The Institute of Biology's
Studies in Biology, no. 130

Evolution and Pollution

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General Preface to the Series

Because it is no longer possible for one textbook to cover the whole field of biology while remaining sufficiently up to date, the Institute of Biology proposed this series so that teachers and students can learn about significant developments. The enthusiastic acceptance of 'Studies in Biology' shows that the books are providing authoritative views of biological topics.

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Readers' comments will be welcomed by the Education Officer of the Institute.

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Preface

Pollution is, unfortunately, an inevitable part of our world. At its worst it can have very severe effects: plants and animals are progressively stressed and finally eliminated. But ecosystems and species do have a considerable resilience. This book discusses the remarkable resilience in species which can be provided by evolution. Natural selection can cause substantial genetic changes in populations which allow species to tolerate high levels of pollution. This is of interest not only to people concerned with pollution but also to everyone interested in the mechanism of evolution, because some of the best examples of evolution in action now available to us, are of evolution in relation to pollution.

This book looks at the evolution that occurs in plants growing on sites contaminated with metals, influenced by air pollutants, and even treated with herbicides. We find that evolution can be very rapid and exciting. The same is being found in animals. We have chosen not to use the word 'plants' in our title because the remarkable examples that we discuss are of importance and relevance to everyone, whether they are interested in plants, animals, or micro-organisms.

Liverpool, 1981

A.D.B.
T.McN.

Contents

1 Variation and Selection

1.1 Evolution and pollution

Pollution is a problem that is as old as civilization. The first chimneys and the first metal mines were as much sources of polluting substances as the more gigantic sources we think of today, when we are each responsible every year for about three-quarters of a tonne of pollutants going into the air alone. The damage caused by pollution was recognized a long time ago. In 1650 John Evelyn recorded in his diary 'the hellish and dismal cloud of sea-coale' over London so that 'catarrhs, phthisicks, coughs and consumptions rage more in this one City than in the whole Earth besides', and in 1727 John Fairchild wrote a book *The City Gardener* in which he described the plants which could not be grown in London because of the smoke.

But all these and later writers recorded only the deleterious effects of pollution, damage to trees, disappearance of species and barrenness of polluted areas. They thought of the effects of pollution on living organisms only as a downhill process, resulting in progressively greater damage, in which first one organism and then another succumbed to its effects. To a large extent the ability of individual species to hold out against pollution has been seen as something determined by the inherent characteristics of the species. Thus it seems natural that evergreen conifers such as the Scots pine (*Pinus sylvestris*) should be more susceptible to air pollutants than deciduous tree species such as the London plane (*Platanus acerifolia*) because its leaves would be exposed to the higher levels of atmospheric pollution occurring in the winter. Other variations in susceptibility might not be so easy to explain, but they would, in one way or another, be thought of as being due to the inherent characteristics of the species.

Yet in 1934 an Austrian, PRAT, became puzzled when he found plants of red campion (*Silene dioica*) growing on the highly polluted wastes of a copper mine near Piesky in Austria, on which little else would grow, especially since it was a common plant in normal soils. He collected seed from plants on the mine as well as on ordinary soils, and grew them on soil mixed with different amounts of copper carbonate. In the space of a few weeks he was able to show that while seedlings produced from seed of the mine plants continued to thrive in soil mixed with copper carbonate, seedlings from the plants from normal soil did not, although both lots of seed grew well on normal soil (Fig. 1–1).

