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Geochemistry and ecology

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This paper discusses the importance of geochemistry as a determining factor in the evolutionary development of plant assemblages. Three contrasting examples of geochemical systems are described and considered in relation to their effects on plant growth and development.

Soils derived from serpentines may contain elevated and sometimes toxic concentrations of Cr and Ni depending on mineral composition and weathering processes. These conditions have so modified plant growth during the past few million years that specialized floras have evolved on particular sites.

Extensive areas throughout the world contain high concentrations of Se but these have not always been accompanied by the development of specific floras. Geochemistry can help explain how Se-specific floras have developed in several Western States of America but are absent on Se-rich sites in the Republic of Ireland.

Pronounced effects of As toxicity in plants have been recognized in recent years especially from areas polluted by smelter waste and fallout. As-tolerant genotypes have developed during the past 100 years and may still be evolving at the present time.

1. Introduction

Geology and climate are the two major aspects of the physical environment that isolate plant populations and species. The role of climate in controlling broad distributions of plants is undisputed but within areas of climatic similarity, geological variability provides the major source of regional diversity. The contribution of geological phenomena to vegetational discontinuity takes various forms. Variations in physical properties, mineral content and topography account for much of the regional differentiation brought about by geological processes. When these processes interact with the microclimate, a wide range of habitats are created. Discontinuities of vegetational patterns and forms become established which are ubiquitous features of plant distribution. Ecologists then see the floras of the world arrayed in various degrees of discontinuity.

In this paper, only those geological aspects that have given rise to diverse plant distributions will be considered. Of foremost importance is soil diversity and its geochemical implications. Since there is great diversity of geological materials available for soil formation from acid rocks to ultrabasics, the range of geochemical environments is large. Examples can take the form of 'abnormal' soils severely deficient in one or more essential elements, such as the highly acid and infertile soils underlain by sands and siliceous substances. In the U.S.A., typical vegetational discontinuities include the pine barrens of New Jersey, the shale barrens of the Appalachians, the pygmy forests of California and the so-called 'ecological islands' near Ione, California (Gankin & Major 1964; Jenny *et al.* 1969; Kruckeberg 1969*a*). Alternatively, 'abnormal' soils can contain excessive amounts of one or more elements, which again produce exceptional vegetational responses. Three examples have been chosen to illustrate the effect of toxic concentrations of elements on plant growth and development. These are: first, the remarkable floras of the ultrabasics notably serpentines and secondly, floras which have developed on Se-rich soils. Both of these geochemical environments have influenced the evolutionary development of plants for many millions of years. The third example is the recent evolution of vegetation on As-toxic spoil produced during the Industrial Revolution.

2. PLANT LIFE ON SERPENTINES

Probably the most spectacular 'abnormal' soil is that derived from serpentine and other ferromagnesian rocks (ultramafic). These rocks have weathered to soils that exert a profound selective influence on regional floras on every major land mass of the world. Striking contrasts between the barrenness of ultramafic and the comparative luxuriance of adjacent non-mafic sites are familiar features of the landscape (Kruckeberg 1969*b*). Although the most widely known locations are situated in Europe and North America, serpentine floras occur throughout the tropics and temperate areas and include for example, Australia, New Zealand, New Caledonia, Japan, Cuba and Africa (Whittaker 1954; Proctor & Woodell 1975).

The commonest ultramafics are the igneous rocks peridotite and dunite and their metamorphic derivative serpentine, which weathers to soils high in Mg and low in Ca. Because minerals such as chromite are often present in addition to olivine, the soils usually contain high amounts of Cr and Ni. In addition, these soils are deficient in N and P (Spence & Millar 1963).

Ultramafics appeared in the early Precambrian and would have produced specialized soil conditions before the evolutionary development of the angiosperms in the Cretaceous. In tropical areas of the world, such as Rhodesia, Southern Africa and New Caledonia, the origin of at least some of the serpentine endemic species must have closely followed angiosperm development (Wild & Bradshaw 1977). In other parts of the world such as the Northern Hemisphere, the Pleistocene Ice Age will have eliminated all such floras. Present-day floras on these latter sites will therefore be of relatively recent origin.

