

The Soil Factor in Plant Ecology

A. C. S. Wright

The soil factor in plant ecology can be approached from two directions. Usually the approach is made by an ecologist studying the influence of the soil on the composition of a particular plant community, but there is also the less conventional, and perhaps more interesting study of the influence of plants and animals on processes within the soil which may subsequently result in far-reaching ecological changes. Here I wish to illustrate the principles involved by a New Zealand example in each category.

First it is necessary that I give an outline of some of the processes by which soils are produced. Consider a freshly exposed rock surface. At first there is a period when physical weathering is predominant, producing fissures and granulating the rock surface. If water is present chemical weathering attacks the rock minerals, and according to the ease with which their structure is attacked, they decompose to finer particles—*sand*, composed of the more resistant minerals like quartz or tourmaline; *silt*, a finer fraction; and *clay*, composed of the finest and most strongly weathered mineral particles.

At a very early stage in this process life comes to inhabit the more protected corners, and the by-products of living cells help to hasten the rate of chemical weathering. Among the first living components of the organic cycle are bacteria able to derive energy for their growth from chemical transformations without direct recourse to solar energy. They live independently of light and often penetrate deep into the weathering rock. Early arrivals of larger size are the lichens, composite plants each composed of an alga and a fungus. By virtue of this association they successfully colonize bare rock surfaces. The organic cycle gains strength with the addition of other plants until it reaches its maximum development—a fairly stable plant community, usually called the *climax* vegetation.

Soil formation does not stop at the production of a little sand, silt and clay. Weathering processes bit down into the rocks and the layer of soil grows deeper; rain-water draining through the soil leaches out the basic plant foods (in a definite order) and even brings about some rearrangement of the clay and silt fraction of the soil skeleton, so that in vertical section we say that the soil develops a *profile*. The type of profile varies with different kinds of parent rock and with different conditions of soil formation, so that specific *soil types* can be recognized and described.

The *climatic* factor is usually the dominating force in soil formation, mainly because it controls the soil moisture and temperature. In addition it helps to determine the nature of the organic cycle, which includes the vegetation. This results in there being a distinct zonal relationship between the soils of the world. For instance, we speak

of the tundra soils of the subpolar zone and recognize them as a *zonal* soil group.

All the soils in a climatic zone, however, do not necessarily have the same profile characteristics. In a number of cases the influence of the parent rock seems stronger than the impress of climate, resulting in a group of closely related soil profiles extending across a range of climatic zones. This is the case with soils derived from serpentine rock. A commoner example occurs in lowland or basin-like situations where the normal rainfall is reinforced by extra moisture running down from higher land. These soils tend to be much moister than is characteristic for the zone and special soil processes arise which produce rather similar profiles throughout a whole range of climate. They are placed in the *gley* soil group. Soils that appear in more than one climatic zone are grouped by pedologists (for their convenience) as *intrazonal* soils. They usually support vegetation that is conspicuously different from that carried on the zonal soils, and to the plant ecologist they are soils on which *edaphic* factors are largely determining the plant formations.

Thus we arrive at a point where we can discuss the first line of approach mentioned in my introductory remarks. Let us narrow the discussion to one specific suite of intrazonal soils—those derived from highly basic (ultrabasic) rocks. These rocks are well represented in New Zealand by serpentine, of which there are many outcrops in the South Island (Mossburn, Olivine Ranges, Dun Mountain, D'Urville Island) and a few in the North Island (Te Kuiti, North Auckland). The plant cover of the land at the time of the earliest European records included a number of patches of scrub and tussock in regions where one would expect forest. Some of the cases have no apparent relation to soil factors and are possibly connected with Maori history, but elsewhere these patches are clearly associated with the presence of ultrabasic rock. The same thing occurs in New Caledonia, Cuba, etc., and on a world vegetation map the more extensive serpentine areas would be quite easily picked out. What is there about these soils that so modifies the plant cover that it sometimes consists of low scrub with only a few species?

