

The Soil Factor in Plant Ecology (2)

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IN Bulletin No. 24, April, 1951, I made some general comments under this heading to illustrate two important ecological concepts: (1) If the rock from which a soil is derived contains an excessive proportion of one or more mineral elements then over a certain climatic range the soil factor will largely determine the pattern of the vegetation. Serpentine and limestone soils were quoted as examples. (2) If the rock from which the soil is derived contains a more or less normal balance of mineral elements then certain plant species will, over a specific climatic range, largely determine the soil pattern. Various *mull* and *mor* forming species in the New Zealand plant assemblage were quoted as examples.

Since 1951, I have been actively pursuing various manifestations of these two concepts over a much wider range of climates and soil parent materials than hitherto investigated. The most accessible land mass with sufficient variety of environmental conditions to provide more or less continuous sequences of soils from the humid tropics to the cold temperate regions was judged to be the American continent. Field investigations were started in Central America and the West Indian Islands in about 20° North latitude and, by devious ways and means, carried on down to Tierra del Fuego in about latitude 53° South. The main object was to find out what influence the vegetation had on the pedological processes in stable soils of the lowlands of the humid regions in the various latitudes and, as a side issue, what went on as one ascended from the lowlands to the highlands in the various latitudes. The project had to be self-financing as far as possible and so it came about that much of the work was carried out in British Honduras, British Guiana, Brazil and Chile where short-term soil survey jobs were available. During the Central and South American part of the investigation the writer was on leave from the New Zealand Government; on returning to New Zealand in 1954 soil survey work was available in Western Samoa, Fiji and the Chatham Islands, which provided an opportunity to follow out the story on island territories where the plant assemblage is often restricted by chance. The results are of more than passing interest and in the hope that some of the younger ecologists in New Zealand may be tempted into this worth-while field, I have pleasure in setting down my conclusions.

The forest of the lowlands of the humid tropics is a little overwhelming in its exuberance and soil-plant relations are, at first, not easy to see. In part this is due to the fact that, in these regions, soil movement is a very active factor in soil formation. There are not many *stable* soils where the interactions between soils and plants

can adequately be studied. The most profitable hunting grounds for the ecologist interested in soil processes are to be found on the river terraces above flood level and on undissected plateau surfaces occasionally found in the lower foothill regions. Here it is soon evident that instead of individual species with pronounced soil conditioning properties (as was the case with the kauri trees in the mixed podocarp-broadleaved forests of North Auckland) the whole composition of the tropical forest gradually changes as the stable soils become leached and depleted of plant foods. For instance, the forest of the young river terraces is composed of a wide range of gross-feeding species which return to the soil a litter which is rich in basic minerals. With increasing age, weathering and leaching reduce the supply of plant food within root range and gross-feeding species gradually give way to species more tolerant of a lower standard of living. The Amerindian folk who dwell in these forests are well aware that certain indicator species in the vegetation provide good clues to the crop-producing power of the soil and they plan their shifting agriculture accordingly. At a certain stage in the progression the soils start to become really poor and the even canopy of the forest becomes ragged (when seen from the air) by the clear emergence of the crowns of those species best able to tolerate the deteriorated soil conditions. The undercanopy degenerates gradually, successively dominated by low broadleaved trees, then palms and eventually coarse grasses, often with silica-rich cutting edges to the leaves. As the soils become poorer the scattered large trees are replaced by smaller trees of a different physiological type (often species which have resin-charged tissues, and hence are relatively inflammable) and, since the soils have now reached the stage of either iron-pan or clay-pan formation, they are restricted to species tolerant of swamp or semi-swamp (i.e. seasonal swamp) conditions. Many of the grassland areas of the lowland humid tropics are induced communities resulting from the burning of the relatively inflammable type of forest which develops as the soils became poor. At no stage does the forest show a mosaic of *mull* and *mor* forming trees but as the soils deteriorate, there is a general development of acid surface litter. Nevertheless there is little doubt that some species bring about soil deterioration at a faster rate than others. As the Amerindians well know, the maize crop planted on the site of a negrito tree (*Simaruba glauca*) in a forest composed mainly of gross-feeding species, is markedly poorer yielding than the general average of the crop. It would appear that, on stable soils, there is a logical sequence in the plant cover from shade-tolerant, highly competitive succulent gross-feeding species to light-tolerant, resinous frugal-feeding species that matches the change in soil conditions from nutrient-rich to nutrient-poor. Only in the final stage, when rain-water is held perched above the subsoil pan layers, does a deep layer of organic residues accumulate.

