e.g. Chrysanthemum (marigold) and Achillea (yarrow)) were more drought-tolerant. Sheldon (1974) found that the highest germination rate for dandelions (Taraxacum officinale) was obtained when seeds were placed with their long axes at about 45° to the horizontal.

7.1.3 Seedling establishment

The early stages of seedling growth have high mortality rates. Silvertown and Dickie (1981) showed that mortality of nine chalk grassland perennials was usually more than 80% in the first year. The main cause of death was desiccation, but at other sites (e.g. sand dunes, ants nests) burial was a major hazard. Biotic factors, such as predation, disease and competition may also be important.

a) Shade

Several studies have demonstrated that seedlings derived from larger seeds consistently maintain a size advantage over those from smaller seeds e.g. Trifolium subterraneum (burrowing clover) (Black, 1958), Mirabilis hirsuta (Weis, 1982) and Raphanus raphanistrum (wild radish) (Stanton, 1984). Plants characteristic of closed vegetation, e.g. woodlands and scrub, tend to have larger seeds than those from open sites, e.g. grasslands or arable fields (Salisbury, 1942; Werner & Platt, 1976). Even within a given species, woodland populations have larger seeds than grassland populations (Winn, 1985; Maranon & Bartolome, 1989). Neotropical forest trees, that are able to regenerate in small gaps or in shade, have significantly larger seeds than pioneer trees and those which need large light gaps (Foster & Janson, 1985). This difference is presumably the result of the increased food reserves required for seedling establishment in shade, which is reflected in higher seedling mortality among species with smaller seeds in experimental shade conditions (Grime & Jeffrey, 1965).

b) Competition

Competition from neighbouring plants is probably the single greatest hazard faced by colonizing seedlings. Greatest mortality tends to occur during periods favourable to growth (Miles, 1973; Mack, 1976). In chalk grasslands, the species with small seeds tend to be autumn germinators (Silvertown, 1981), presumably because the conditions for establishment are at their least competitive at that time (Al-Mufti *et al.*, 1977). Seedlings of different species vary in their ability to cope with interference from neighbours. Fenner (1978) carried out an experimental comparison of the ability of open and closed habitat species to establish in 2.5 cm gaps in Festuca rubra (red fescue) turf. The seedlings of most of the pioneer species were scarcely able to grow beyond the cotyledon stage, whereas the growth of the closed turf species was much less inhibited. Gross (1984) found that the effects of vegetated cover on seedling emergence and relative growth rate were greater for small-seeded species. The inability of ruderals to withstand competition in the earliest stages of growth may be one of the main causes of their exclusion from closed vegetation types. The value of pre-emption of space by early germination and establishment has been shown by a number of experiments (e.g. Ross & Harper, 1972 on Dactylis glomerata (cocksfoot) and Weaver & Cavers, 1979 on Rumex crispus (common sorrel) and field studies (e.g. Zimmerman & Weis, 1984 on Xanthium strumarium and Cook (1980) on Viola blanda).

c) Drought, burial and predation

In arid environments, a large seed size appears to be an adaptation for drought tolerance by conferring on the seedling the ability to make early rapid root growth to reach the moist layers below the surface. Baker (1972), in a survey of 2490 plant species in California, showed that seed weights are higher for species from dry habitats. A large seed has a two-fold advantage over a smaller one in this situation: its roots can grow more quickly and its shoot can emerge successfully from greater depths. In some cases, where species lack depth-sensing mechanisms, germination at depths too great to allow emergence accounts for a high proportion of seedling deaths. Several factors influence seed burial rates, including soil texture and structure, soil deposition and compression, seed size and morphology, seed longevity, earthworm activity and environmental conditions such as cold or low pH (Parker *et al.*, 1989). Seedling predators include both generalist herbivores, such as molluscs, and specialists associated with the parent plant. Susceptibility to grazing is determined by factors such as seedling size and morphology (Fenner, 1985). Pathogens also have an important effect on seedlings. The impact of both disease and herbivory

may depend upon factors such as distance from the parent plant or seedling density and light conditions (Vaartaja, 1962; Maiorana, 1981; Augspurger, 1984; Augspurger & Kelly, 1984).

d) The nurse effect

In some cases, the presence of established plants in the vicinity of a seedling increases the chances of survival. This is especially likely to occur in harsh environments, where neighbouring vegetation may ameliorate the conditions locally. In the Sonoran desert, Franco and Nobel (1988) found that seedlings of the desert succulent Agave deserti were only found in sheltered micro-habitats, 81% under the canopy of the desert bunchgrass (Hilaria rigida). Apparently, because soil surface temperatures can reach 71 °C in exposed areas, seedlings were generally located near the centre or on the northern side of this 'nurse plant'. Similarly, 89% of seedlings of the cactus Carnegiea gigantea occurred under the canopy of Ambrosia deltoidea and Cercidium microphyllum (Franco & Nobel, 1989). In both cases, the nurse plants facilitate seedling establishment by reducing high temperatures near the soil surface and provide a microhabitat with a higher soil nitrogen level. This 'nurse effect' is by no means confined to such extreme environments. In calcareous grasslands, Keizer *et al.*, 1985 found that Carlina vulgaris (carline thistle) and Linum catharticum (purging flax) seedlings had lower rates of mortality where the bryophyte cover was highest and Ryser (1993) found that shelter by neighbouring vegetation appeared to be necessary for the establishment of Arabis hirsuta (hairy rockcress) and Primula veris (cowslip).

7.2 Invertebrates

Small animals have a very large surface area in proportion to their mass. Consequently, the conservation of water is the prime physiological problem of their existence (Buxton, 1932; Mellanby, 1935). Worms, leeches, slugs and terrestrial arthropods such as woodlice, centipedes, millipedes, spring-tails and other soil dwellers, avoid desiccation by remaining most, if not all, of the time in a damp or humid environment. Other groups such as many insects, spiders, scorpions and mites, possess a thin epicuticular layer of wax which is relatively impervious to water vapour and thereby reduces water loss, by transpiration. The exigencies of the physical environment press less heavily upon them, and their distribution is not limited by microclimatic factors to the same extent (Cloudsley-Thompson, 1962).