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The slow process of succession

from Peter D. Moore

THERE are certain areas of ecology which are made more difficult to investigate by the current tendency to limit research grants to three years. Take the long-term study of plant competition between bracken (*Pteridium aquilinum*) and heather (*Calluna vulgaris*) on the Brecklands of East Anglia. If Alex Watt (*J. Ecol.* **43**, 490; 1955) had been restricted to a three-year study period, plant ecology would be much the poorer. Then there is the study of successional processes, which may take several hundred years to reach completion. The subject is of considerable interest to both pure and applied ecologists but short-term studies have considerable weaknesses.

Some brief research projects concerning succession have been undertaken, such as that of Tramer (*Ecology* **56**, 905; 1975) who observed abandoned agricultural plots over a three-year period. But it is difficult to derive general statements concerning the nature of the process from such a restricted view. Many researchers have tried to solve this problem by observing the extant stages in successions which have been proceeding for different lengths of time. Classical studies such as those of Crocker and Major (*J.Ecol.* **43**, 427; 1955) on a glacial retreat recolonization and Olson (*Bot. Gaz.* **119**, 125; 1958) on the sand dunes of the Great Lakes region are of this type. Similar studies have used abandoned agricultural land of known history, such as those of Bazzaz (*Ecology* **56**, 485; 1975) and Nicholson and Monk (*Ecology* **55**, 1075; 1974). This approach suffers from the disadvantage that one must assume that study sites are alike in all but the developmental time factor. Naturally, this is hardly ever the case.

Ideally, one would like to take a single location and study the changes in plant and animal populations over many decades, or even centuries. In Britain we are fortunate in that one such experiment has been in progress for over a century, and some of the resulting data has now been analysed by Silvertown (*J. appl. Ecol.* **17**, 491; 1980). This is the Park Grass Experiment at Rothamsted Experimental Station, which was begun in 1856 and which was originally intended to study the effects of various fertilizer regimes on grassland composition and productivity. The subdivision and replication of treatment plots was improved in 1964, but the data analysed by Silvertown covers only the period up to this revision.

From 1862, samples were cropped from the plots, were separated into species, dried and weighed. Plots which had received regular applications of ammonium sulphate were of lower pH and lower diversity (Shannon function), and all plots showed a negative relationship between overall biomass and diversity (and species richness).

The succession at Rothamsted has reached an equilibrium condition, under the constraints of harvesting imposed upon it. It is essentially a plagioclimax in the Tansley sense. Yet the variation of the equilibrium point in relation to nutrient capital and therefore biomass is of considerable interest for the theory of succession.

It adds considerable weight to the ideas of Green (*Biol. Conserv.* **4**, 378; 1972) who regarded the successional process in chalk grassland to be an accretion of nutrients in the biomass and litter, resulting in increased dominance and consequently reduced diversity among the plants. The results also fit well into the Grime model (*Nature* **242**, 344; 1973) if one regards increased fertilization as 'reduced stress', but the term over-simplifies the complexity of the system by reducing it to one dimension.

One of the particularly interesting features of the development of short turf into tall turf (increasing biomass) in grassland succession is that its influence upon invertebrate diversity is the reverse of that found in plants. As plant diversity falls, invertebrate diversity increases. This is considered by Morris (In *The Scientific Management of Plant and Animal Communities for Conservation,* ed. E. Duffey and A.S. Watt, Blackwell, Oxford, 527; 1971) to be a consequence of the increased opportunities for herbivorous grazers in the structurally and microclimatically more complex environment offered by tall grassland plants. This, of course, will increase diversity at higher trophic levels also.

An Australian experiment has recently confirmed this relationship by monitoring the invertebrate faunas associated with different stock density of sheep. Hutchinson and King (*J. appl. Ecol.* **17**, 369; 1980) sampled sites over a three year period which were grazed at densities of 10 sheep ha^{-1}, 20 ha^{-1} and 30 ha^{-1}. Apart from Scarabaeid beetle larvae and Oligochaeta, which showed greatest mean abundance (no. m^{-2}) and biomass in intermediate grazing levels, other groups showed a reduction in biomass and density as the grazing pressure increased. Here again, grazing pressure can be considered as a controlling influence upon habitat structure.

But what of vertebrates? Small mammals, like invertebrates, are more abundant in taller, undisturbed turf (Duffey, *J. Anim. Ecol.* **31**, 571; 1962), but birds, particularly those which use grassland for feeding, seem to prefer short turf. In Sweden, Larsson (*Oikos* **20**, 136; 1969) has shown a considerable decrease in the numbers and diversity of birds frequenting the grassland areas around some Swedish lakes, following the removal of cattle grazing, and the consequent increase in vegetation cover.

This change in avifaunal diversity and density with the successional development from short to long turf has some interesting implications for applied ecology. A survey by Brough and Bridgman (*J. appl. Ecol.* **17**, 243; 1980) of thirteen airfields in Britain has shown very considerable differences in the density of feeding birds in short and long turf. The total counts over a two year period showed that three times as many birds overall used the short turf sites (which was defined as being a grass height of 5-10cm) when compared to long turf sites (grass height 15-20cm). In the case of gulls, the numbers feeding in long grass were only one fifth of those in short turf habitats. Their distaste for long turf may be associated with a greater difficulty in feeding upon soil invertebrates, coupled with a lack of visibility which might allow the approach of predators.

There thus seems to be a strong case for allowing the grassland succession on airfields to proceed beyond the short-turf stage and thus reduce the risk of bird strikes for aircraft. As Brough and Bridgman point out, however, there is one snag. The increased small mammal populations of the long grass may attract avian predators, such as kestrels and short-eared owls. But the data which they present suggests that these species are unlikely to reach seriously high population levels.

It would be pleasant to think that such a practical application of the study of what are essentially successional processes might encourage further and longer term studies.

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