The paper is short, and Prat was content to record the differences

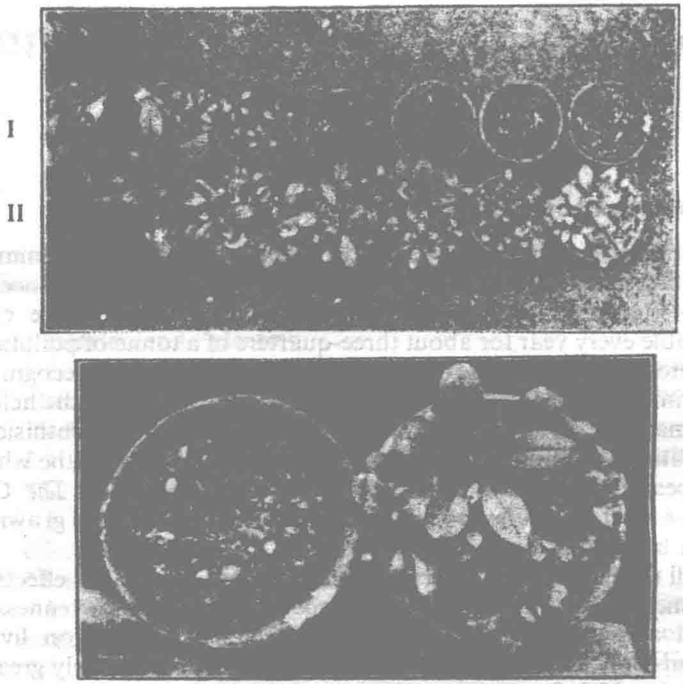


Fig. 1–1 **The first indication that plant evolution could occur in polluted environments: growth of populations of red campion, I from a normal soil, II from a copper mine, on soil mixed with different amounts of copper carbonate (look particularly at the close up of I and II at the highest copper level) (PRAT, 1934).**

between the two populations, and to suggest only briefly that they might be the outcome of natural selection. By this time the process of evolution was well understood and good evidence for the way in which it could cause local differences between populations within plant species had been described. But Prat had discovered an important extension of the principles of evolution: that evolutionary change could occur in man-made as well as natural environments. Like so many scientific discoveries, it was virtually ignored for thirty years. But it is the starting point of a great deal of work showing us just how the evolutionary mechanisms proposed by Charles Darwin operate in practice in plants.

1.2 The basis of evolution

Darwin's explanation for the way in which evolution occurs is very simple. His starting point was four observations, from which he made three crucial deductions:

Observation *i*) The numbers of all organisms tend to increase logarithmically.

Observation *ii*) Yet on the whole their numbers remain more or less constant.

deduction ∴ There must be a *struggle for existence* – some organisms survive and some die.

Observation *iii*) Organisms vary – some are better adapted to their environments than others.

deduction ∴ In the struggle for existence it will be these that tend to survive – there is *natural selection.*

Observation *iv*) Much of this variation is inherited.

deduction ∴ The results of natural selection will accumulate as one generation replaces another – there will be *evolutionary change*.

This remains the only explanation of evolution that is plausible today.

Darwin's main problem was that he had no direct observations to illustrate his deductions. It is surprising to realize that nowhere in the *Origin of Species* is there any example of natural selection in action. Nor is his evidence on the origin and inheritance of variation satisfactory. It required later work to demonstrate that characters are determined by genes which are passed on from one generation to another in a complex manner. The final surprise is that he gives no examples of evolution actually occurring naturally: he had to make do with the results of animal breeding, which had impressed him greatly.

We are now, one hundred years later, in a very different position. Not only do we understand the mechanisms of variation but we have excellent evidence for natural selection, and can show how the two interact to give evolution. This occurs so rapidly that we can observe it taking place.

Evolution has usually had time to bring species, and more particularly their constituent populations, into equilibrium with their environments. This is not to say that better, more adapted, individuals could not occur, but their evolution is limited by the amount of variation available. There may either not be the genetic variation available to allow natural selection to create populations of superior individuals, or the variation present may not be suitable for creating individuals which are superior in the existing habitat of the species.

Pollution, on the other hand, creates new environments. Suddenly the populations of a species are no longer in equilibrium with an environment they have long experienced. Conditions are completely new and we can see natural selection starting afresh to mould the species in a remarkable manner. To understand how this can occur, we must first look at the mechanism of evolution and one or two examples of selection in ordinary situations.

1.3 Types of variation

All characters are ultimately determined by genes; this ensures that there is continuity of characteristics between one generation and the next. Actual patterns of inheritance can differ however, depending on whether a character is determined by one or by several pairs of genes. When only one pair of genes is involved the pattern of inheritance is very simple although it was a considerable intellectual feat by Mendel to be