Serpentine vegetation is in general rather sparse, with intervening barren ground; xerophytic characters and dwarfing are common features. The floras are impoverished but often contain unique or endemic species, taxonomically separate from populations on surrounding soils. In Rhodesia, for example, there are some 320 serpentine tolerant angiosperm species of which 22 are endemics (Wild 1965, 1974*a*; Wild & Bradshaw 1977). Adjacent areas, by way of contrast, contain nearly three times as many angiosperm species. In the Pacific North West of the U.S.A., endemics on ultramafics are fewer in number than in Rhodesia but many of the species occur in greatest abundance on this substrate (Kruckeberg 1969*b*). In New Caledonia, too, there are fewer endemics but they occur in a similar proportion to the Rhodesian situation (Jaffré 1974).

From an ecological point of view the high concentration of Mg and the low concentrations of Ca, N, P and K undoubtedly influence plant growth and evolutionary development (Walker 1954; Kruckeberg 1954; Proctor 1970). Several ecologists, however, consider that the high levels of Cr (up to 10% in air-dry soils) and Ni (commonly 0.5% in air-dry soils) are determining factors (Hunter & Vergnano 1953; Menezes de Sequeira 1968; Lyon *et al.* 1968, 1971; Anderson *et al.* 1973; Shewry & Peterson 1976). Undoubtedly these differences of opinion have arisen as a result of regional geochemical differences and variation in rates of weathering. A selection of published data has been compiled by Shewry & Peterson (1976) to illustrate this point.

In geochemical terms, soluble Cr is very low, usually below 1 μg/g in air-dry soil, and probably has only a minor effect on root growth. Serpentine ecotypes examined in our laboratories have failed to show a marked tolerance towards either Cr III or Cr VI. Further work is certainly needed to identify the forms of soluble Cr in soils. Nevertheless, Cr is accumulated by some plants to extreme levels, e.g. *Sutera fodina*, a geophyte from Rhodesia, can contain up to 50 mg/g ash mass (see table 1). Other species, however, may accumulate Cr only to low levels. Since soil Cr concentrations vary widely from region to region, the relative accumulation (i.e. the plant : soil ratio) is often calculated. The overall results show that Cr concentrations in plants are below the soil concentrations (table 1).

TABLE 1. TOTAL Cr CONCENTRATIONS IN SERPENTINE SOILS AND ASSOCIATED PLANT SPECIES

species	plant concentration μg/g ash mass	soil concentration μg/g ash mass	plant/soil	reference
Sutera fodina	48000	125000	0.38	Wild (1974*b*)
Leptospermum scoparium	2470	8950	0.28	Lyon *et al.* (1971)
Dicoma niccolifera	30000	125000	0.24	Wild (1974*b*)
Cerastium nigrescens	147	1800	0.08	Shewry & Peterson (1976)
Hebe odora	330	13800	0.02	Lyon *et al.* (1971)
Silene maritima	22	1800	0.01	Shewry & Peterson (1976)

Some species exhibit highly significant plant Cr–soil Cr correlations (see figure 1) and could be used for biogeochemical prospecting purposes (Lyon *et al.* 1968, 1971). However, correlations were not noted in other species collected at the same time and from the same soils. Presumably in this latter group of species their genetic and nutritional diversity outweighed plant–soil effects.

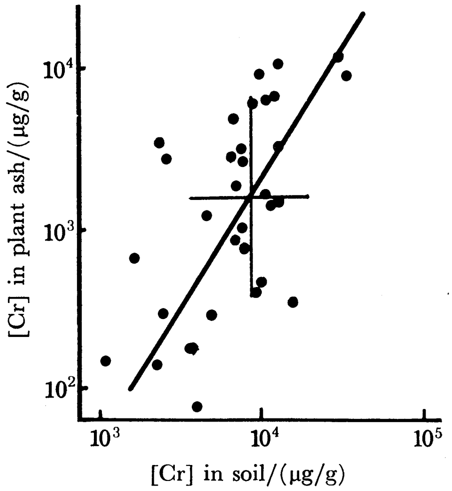

FIGURE 1

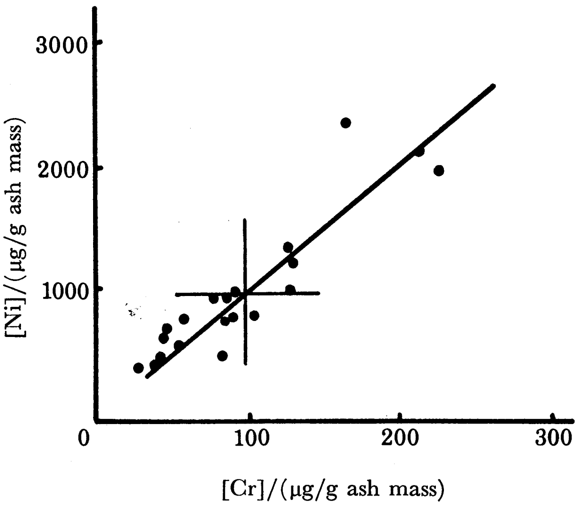

FIGURE 2

FIGURE 1. Relation between the concentration of Cr in leaf ash from individual *Leptospermum scoparium* plants and the concentration in associated serpentine soils from Dun Mountain, New Zealand. The regression line is shown, together with the mean. Data modified from Lyon *et al.* (1968).

