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CHANGES IN PLANT DISTRIBUTION FOLLOWING CHANGES IN LOCAL CLIMATE

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Causes of change

An examination of Godwin (1956) and the numerous papers written during the past three decades on pollen stratigraphy of peat deposits reveals that the composition of the flora in any one area has been in a state of continual change over the last 10,000 years. In the past these changes in vegetation were mainly due to the relatively slight changes in climate; but during the last few thousand years man has had an increasing influence on the distribution and abundance of species. The changes in climate have not only affected the environment above ground level, but have also resulted in marked alterations in the structure and mineral content of the soil. The loss of several species which require a base-rich soil, with good drainage, from western parts of Britain during the last few thousand years is the result of the higher rainfall totals and cooler climate of these areas leading to the leaching of minerals and the gradual accumulation of organic matter which makes the soils more acidic and waterlogged.

The effects of climate can be readily observed on mountains and hills where the warmer, drier southern slopes are characterised by good quality hill grazing pastures containing *Agrostis tenuis, A. canina, Festuca ovina, Galium saxatile* and frequently *Pteridium aquilinum;* whereas the cooler, moister and more peaty soils of the northern slopes are covered by heaths *(Calluna vulgaris, Erica tetralix, Vaccinium myrtillus), Carex binervis, Luzula campestris, Nardus stricta, Sieglingia decumbens,* and numerous mosses and lichens. Other environmental factors may also be involved as when we find additional species such as *Plantago lanceolata, Thymus drucei, Trifolium repens, Veronica officinalis* and *Viola riviniana* which will only occur on the more mineral rich soils. Some of the differences are reinforced by selective grazing of domestic and wild animals. Farmers take advantage of these climatic differences associated with aspect: a short journey through hill country will soon show that the more productive and improved fields are on south-facing slopes.

Other obvious ways in which the climate determines the distribution of species can be seen by looking at the maps in the *Atlas of the British Flora*. Species, such as *Cirsium eriophorum, Galium pumilum* and *Tamus communis* are confined to the warmer, drier localities of England and Wales, while, at the other extreme, in the cooler, moister sites at high elevations in north-west Scotland we find the only localities for *Juncus trifidus, Luzula spicata, Veronica alpina* and a number of other species. The first group includes those continental species that are at their northern limit of distribution, while the second group contains those that are at their southernmost stations. The species of these two contrasting groups have, during the course of their evolution, become adapted to very different environmental conditions and will normally only thrive, flower and fruit providing certain environmental factors are present.

A few species appear to be particularly good indicators of climatic change, an example being *Nardus stricta* which is the dominant grass in areas adjacent to permanent and temporary snow-beds. In fact, it is such a good indicator species that Green (1968) and others have used it as a guide to areas where one can expect snow to persist for the greater part of the year in Scotland. These areas of quasi-permanent snow-beds in parts of Scotland appear to be on the increase (Spink 1968, 1969) and could well have a more pronounced effect on the vegetation of these regions if the climate continues to become cooler and moister.

The changes in climate outlined by Lamb (p. 11) will certainly lead to changes in the distribution of species in the British flora, but these changes will affect different species in differing ways. In considering these changes it is vitally important to consider certain genetical and evolutionary implications.

The response to change

Every species has its own range of tolerance to environmental factors—some grow almost anywhere; others are restricted to just one or a few localities. Generally speaking, those species which are widespread (weeds excluded) are outbreeding and possess a considerable amount of genetic diversity, whereas rare species are invariably inbreeding, frequently apomictic, as in *Hieracium*, and have a limited degree of genetic variability. Because their populations are virtually isolated there is no gene exchange between them as occurs in closely adjacent populations of more common species. It is these rare species, with little or no genetic diversity, that are most likely to become extinct if there are marked climatic changes, especially alterations in the local environment.

Some of the rarer species could benefit from certain climatic changes. For instance, if the British climate becomes cooler, wetter, and more humid as suggested by Lamb, a number of arctic-alpine species may extend their range, providing that soil conditions are suitable in adjacent areas. However his suggestion that dry easterly winds may become more frequent could result in some species, which require a continual high humidity, becoming less abundant as a result of occasional periods of desiccation. Continental species which require a warm soil, with a temperature of at least 12°C. for germination, and high summer and autumn temperatures for seed ripening, may well become extinct if the climate becomes cooler and the growing season shorter unless they can adapt themselves to the new conditions.