Research workers in the different countries have reached no agreement on this point, other than the general one, that it is related to the unusual chemistry of the soil. To a varying degree the blame is laid upon high pH, low calcium magnesium ratio, low calcium, high magnesium, and the presence of toxic amounts of elements like chromium, nickel and cobalt. This confusion becomes understandable, however, if we consider the problem from the angle of soil formation.

The highest latitude in which I have seen these soils was on the island of Skye. Much of the area is under a blanket of peat. Chemical weathering of rock minerals is slight and the rate of leaching is high, so that soils have a low pH, low calcium and low magnesium. These features and the calcium magnesium ratio are normal, and plants show only a slight accumulation of chromium. There are few characteristic

herbaceous plants ("serpentine species") on these soils and most species of the normal district flora appear to be serpentine tolerant, few being completely absent.

In New Zealand, e.g., in the Nelson "mineral belt", there is less leaching but more weathering. In conformity with the greater degree of chemical weathering the uptake of chromium from the soil is slightly greater. But the main feature of the soil chemistry is the high level of magnesium, high pH, and the very low calcium magnesium ratio, which is in conformity with a moderate rate of leaching. The list of "serpentine species" is longer and that of the serpentine-tolerant plants shorter.

At the other end of the scale, represented by New Caledonia, where the soil minerals are completely weathered and leaching is moderate to high, the soil magnesium content is more normal but there is a high level of exchangeable chromium, etc. Rather large amounts of these elements are taken up and as they are toxic to most plants there is a low scrub composed of relatively few species, almost all of them specific to the serpentine areas. The point that I wish to emphasize is that the modification of the zonal vegetation is most probably brought about by a different set of soil conditions in each climatic zone.

Other intrazonal suites, e.g., limestone and basalt, have a similar but narrower zonal range over which the peculiar soil parent materials may be expected to influence the composition of the plant formations. If you are in the right climatic region, you may expect limestone soils, for instance, to modify the plant cover.

About the other aspect, modification of the soil by plants, there is a lot more that we would like to know. There are many pertinent questions that need an answer, and in my opinion New Zealand is particularly well favoured for finding the answers, so that if anyone can develop fruitful concepts from this line of work it *should* be the ecologists of this country.

I have already indicated that soil formation is profoundly modified by the presence of an organic cycle. The fully developed plant cover is the most important component of the organic cycle and is a powerful conditioning agent on soil processes. In the great majority of New Zealand soils, nutrients released by weathering of soil minerals are either lost by leaching or taken up by plant roots. Once within the plant they are protected from normal leaching until returned to the soil surface through the leaf, twig and bark litter. Thus the organic cycle helps to sustain the nutrient level in the soil, but the efficiency of the system varies widely with different plant species. Some have a high level of nutrient intake and only slight withdrawal of nutrient elements from the leaves and twigs before abscission, so that their litter is rich in plant nutrients, able to support a large and varied population of decay organisms. In this particular cycle there is a relatively high level of circulation of nutrients and little fertility is lost by leaching. Puriri is a species of this type; there is no litter

accumulation beneath this tree and the soils are brown and crumbly. There are few soil fungi but many worms and a large population of soil bacteria.

On the other hand, many trees use only a small proportion of the soil nutrients available and generally their litter is less well supplied with elements like calcium and magnesium. This litter is less palatable to decay organisms and it tends to accumulate and become peaty. Normal leaching is accelerated because there is acidification of the rain-water percolating into the soil. This is characteristic of the litters of rimu, kauri and kamahi in almost all of their New Zealand stations. The soil beneath is acid, bleached and structureless, with few worms or soil bacteria but many soil fungi.