FIGURE 2. Relation between the concentration of Cr and Ni in leaf ash from individual *Armeria maritima* plants collected from serpentine soils, Unst, Shetland Islands. The regression line is shown, together with the mean. Data modified from Shewry & Peterson (1976).

Interelement correlations have also been established in many species (Lyon *et al.* 1968, 1971; Shewry & Peterson 1976), of particular interest being the plant Cr – plant Ni correlation (see figure 2) which perhaps indicates that both elements are accumulated by the same mechanism.

Soluble Ni in serpentine soils can be readily measured and has been shown to exist predominantly as the hydrated Ni ion (Shewry & Peterson 1976). Test plants, such as barley, when grown on serpentine soils containing approximately 5 μg/g soluble Ni have been reported to develop toxicity symptoms (Anderson *et al.* 1973). When grown in solution cultures in the presence of Ni ions, barley seedlings develop similar toxicity symptoms. Endemics and tolerant ecotypes must, therefore, have evolved tolerance at the root–soil level and then at the cellular level. Indeed, serpentine ecotypes of *Silene maritima* will develop in Ni-enriched solutions without the appearance of toxicity symptoms (R. A. Skeffington & P. J. Peterson, unpublished data).

Table 2. Total Ni concentrations in serpentine soils and associated plant species

species	plant concentration (% ash mass)	soil concentration (% ash mass)	plant/soil	reference
Hybanthus floribundus	13	0.08	162.5	Severne (1974)
H. austro-caledonicus	27	0.50	54.0	Brooks *et al.* (1974)
Pearsonia metallifera	15.3	0.55	27.8	Wild (1974*b*)
Alyssum serpyllifolium	10.3	0.40	25.8	Menezes de Sequeira (1968)
Dicoma niccolifera	2.8	0.70	4.0	Wild (1970, 1971)
Pimelea suteri	0.59	0.33	1.8	Lyon *et al.* (1971)
Silene acaulis	0.18	0.33	0.5	Shewry & Peterson (1976)

Over the past several years an increasing number of outstanding Ni accumulators, or hyperaccumulators, have been reported especially from New Caledonia, Australia and Rhodesia (Severne & Brooks 1972; Cole 1973; Jaffré & Schmid 1974; Brooks *et al.* 1974; Jaffré *et al.* 1976). The range of accumulation encountered in various species is listed in table 2. It can be seen that the relative accumulation index for Ni exceeds unity by one or two orders of magnitude, which contrasts with the low index values for Cr already mentioned (table 1). Plants must therefore have evolved tolerance to extreme concentrations of Ni. Indeed, they have developed different cellular approaches, e.g. in *Hybanthus floribundus* Ni is especially located as deposits in some cells (Severne 1974), while in *Psychotria douarrei* Ni is stored as the hydrated ion. In other species such as *Sebertia acuminata*, Ni is metabolized in the cell to form a Ni–citrate complex (Lee *et al.* 1977) which can be compared with the Cr–trioxalate complex isolated from the Cr-accumulating *Leptospermum scoparium* (Lyon *et al.* 1969).

The extensive serpentine areas throughout the world have provided situations where evolution has continued over geological time. Geochemically the areas may appear similar, but the individual species have evolved along different physiological lines.

3. Plant growth on seleniferous soils

Se-rich soils with their characteristic floras have been recognized for many years from parts of the U.S.A. such as the Great Plains as being particularly toxic to livestock (Rosenfeld & Beath 1964). In parts of Australia, likewise, seleniferous plants have given rise to Se-toxic symptoms in cattle and horses while in South America seeds of *Lecythis ollaria* are toxic to man. Similar disorders in animals have been reported from seleniferous areas in the Republic of Ireland (Walsh *et al.* 1951).