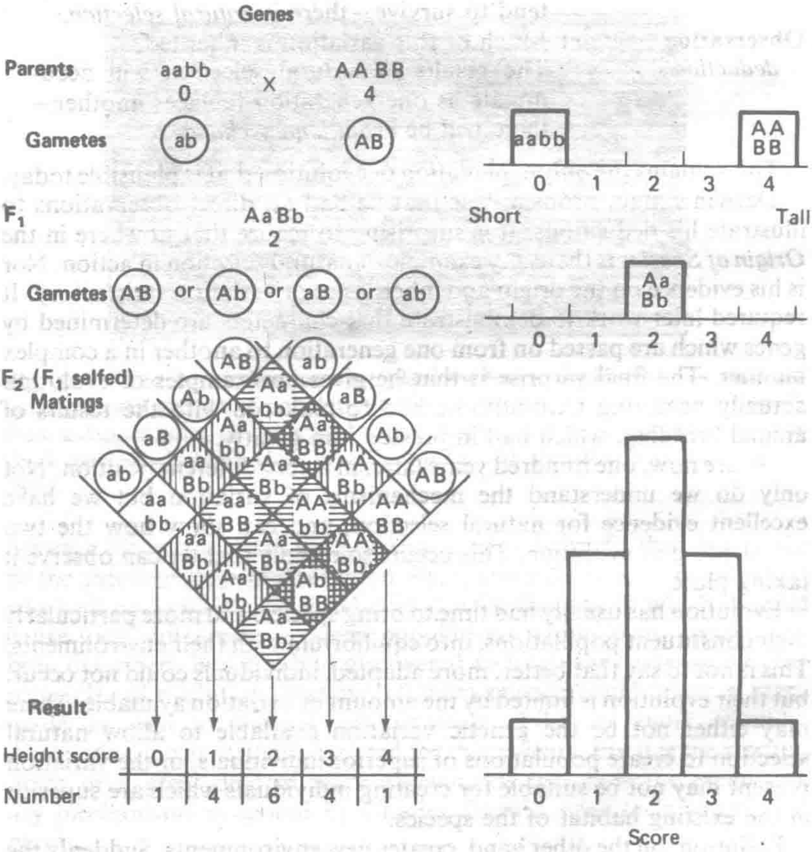


Fig. 1–2 The result of crossing pure breeding short and tall plants when the character is determined by two pairs of genes acting in an additive manner: there is a continuous range of variation in the F_2 generation. (Each capital letter represents an additive gene scoring one height unit.)

the first person to understand it. He worked with genes which had major effects on the garden pea. He showed that, for example, when a tall and a short plant were crossed, the progeny were all tall; shortness had effectively disappeared because tall was dominant. However when these tall plants were crossed, their progeny contained both tall and short plants, in a ratio of approximately 3 tall: 1 short. Although dominance can cause the character to disappear for a generation, it has the potential to reappear in any subsequent generation. When a character is determined by *major genes* like this the variation is *discontinuous* and easy to see.

Most characters in living organisms are, however, more complex since they are determined by several processes and therefore by several pairs of genes. In this case the resulting patterns of inheritance are more complex (and explain why biologists originally dismissed Mendel's proposals). But they can be understood if we assume the simplest situation in which the character is determined by only two pairs of genes, which are inherited independently of each other and whose effects add up to give the final character (Fig. 1–2). Now we have a situation which looks like blending inheritance, where the differences between the original parents seem to disappear as we progress from one generation to another. But this is not true because the continuous range of variability which appears in the second (F_2) generation is genetically determined, and if we breed from particular F_2 individuals we can get very different families in the next (F_3) generation. So when a character is determined by many genes with small effect, *polygenes*, although the variation is now *continuous*, it is still genetically determined, just as if it was discontinuous. This is because the individual polygenes are still behaving in a Mendelian manner.

1.4 Effects of selection

If a character is genetically determined it is heritable and can be selected for. The action of selection on a population containing a pair of major genes can easily be demonstrated if we know the fitness of the different genotypes – the relative amounts they contribute to the next generation. Figure 1–3 shows the change in the proportion of a gene present in a population (gene frequency) where individuals possessing that gene produce 20 % fewer offspring (i.e. their fitness is 20 % less) than individuals lacking the gene. What is surprising perhaps is that even with a difference in fitness as little as this the population changes markedly in few generations. If one genotype had been 40 % less fit than the other the rate of change would have been twice as fast.

When a character is determined by polygenes similar changes in gene frequency can occur. However we are unable to see individual gene effects and so must use the average characteristics of the population. In

1900 a selection experiment on corn (*Zea mays*) was set up in the University of Illinois, in which there was selection for high, and also for low, oil content in the grain in an old unselected variety, 'Burr White'. This experiment is still continuing. The results of the first fifty years (Fig.