This process of soil deterioration goes on much faster in soils derived from quartz-rich parent materials. Where these occur at stable sites in landscapes in the humid tropics the vegetation is commonly coarse and wiry grassland and the only forest in the region is that on the unstable hill slopes or along the streams. The surface soil consists of several feet of white quartz sand which may be submerged by surface water during the wet season. These are the tropical podzols. On quartz-poor parent materials—such as basalt—the soils develop a bright red colour and are loosely honey-combed with a hard framework composed of oxides of iron and alumina and are known as laterites or lateritic soils. They correspond, in a measure, to the 'ironstone' soils of North Auckland. In many places the lateritic and the podzol stage of soil development may be reached before the forest becomes open and interspersed with patches of grassland, and it has yet to be shown that the majority of the grasslands in the humid lowlands of the tropics are not, in fact, promoted by the hand of man carrying his all important and ever-present fire-brand.

This is the pattern of the relationship between soils and vegetation on stable lowland landscapes in British Honduras, in British Guiana and Brazil. The Maya Mountains of British Honduras, the Pakaraima Mountains of British Guiana and the foothills of the Andes in Brazil and Peru, all show in exciting succession a gradual separation of the components of the forest vegetation into *mor*-forming and *mull*-forming species and the development of forest mosaics in the soil as individual trees achieve marked local powers of soil conditioning. As in New Zealand it is the trees of ancient lineage—the conifer stands—which first appear as *mor*-formers in a mixed broadleaved forest, and at the higher altitudes (as on the Western Andes) most species in the plant assemblage become peat-forming and the soils are fairly uniformly podzolized.

The Pacific lowlands of the South American continent are too dry to be of interest to the present discussion until the latitude of about 38°S is reached (equivalent to the Bay of Plenty), where forests of *Nothofagus* become a general feature of the Chilean landscape. Much of the landscape of Chile is covered with andesitic ash and the soils are both younger and less weathered than the equivalent soils in New Zealand but nevertheless progressing southward through Southern Chile, the gradual development of *mor*-forming *Nothofagus* forest is clearly associated with a sharp increase in the intensity of soil leaching, culminating in widespread podzolization of the soil in about latitude 42°S, on almost all parent materials other than recent volcanic ash or recent alluvium. The chief interest that this region of Chile holds for the pedologist lies in the presence of areas of podocarp-broadleaved forest very similar in composition to that of the Catlins region of South Otago and Southland, and the presence of *Araucaria*, *Libocedrus* and *Fitzroya* forests in various parts of the

highlands and lowlands. The *Libocedrus* forests are almost exactly comparable to those of New Zealand and, where on the older types of rock, produce podzols identical in appearance with those found in the Catlin ranges. The *Araucaria* forests rarely occur other than on young volcanic soils high on the flanks of the Andes but they are, nevertheless, strongly mor-forming. *Fitzroya*, the Chilean cedar, is now found mainly on Chiloe Island and in pockets on the foothills of the Andes south of latitude 41°S, and it appears to have a prodigious propensity for accelerating soil leaching through the accumulation of thick mounds of resinous litter. There are also several species of *Podocarpus* and *Dacrydium* which have an equivalent effect on soil processes to their counterparts in similar latitudes in New Zealand.

Progressing further southward, the gradual development of heath and bog vegetation, *Dracophyllum* forest, and *Nothofagus antarctica* (equivalent to *N. cliffortioides* in New Zealand) contribute to the gradual thickening layer of forest peat on the soil and the development of podzol characteristics in the soil. The Chronos Islands were not visited but from local descriptions and from Charles Darwin's accounts, they sound uncommonly like Chatham Island landscapes. Indeed, if it were not for the remarkable absence of sandflies, a New Zealander might feel completely at home in this part of Chile.

