in eye shape is caused by genes at at least eight loci. It seems that no macromutation was involved in this case. I know of no example pointing the other way, but shall not be surprised if one crops up.

Genetic analysis cannot, of course, be applied to the more extreme differences between bauplans, so it is still possible to argue that the origins of major taxa require special genetic events. However, no-one at the conference was prepared to challenge Stebbins's remark that the most striking morphological novelty among the higher plants was the flower head of *Zea mays*, which is largely the result of selective breeding under domestication and is known to be under the control of many genes with small effects.

It will be apparent that this report has been written by a geneticist, not a palaeontologist. Despite my reservations, I found the meeting immensely stimulating. It can only be good for evolutionary biology that people from such different disciplines should meet, talk and, occasionally, listen. It was only to be expected that there would be much misunderstanding, confusion and even indignation. I hope we shall meet again in a year or two, and that next time the confusion may be slightly diminished. □

Why is a plant where it is?

from Peter D. Moore

ONE of the simplest questions to ask, yet one of the most difficult to answer is why a particular individual of a given plant species should be found growing at a particular location. The answer may be sought in its physiological requirements and the degree to which they are satisfied by the physical framework of that spot; or in the complex of biological interactions with other organisms, competitors, predators, parasites, and so on; or in the tangled web of historical events which has moulded both of these former factors; or, finally, in the sheer chance which brought a propagule to that site and which left it untouched by random catastrophe. The interaction of all these forces permits no easy answer to the apparently simple question.

Any attempt must seek first to locate the physical environmental stress and physiological sensitivity which, in combination, allow the identification of a limiting factor. This factor can be regarded as a necessary resource in such short supply that any increase in its availability will result in an increase in the performance of the individual or density of the population. But the model, stated in these terms, needs to be flexible enough for such factors as temperature at specific times of day or year to be regarded as a resource.

One may examine any aspect of the plant's physiology, or any time in the plant's life history, to find where resource restriction meets the plant at its most vulnerable point and prevents further reproduction, growth, or even survival. Perhaps the most obvious place to start is at the beginning and to define those resource limitations which restrict the germination of the seed and thus determine whether the plant is to be given the opportunity to meet further tests. Thompson (*Ann. Bot.* **34**, 427; 1970) has approached from this direction in his studies of various species of Caryophyllaceae. He devised a metal bar along which a temperature gradient was maintained and observed the germination characteristics of each species in relation to temperature, and found that their requirements correlated well with the biogeographical characteristics of each species. For example, a species (*Silene secundiflora*) from the Mediterranean germinated at low temperature, this being advantageous to species in which autumn germination means a mild, damp period before meeting the unfavourable drought of the following summer. A more northerly species, on the other hand (*Lychnis flos-cuculi*), had a higher temperature germination requirement; it thus remains dormant through the winter after seed set and germinates in the spring.

Subsequently Thompson (*Ann. Bot.* **39**, 1; 1975) has examined in detail the geographical variation between populations of a single species, namely *Silene dioica*. He has found considerable variation both within and between populations and also a different response among after ripened seeds from those which were fresh. The populations from regions with milder winter contained more individuals which were capable of germination at low temperature, thus confirming the trend indicated by the previous experiments.

Silene dioica, the red campion, is a woodland herb, widespread in Europe, which, in the western, deciduous woods of Britain and northern France is often accompanied by the bluebell, *Hycanin-thoides non-scriptus*. The seeds of this species were also subjected to the attentions of Thomson and Cox (*Ann. Bot.* **42**, 51; 1978), and on the basis of their experiments they propose that the seeds germinate naturally at about 11°C, in the late autumn and that they therefore overwinter as seedlings. This obviously leaves the species somewhat vulnerable to winter frost; its distribution appears to correlate well with the isotherm of the main daily maximum temperature of the coldest winter month at 0°C, and also with a mean daily maximum of the warmest summer month at 25°C. Its sensitivity to winter frost and summer drought account for its western distribution and its confinement to the woodland habitat, where it is protected from both. The survival of bluebells in open habitats in the extreme west of Britain (often as a relict of former woodland) may be a reflection of the mild, oceanic conditions prevailing there.

The examination of seed from one further woodland species, the wood millet grass, *Millium effusum*, has shown a rather more complex pattern of reaction. Thompson (*Ann. Bot.* **46**, 593; 1980) found that seed germinated immediately after harvesting had an optimum temperature requirement of 16°C but, after storage for 2.5 months, the optimum temperature for germination was 21°C and germination took place over a wider temperature range. The breadth of tolerance increased yet further after 10 months. Also, germination was faster after a period of storage but, rather surprisingly, a higher temperature (26°C) of storage reduced the subsequent germination rate. The ecological significance of this high temperature inhibition of the after ripening process is difficult to discern, but Thompson suggests that it could reduce the chances of an ill-advised, rapid response to mild conditions soon after shedding.

Millium effusum has a wide distribution in Europe and, in view of the late flowering and fruiting in the north of its range (late August in areas to the north of the Baltic), temperatures will already be below those needed for germination, which is thus delayed until spring. In the south (southern France and Iberia), seed is shed in early summer, so it experiences a hot, dry period followed by a warm, moist one. This results in the bulk of the seed germinating before winter arrives. In between these two extremes, the complex microclimatic variations caused by site factors (microtopography, aspect, etc.) and fluctuations in weather conditions, can result in a range of responses. Indeed, the plasticity of this species may be a key to its success.

Thompson's germination studies illustrate the possibilities which exist for pinpointing the limits of a plant's capacity to meet the stresses of the environment, but seed germination is only one of many critical phases in the plant's life cycle. Also, the fact that one factor may limit a species on a continental scale, does not preclude the possibility that other factors will limit its local distribution pattern. At the level of the individual one must still account for the part played by chance. At this scale is vegetation simply, in the words of Gleason, a "fortuitous juxtaposition of plant individuals"?

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