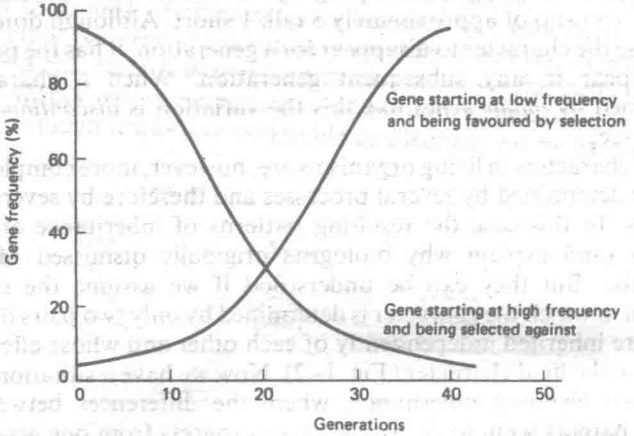


Fig. 1–3 The changes which occur in the frequency of a dominant gene which is either favoured or disfavoured by a selection intensity of 20%: the change in gene frequency is very rapid.

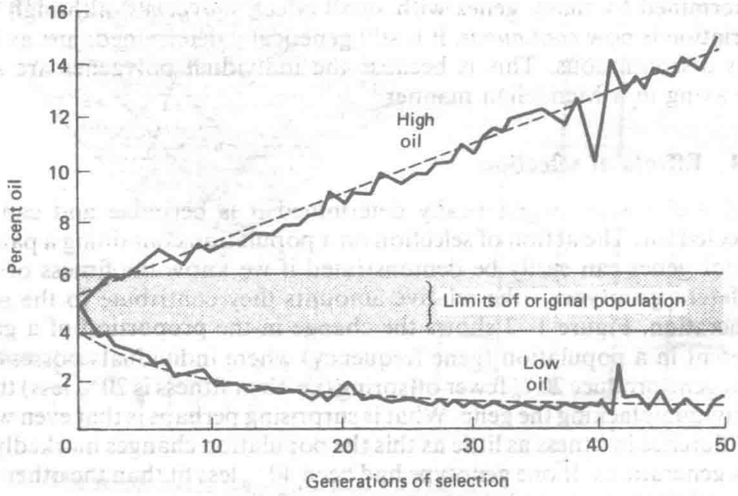


Fig. 1–4 The outcome of selection for high and low oil content in the Illinois corn experiment: response to selection is considerable (WOODWORTH, *et al.*, 1952; by permission of the American Society of Agronomy).

1–4) show that there is an enormous store of variability, which is available for selection, in a character determined by polygenes. In particular the two selected populations have reached levels of oil content which are far outside the range of the initial population.

This can be explained if some of the original variation was in the form AAbb and aaBB, each of which would score 2 in the scheme shown in Fig. 1–3. With crossing and subsequent recombination of genes, genotypes such as $\underset{4}{\text{AABB}}$ and $\underset{0}{\text{aabb}}$ would be produced which would score more (or less) than their parents. This hidden, or transgressive segregation, as it is called, is now well understood (EDWARDS, 1977). Plant breeders, in particular, rely on it to achieve increases in yield. But it is also a widespread property of characters in natural populations, and, just as in maize under artificial selection, it allows populations to respond in remarkable ways to natural selection.

In the end, however, the store of genetic variation in a population available for selection must become exhausted, because the number of genes in the population is finite. Some new variability may arise due to gene mutation but this is a slow and largely unpredictable source. As a result a population being subjected to selection ultimately stops responding and reaches a plateau (Fig. 1–5). It will be unable to respond further unless it receives new genetic variation by mutation, or by hybridization with some related organism carrying different genes. It seems likely that most established populations are in the plateau situation, where they have run out of all immediately available variation of value in their existing environment.