Thus, in continental regions, the processes associated with the ageing of stable soils are matched by a changing plant cover and, under appropriate climatic conditions, are visibly accelerated by the presence of an ever-increasing proportion of plants which make but frugal use of the plant food available and whose accumulating organic residues intensify the mechanism of leaching. When an ecological niche becomes sub-optional for one species, some plant more tolerant of lower nutritional levels moves in. This sequence of events also operates in island territories—but with a difference. On islands the original assemblage of plants present may not include species adapted to the poor soils that will arise eventually on stable land surfaces. What happens in the case of an isolated island derived from base-rich volcanic rocks, such as the basalts of Western Samoa, where youthful soils will initially favour the shade-tolerant, highly competitive, gross-feeding colonizers, and stray arrivals adapted to poorer soils may quite easily fail to secure a foothold? Plants of this category arriving at a much later date will find many ecological niches ready-made for them, but at the outset, when all the soils are youthful, they may find themselves excluded. The present ecological pattern on the islands of Upolo and Savai'i may provide some answers. Many of the lava flows are of gentle relief and here, in the course of time, deep and comparatively stable soils have developed. These soils are very poor but, under natural conditions, are still occupied by gross-feeding forest trees, albeit much reduced in height and more spindly in shape than normally. When trees are blown

down, or when a larger tree than usual falls, the gap in the canopy remains open for a very long time. A natural clearing is formed which for many years is occupied by native grasses (or by introduced herbs, grasses or vines if not too remote from occupied land). Regrowth of a forest cover is by means of a slow advance from the forested periphery of the clearing—none of the adjacent species seem able to jump out into the high light and nutrient poor condition in the centre but can advance centripetally only from the shade of the surrounding trees and with the help of the small nutrient return provided by their litter. If there were present in the plant assemblage of Samoa species better adapted to these poor soils the present day vegetation pattern of Western Samoa would surely be very different. In Fiji, where there have always been small areas of quartz-rich but nutrient-poor sands, chance arrivals adapted to poor soil conditions have been able to survive and these have, in the course of time, spread and now occupy most of the poor soils that developed on land of easy relief. The present day vegetation pattern of Fiji is much more elaborate than that of the islands of Western Samoa.

Another Pacific Island of great ecological interest is Chatham or Rekohu Island off the New Zealand coast. Here, under a cool, damp and windy climate like that of Invercargill (although not so wet), many common plants of the Southland assemblage, those of the podocarp forest, manuka scrub and tussock grassland for instance, are missing and their various ecological niches have been taken over by *Dracophyllum* forest. *Dracophyllum*, in this type of climate, is an exceedingly active agent of peat formation. The grass-like foliage, so rich in complex organic compounds of a resinous nature, are very slow to break down and deep layers of forest peat (mor) quickly build up and add greatly to the rate of soil leaching. Under *Dracophyllum* forest, recently stabilized dune sands rapidly develop podzol characteristics, including humus, silica and iron pans. These impede drainage to such an extent that, on landscapes of gentle relief, bog conditions soon develop. It is interesting to speculate on how much of the blanket peat covering the landscape of the Chathams is due to the absence of podocarp species, manuka and tussock, and to the peat-forming propensities of *Dracophyllum*.

Continued from page 5: Gastrodia and Mycorrhiza—between the *Orobanche* tuberous, and apparently mycorrhizic, rhizome and the roots of the other plant. Possibly a connection exists through a fungus common to both. Again, further investigation would be interesting.

Many years ago G. M. Thomson examined the rhizomes of *Gastrodia* (*Proc. N.Z. Inst.* 40, 579) of which he gave an account that is still interesting to read. He remarks that 'It is desirable that the parasitic habit of these orchids should be more closely investigated. I have no record of the roots on which they grow, nor can I find that any careful investigation of these has been made'.