The dominant members of the vegetation in New Zealand can be divided into *mor* formers like the kauri, and *mull* formers like the puriri. The difference between these two categories is partly physiological, linked with, perhaps, root respiration rate, rhizosphere associations, nitrogen intake, level of carbohydrate metabolism, fat translocation, leaf morphology and many other factors. Trees like broadleaf and mahoe are mull formers almost throughout New Zealand. The only known exception is in certain locations in Fiordland where extremely wet conditions occasionally cause accumulation of litter, and a kind of base-rich or *fen* peat is produced. In the other category the New Zealand kauri is a confirmed *mor* former, but the Fijian species is a *mull* former. This may be a species difference or it may be the result of tropical conditions under which most litters decay readily.

The effect of a layer of *mor* on the surface of the soil is always acceleration of the normal rate of leaching. Often the order of removal of soil minerals is modified by different kinds of *mor*. When the vegetation is made up of a mixture of *mull* and *mor* formers, the soil pattern shows a mosaic of different profiles corresponding to the different species of trees. This mosaic is not etched permanently in the soil, but during the adult life of one tree—often a long time in the case of podocarps and kauri—the influence of that individual tree may be considerable. In plant successions the trees and shrubs of one stage condition the soil ahead of the next stage. Little, however, is known about the process. There is a great abundance of problems awaiting the plant ecologist in this field. Let me indicate a few of them.

Foremost is the problem of the dynamics of the climax vegetation. If the soil is changing continuously, how is an apparently stable plant cover maintained? Is there alternation between *mor*-forming and *mull*-forming dominants to maintain the soil "status quo"? Some botanists and pedologists think that this does occur. If this is so, what is the mechanism by which it operates? Then there is the case of the stability of a forest dominated by a single species, like silver beech, and the development of pure stands of trees—miro and kauri both show this tendency—in a mosaic forest. It seems likely that

mor formers as a group can make fairly good growth at a very low level of nutrition, using nothing more than the nutrient in their own organic residues plus a little extra mineral nutrient supplied in the rain and in atmospheric dust. Several cycles of trees growing on their own litter will naturally have a strong conditioning influence on soil processes and can produce very marked, permanent changes in the soil profile. Usually impervious pans develop and these hold up the rain-water and lead to the formation of gley soils which carry a swamp vegetation. This has occurred in the case of most terrace pakihi and flat gumlands.

In concluding I hope that I have said enough to make it plain that here is a field of plant ecology the surface of which has barely been scratched.

Typha in New Zealand

R. Mason and N. T. Moar

Raupo is one of the most conspicuous plants in swamps and wet places, and may be regarded as commonplace and known to everyone; yet whether we have more than one form, and if so what botanical names should be applied to them, are questions which most of us would not care to answer from our own knowledge.

Typha is a genus with an almost worldwide distribution and some widely distributed species. Our plants were put by Forster under *T. latifolia* L., a species of Europe, North America, and parts of Asia, but all later botanists, except T. Kirk, have put them under *T. angustifolia* L., a species with a similar distribution. Kirk, who was familiar with both species in England, considered ours to be *T. latifolia*, and always used that name. The more obvious characters such as size and robustness, and the distance between the male and female spikes, were used to distinguish the species. Our plants certainly seem to be taller than *T. angustifolia* and to have broader leaves.

Cheeseman quotes Graebner (1900) as classifying our plants as *T. angustifolia* var. *brownii* and *T. angustifolia* var. *muelleri*, and states that var. *brownii* includes the larger and coarser states with contiguous spikes, and var. *muelleri* the smaller plants with a gap between the male and female spikes. Graebner, in fact, placed our plants under *T. angustifolia* in a proles *brownii* and in a subspecies *T. muelleri*. Although he stated both were found in New Zealand, he does not seem to have seen New Zealand material himself, and perhaps he was here relying on Rohrbach, who (according to Melvaine, 1940) referred to New Zealand specimens of *T.a.* var. *brownii*, and on Kronfeld, whose monograph of 1889 we have not seen. Graebner based his classification mainly on details of the floral structure.