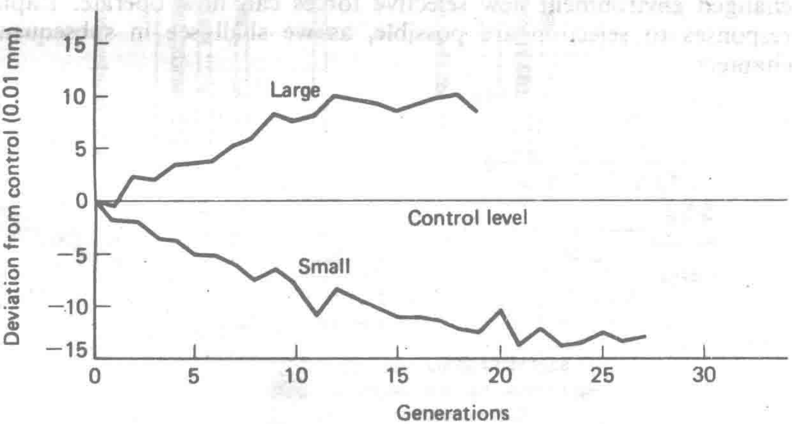


Fig. 1–5 The outcome of selection for body size (thorax length) in *Drosophila melanogaster*: eventually there is no further response to selection (ROBERTSON, 1955).

However we must not lose sight of the fact that what we see as a population in the field is a collection of phenotypes, the product of the effects of the environment on the expression of the genotype of an individual. These effects can make genetically different individuals look phenotypically similar and so prevent selection from acting on these *hidden genetic differences.*

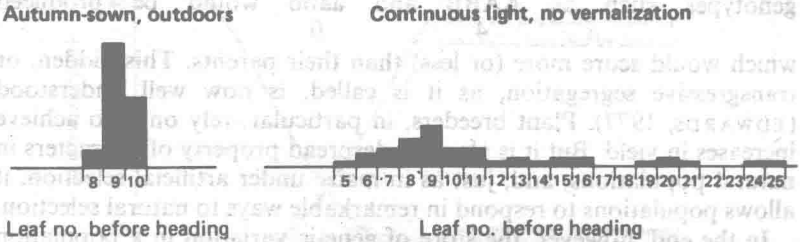


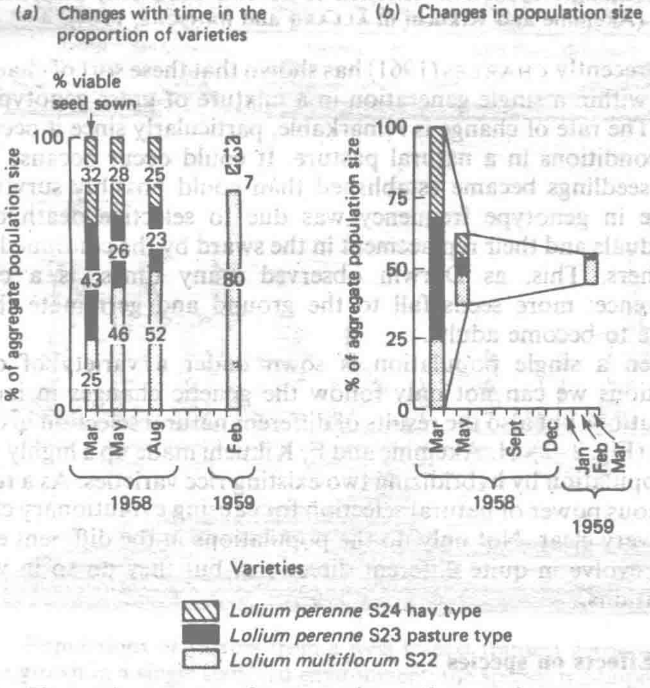
Fig. 1–6 Flowering time in a population of ryegrass grown in normal and abnormal conditions: an apparently uniform population reveals that it contains hidden variation when it is exposed to a new environment (COOPER, 1954).

If a population becomes subjected to a new environment, some of these genetic differences within it may now be revealed, for instance when a ryegrass population (*Lolium perenne*) is transferred to a new environment (Fig. 1–6). It can now respond again to selection. This will also happen when the population becomes exposed to a pollutant; in this changed environment new selective forces can now operate. Rapid responses to selection are possible, as we shall see in subsequent chapters.

2 Evolution in Natural Conditions

2.1 Effects on artificial populations

The power of selection in natural conditions can be demonstrated by very simple experiments. If an artificial mixture of different genotypes is sown out in a field under normal conditions, allowed to grow to maturity, the seed collected and re-sown the next year, the proportions of the different genotypes change very rapidly, and in a few generations some get completely eliminated. This was shown first by H. V. Harlan and M. J. Martini in a large scale experiment in the United States involving a mixture of barley varieties.