On the other hand, widespread species are not so likely to be affected by changes in climate since they usually have the ability to undergo genetic change as a result of natural selection. This has been clearly shown by the work of Clausen, Keck, and Hiesey (1940 *et seq.*) in the United States who have worked on variation within and between populations and races of *Potentilla* spp. and *Achillea* spp., and by Bradshaw (1960) and his colleagues in this country who have been looking at species of *Agrostis*. In *Agrostis*, and also in *Silene maritima*, there are considerable morphological and physiological differences between populations within a relatively short distance of one another and, in many instances, it can be shown that these differences are brought about by the selection of certain character combinations for specific sets of environmental parameters.

Most of us are concerned with changes in plant distribution within our own county, region, or locality rather than overall changes in distribution throughout the British Isles. By knowing our local climate we shall eventually obtain a better understanding of how important climate is, both directly and indirectly, in determining the composition of the vegetation within relatively small areas as well as throughout the whole of the area under investigation. Areas with a diverse topography are particularly good for studies of local climate. Investigations will show how the local climate is affected by aspect, angle of slope, and altitude and that for example some species only occur on warm well drained south-facing slopes while others are restricted to cooler and moister north-facing slopes.

Extremes of climate are also important and every opportunity should be taken to find out the consequences of extremes on less common species, especially those that are at the limits of their range. For example, the severe winter of 1962–3 killed over 60% of gorse bushes (*Ulex europaeus*) in lowland parts of mid Wales and most of those that survived died back almost to the base. Some of these eventually recovered, but most of the more vigorous bushes in 1969 were those that had germinated since 1963. This shows that the distribution of *Ulex europaeus* is partly determined by temperature and that it cannot stand severe prolonged cold spells: for this reason it rarely occurs above 150m and then only on south-facing slopes.

For *Ulex europaeus* a single cold winter was not sufficient to cause extinction; but a succession of cold winters could have had a disastrous effect on the distribution of this species, although since gorse seeds appear to survive in the ground for many years it could extend its range again if the winters became less severe. Two points arise from this case: first, the survival of a species partly depends on how long its seeds remain viable; secondly, it is concurrent extremes that can result in a species becoming extinct.

This is where the local observer is at a great advantage since the same extreme climatic events rarely occur throughout the whole of the British Isles. For example, during the summers of both 1968 and 1969 a number of species have wilted and become completely desiccated on shallow Powys-type soils in west Wales where we have had rainfall totals of only about 40% of average; but in eastern England such observations could not be made since rainfall totals have been well above average in each of these two summers.

So far I have avoided giving examples of species which have become either much rarer or more abundant throughout Britain within recent years as a result of climatic change. This is because it is difficult to be sure if any marked changes in distribution *are* primarily due to the gradual changes that have occurred in our climate over the last few hundred years. One might, for instance, think that the occurrence for the first time during the present century of the many hundred of alien species, of a continental distribution type, in southern Britain could be because our winters have become much milder since the middle of the 18th century. These aliens certainly grow more successfully in hot, dry summers and may overwinter in mild winters, but their presence in Britain is more the result of human influence than climatic change. Again, the disappearance of species such as *Agrostemma githago* and *Chrysanthemum segetum* is unlikely to be due to climatic change, but rather to improved seed cleaning techniques and agricultural practices.

Climatic changes have certainly resulted in changes in the distribution of plants in the past and the process is continuing. The most satisfactory way of finding out how important climatic changes are, compared to changes in other environmental factors, in altering the range of a species, is to carry out detailed recording at the same site, especially one at which changes are suspected to occur, at regular intervals. The records should include details on the performance of the species, the time they come into flower, the amount of good seeds produced each year, and how many new plants are added to the population each year. The value of this type of study is very well illustrated in Pigott's paper (p. 32). This information will enable us to build up an environmental spectrum for each species which should tell us the main factors involved in determining the distribution of each species and, finally, to see if certain populations can become adapted to a new range of environmental tolerance rather than become extinct.

The environmental spectrum

In Wales we are trying to produce an environmental spectrum for each species by means of our '00' survey in which we are making a detailed record of the performance of species in the one kilometre square (the '00' square) at the bottom left-hand corner of each of the 10km national grid squares. Recently we have also been looking at other representative 1km squares in order to obtain a fuller coverage. This has provided us with information on the range of tolerance for all but the rare species and by resampling, say at ten yearly intervals, we hope to record changes in distribution and to relate these modifications to climatic factors, changes in land-use, etc.

In areas of diverse topography, like most of Wales, there can be considerable environmental variations within a 1km square and a smaller sampling area is necessary to be sure of arriving at genuine conclusions. So, to supplement the '00' survey, we are now collecting quadrat data for selected areas and habitats within each 1km square. A quadrat size of 2m has been chosen as we wish to compare our results with those obtained in recent Scottish surveys. In the 2m quadrats we record the area occupied by each species, note the relevant environmental factors, and collect a soil sample for detailed analysis.