Seleniferous floras, in keeping with serpentine floras already mentioned, contain many tolerant species, some of which are considered Se endemics. In the Great Plains areas, weathering of rocks *in situ* under arid or semi-arid conditions has given rise to soils high in Se – up to approximately 5 µg/g in air-dry soil is common (Olson *et al.* 1942). The soils of Ireland, on the other hand, have their origins in the marine black shales of Carboniferous and Jurassic ages and probably developed under humid conditions to give organic-rich seleniferous basins (Fleming 1962). These soils contain up to 100 µg Se/g. However, little experimental geochemistry has been carried out on the ionic species in seleniferous soils. High voltage electrophoretic separations of water soluble Se compounds in soils from South Dakota and from County Meath, Ireland, followed by analysis revealed that Se VI (selenate) predominates in the former soil but Se IV (selenite) predominates in the latter (see figure 3). On a quantitative basis soluble Se VI accounted for up to one half the total Se in the soil, i.e. 2 µg/g, a concentration at which toxicity symptoms in plants can be found. Seleniferous plants are, however, scarcely affected during growth under these conditions. Indeed, they accumulate the element to very high concentrations – up to 1% dry mass and normally metabolize Se to seleno-acids (Peterson 1971).

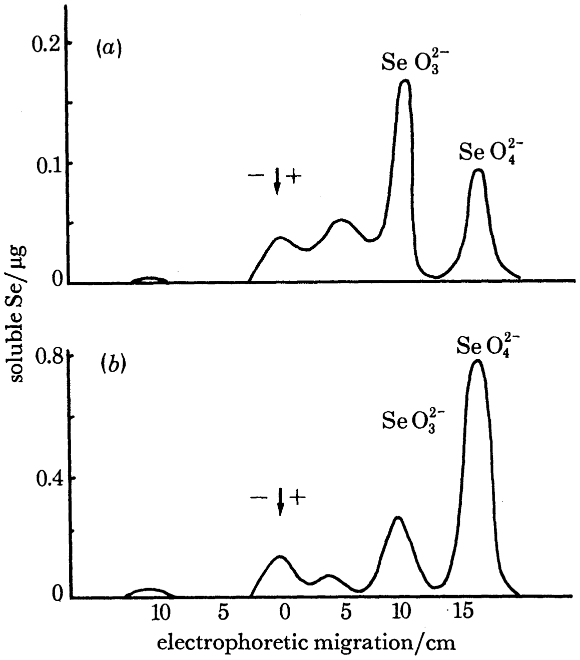

FIGURE 3. High voltage paper electrophoretic separation of Se compounds in aqueous extracts of two toxic seleniferous soils: (*a*) Co. Meath, Ireland; (*b*) South Dakota, U.S.A. The position of sample application is shown, together with the occurrence of selenite and selenate ions. Data modified from Nye & Peterson (1975).

The Irish seleniferous areas, on the other hand, contain less than 0.2 µg/g soluble Se and often only 0.02 µg/g. At these concentrations, plants were not subjected to environmental stress and species would not need tolerance mechanisms to avoid this element. This geochemical difference between the two soils probably helps to explain the absence of a Se-specific flora in Ireland. There is also a metabolic difference between Se IV and Se VI which is probably involved in the evolutionary development of tolerance. Selenium vi is accumulated metabolically and a tolerance mechanism is definitely required, whereas Se iv is accumulated passively and to lower levels. Geochemistry has, therefore, helped to solve this intriguing ecological problem.

Analysis of the concentration of Se in plants collected from various Irish seleniferous sites with their respective soils have shown a direct relation between plant and total soil Se (figure 4). There was no relation between plant Se and 'available' Se. However, as the predominant form of soluble Se in Irish soils was Se iv, a reexamination of the soil and the plant data revealed a linear relation between soluble Se iv and plant Se (Nye & Peterson 1975). The concentration of Se in ryegrass was shown by Williams & Thornton (1972) to be related to the total soil Se and to water soluble Se.