(a) Changes with time in the proportion of varieties

(b) Changes in population size

Fig. 2–1 Change in genotype frequency in a mixture of ryegrass varieties sown in natural conditions: population changes can occur within a single generation (CHARLES, 1961).

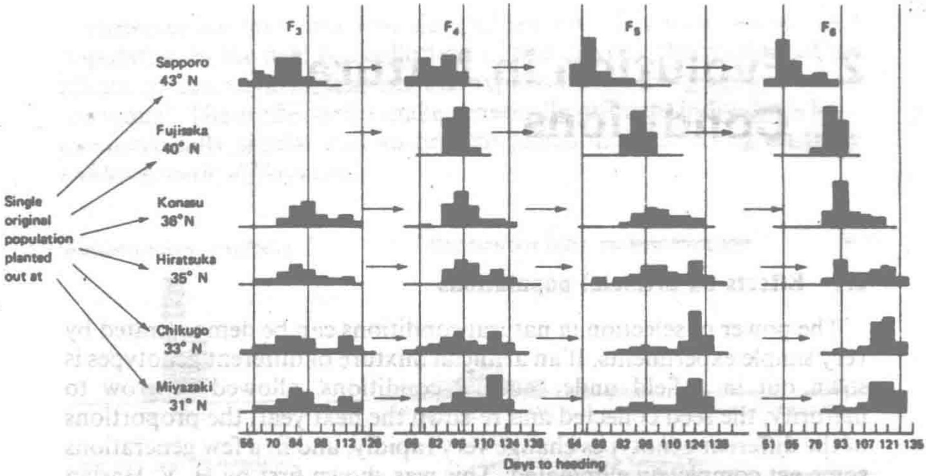


Fig. 2–2 Histograms of heading dates in a rice population grown for successive generations in different regions of Japan: the original population rapidly changes by natural selection to become completely different in each region (Akemine and Kikuchi in ALLARD and HANSCHE, 1964).

But recently CHARLES (1961) has shown that these sort of changes can occur within a single generation in a mixture of grass genotypes (Fig. 2–1). The rate of change is remarkable, particularly since it occurred in field conditions in a natural pasture. It could occur because initially more seedlings became established than could possibly survive later: change in genotype frequency was due to selective death of some individuals and their replacement in the sward by the continued growth of others. This, as Darwin observed many times, is a common occurrence: more seeds fall to the ground and germinate than can survive to become adults.

When a single population is sown under a variety of different conditions we can not only follow the genetic changes in individual populations but also the results of different natural selection in different places (Fig. 2–2). H. Akemine and F. Kikuchi made up a highly variable rice population by hybridizing two existing rice varieties. As a result the enormous power of natural selection for causing evolutionary change is made very clear. Not only do the populations in the different environments evolve in quite different directions, but they do so in very few generations.

2.2 Effects on species

When a wild species in the course of time enlarges its range it inevitably spreads into different, new, environments. Consequently, in each new situation it becomes subject to all the effects of each particular environment. Natural selection then begins to act, to refine each character of the species in relation to its new conditions of life. Darwin recognized this likelihood, very clearly, in the *Origin of Species* (Chapter IV).