One of the main problems of this type of survey in the past has been the analysis of the data. But, with the advent of computers, this task is relatively easy. Projects of this type are ideal for a team of keen amateur and professional botanists with the latter having access to computer facilities. This applies particularly to the compilation of county and regional Floras which can be made far more informative if details are provided on changes in distribution, and the reasons for these changes, in addition to supplying lists of localities in which the species have been found. This extention of the original '00' survey appears to be providing us with the type of data we require to determine the environmental tolerance of species and, furthermore, it is now revealing that there are considerable differences in tolerance within the same species depending on location and habitat.

Rather more detailed work is being carried out at the University College of Wales, Aberystwyth on certain areas which are particularly heterogeneous for both environmental factors and habitats. For this we are using association analysis and other techniques. So far, most workers have used association analysis methods for examining the vegetation in just a single area but, as Williams and Lambert (1960) have pointed out, these methods of finding associations between species and relating distribution to environmental factors are especially suitable for general survey work covering a large area. To date our work has been mainly concerned with hill-pastures and we have selected areas consisting of a mosaic of different sub-habitats and plant associations. Four areas have already been investigated but we intend to extend the survey and to resample at ten-yearly intervals.

Recording climatic change

One of the main difficulties in surveys of this type is relating changes in vegetation to changes in local climate. The information obtained by the Meteorological Office and others from Stevenson's Screens some 1·5m above ground level can be of some value, but what we need is records of day to day and seasonal changes where the more interesting species occur and, in particular, records relating to climate just above ground level and in the soil. The ideal would be to have a number of comprehensive, and preferably automatic, environmental weather stations recording in the more important nature reserves. A start has been made, but the high cost of the instruments inevitably means that we cannot obtain an overall picture of the extremes that occur which are so important to the proper understanding of plant/climate relationships.

The complex interaction of climatic and other factors can lead to changes in the distribution patterns of all species. Furthermore, climatic factors can act indirectly through modifying the soil and the distribution of species, both above and below ground level, which compete with the particular species we are investigating. Competition between species may be more important than was first realised: it is now known that certain species produce toxic substances which inhibit the germination and growth of other species.

Changes in nature reserves

Nature reserves frequently provide the most dramatic illustrations of how the distribution of species can be rapidly modified as a result of micro-climatic changes brought about by bad reserve management. In several instances a heavily grazed species-rich reserve has, within a few years, become a species poor reserve dominated by *Dactylis glomerata* and *Deschampsia cespitosa* because a fence was put around the reserve and no regular grazing allowed. By their vigorous growth, these two rank species of grass radically altered the climate, at and just above, ground level. As they grew the patches between the clumps of grass became overgrown, the amount of light reaching the ground decreased, and the soil became moister and cooler as evaporation was reduced. As a result many of the smaller and more interesting species of both plants and animals, for which the reserve was established, have become extinct. This illustrates why it is most important to find out the environmental factors which control the growth of the more interesting species which we wish to preserve: in most instances it is best to maintain the same management policy since it was the system of previous land-use that led to the area being sufficiently interesting for it to be acquired as a nature reserve in the first instance.

Perhaps we should look ahead and consider whether we should alter the micro-climate of parts of our larger reserves to create new climates which would lead to additional species coming into the reserve preferably on their own accord rather than being deliberately introduced. This would help us in our study of the effect of climate on various species since we could then see how quickly the new species arrived, how rapidly they spread, and whether they maintained themselves or gradually decreased after reaching a certain level, to be replaced by more successful, later, introductions. By doing this we shall find out just how the climate affects all the species in our reserves: this, one hopes, will result in the production of efficient management plans designed to maintain the diversity of both the environment and the species within our reserves.

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DISCUSSION

C. J. Cadbury asked whether Dr. Savidge had found any clines in flower colour in relation to microclimate in Wales: he had found a change in *Cirsium palustre* in Monmouthshire from nearly 100% white at 1,000 ft to nearly 100% purple at 750 ft only a mile away.

Dr. Savidge said it had been noticed in *Silene vulgaris:* it applied not only to flower colour but to the pigmentation of the whole plant. The physiological importance of the pigmentation is not understood.

Dr. F. Merton asked what sampling has been done to obtain adequate paramenters of the climate.

Dr. Savidge replied that they had sampled over 1,300 quadrats in which over 200 species had been recorded. This gave a good range of parameters for any particlar species: however at present they had not been able to measure the microclimate directly.

M. Jones asked how the microclimate in a nature reserve might be altered.

Dr. Savidge said this could be achieved by the creation of small pools, by planting trees in open landscapes or by creating glades in woods.