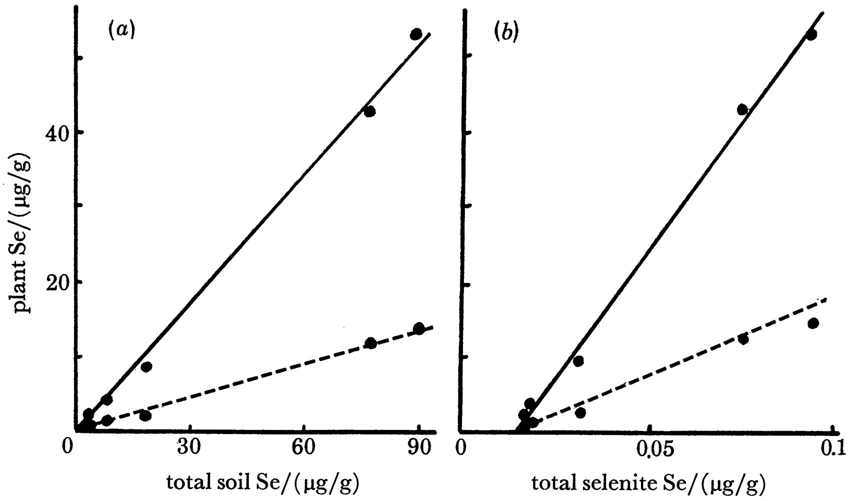

Figure 4. Relation between (*a*) mean Se concentration in plants and the respective soil concentration; (*b*) mean Se concentration in plants and the concentration of water-soluble selenite in soil extracts. ——, *Rumex acetosa*; – –, *Holcus lanatus*. Data modified from Nye & Peterson (1975).

4. Development of As-tolerant vegetation

Together with associated elements, As has been mined and smelted in Devon and Cornwall for several centuries. Initially, As was a waste product from Cu and Sn mines but by the late 1800s the production of As from arsenopyrites was an important operation. Consequently As-rich areas have arisen either directly from smelting of ore, or indirectly by association with mining and smelting of Cu and Sn. The grossly contaminated sites are largely barren (plant cover less than 1%) and support a depauperate flora (Porter & Peterson 1975). Arsenic toxic areas have also been described from parts of the U.S.A., Canada, Rhodesia and from Australia, to mention a few of the important sites. Plants that have colonized these areas are known to have evolved tolerance to the high concentrations of As in the soils (Porter & Peterson 1977*a*). Such plants actually accumulate the element to extreme levels which are considered toxic to normal plants. Individuals of *Agrostis tenuis* can contain up to 1% As dry mass and plants of *Jassione montana* up to 0.7%. The magnitude of accumulation can be gauged with reference to 'normal' plants which contain around 1 μg/g which collected from urban areas, or, less than 0.1 μg/g from remote environments.

Soils in which these plants accumulating As were growing contained between 1 and 2% total

As with water soluble values of approximately 1–5 μg/g and up to 20 μg/g. Analysis of the oxidation state of the As in water soluble extracts has shown that arsenate predominates down the profile (Porter & Peterson 1977*b*). Arsenite, on the other hand, occurred at low concentrations. Dimethylarsine was identified in the uppermost horizons and underneath plants during the dry periods, but it could be assayed down the profile during wet weather.

Clonal material of *A. tenuis* from high-As soils exhibited tolerance to arsenate, but not arsenite (Porter & Peterson 1977*a*). Clonal material from low-As sites was not tolerant to either form of As. Dimethylarsine is also toxic to plants, but at the concentrations encountered in soil solution its effect on plants can be considered minimal.

In the short time available for colonization (60–100 years), individuals of various species have evolved tolerance of this toxic soil and will have differentiated physiologically from individuals on non-toxic areas. It seemed of interest, therefore, to investigate whether tolerant populations consist of a number of genotypes, or whether all have been derived from the same genotype. Isoenzyme complements have been used to identify genotypic variation in various organisms (Shaw 1965; Gottlieb 1971). *Agrostis tenuis* clones were examined and shown to possess active and well defined esterase isoenzymes. Analysis of different plants from the same clone showed that they contained identical isoenzymes whereas different clones often exhibited different isoenzymes. Thus the As-toxic soils from even one area support a number of different genotypes. There is, therefore, no selective pressure for a particular isoenzyme or for a particular degree of tolerance despite very strong selection pressures from the geochemical environment. Individuals from any one site may be genetically different which presumably indicates separate evolutionary origins for at least some of the plants. In a comparable study with *A. stolonifera*, Wu *et al.* (1975) concluded that Cu-tolerant populations also consisted of a number of different genotypes. These populations must have evolved by the rapid selection of a number of tolerant plants from apparently non-tolerant populations.

5. Conclusions

The geochemical parameters in soils can be seen to operate as agents of natural selection on plant populations. Geochemical discontinuities can give rise to discontinuous floras as already mentioned. Macro-evolutionary trends have given rise to endemic species while micro-evolutionary reactions will affect the degree of tolerance in an individual. Although selection of some tolerant types presumably took place millions of years ago, development of As-tolerant ecotypes shows that rapid selection of exceptional genotypes can take place today.

I contend, then, that geochemistry is a potent selective force in the evolutionary development of plant assemblages.

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