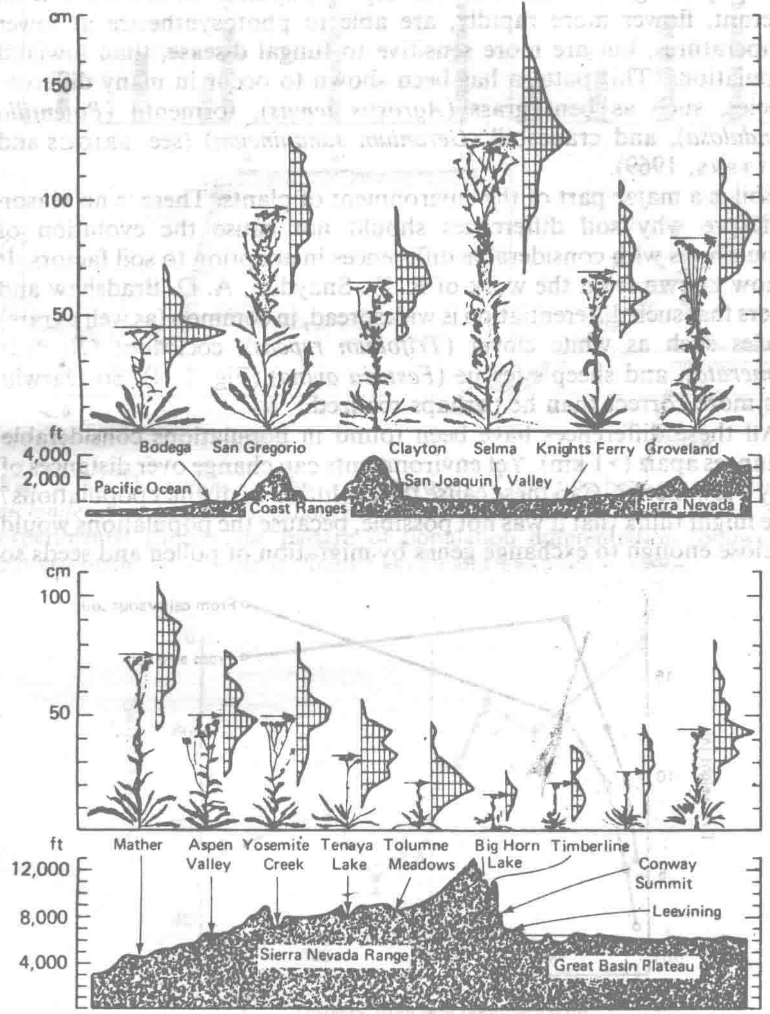


Fig. 2–3 Populations of yarrow from a west-to-east transect across central California grown in a single standard environment: the species is composed of very different populations, the result of natural selection (CLAUSEN, 1962; by permission of Cornell University Press).

As a result we find that species are differentiated into local, adapted, populations, called *ecotypes* by G. Turesson. One of the best examples is the work by J. Clausen, D. D. Keck and W. M. Hiesey on the common plant, yarrow (*Achillea lanulosa* and *A. borealis*) (Fig. 2–3). They showed that the populations are not only morphologically, but also physiologically, distinct. The alpine populations are more frost tolerant, flower more rapidly, are able to photosynthesize at lower temperatures, but are more sensitive to fungal disease, than lowland populations. This pattern has been shown to occur in many different species, such as bent grass (*Agrostis tenuis*), tormentil (*Potentilla glandulosa*), and cranesbill (*Geranium sanguineum*) (see BRIGGS and WALTERS, 1969).

Soil is a major part of the environment of plants. There is no reason therefore why soil differences should not cause the evolution of populations with considerable differences in adaption to soil factors. It is now known from the work of R. W. Snaydon, A. D. Bradshaw and others that such differentiation is widespread, in common (as well as rare) species such as white clover (*Trifolium repens*), cocksfoot (*Dactylis glomerata*), and sheep's fescue (*Festuca ovina*) (Fig. 2–4). So Darwin was more correct than he perhaps realized.

All these differences have been found in populations considerable distances apart (> 1 km). Yet environments can change over distances of only a few metres. Can these cause the evolution of distinct populations? One might think that it was not possible, because the populations would be close enough to exchange genes by migration of pollen and seeds so

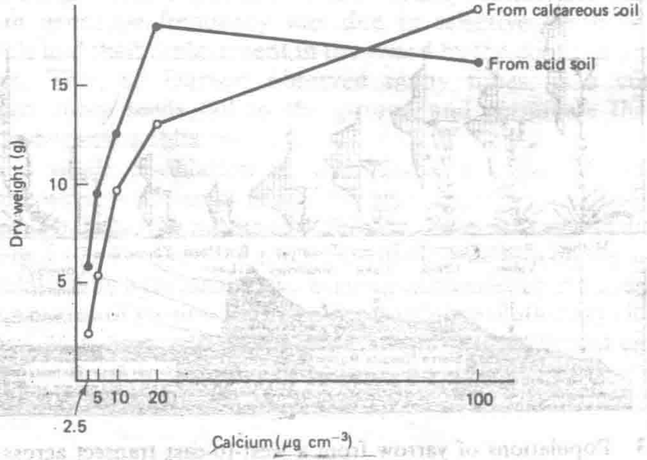


Fig. 2–4 The growth of two populations of sheep's fescue coming from contrasting soils, at various calcium levels: they have completely different patterns of response (SNAYDON and BRADSHAW, 1961).