PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The Precursor Environment for Vascular Plant Colonization

V. P. Wright

Phil. Trans. R. Soc. Lond. B 1985 **309**, 143-145
doi: 10.1098/rstb.1985.0075

Phil. Trans. R. Soc. Lond. B **309**, 143–145 (1985)

Printed in Great Britain

The precursor environment for vascular plant colonization

By V. P. Wright

Department of Earth Sciences, Open University, Milton Keynes, MK7 6AA, U.K.

There is evidence, although inconclusive, that a biologically active soil cover existed long before the late Silurian. The earliest vascular plants may have colonized a land surface containing well-developed soils which were functioning biologically and biochemically in similar ways to modern soils.

In any discussion of the late Silurian–early Devonian 'invasion of the land', two basic questions arise in relation to the history of the land cover and its soils:

(i) Did vascular plants colonize a barren landscape or did biologically functioning soils already exist?

(ii) What changes did the vascular plant cover cause to the land surface and its soils?

This latter question has been tackled by Retallack (this symposium) and the following is a discussion of some aspects of the former.

Many soil-forming processes are purely physical or physico-chemical in origin and examples of such pedogenic modifications of the land surface have now been documented from the Precambrian and lower Palaeozoic (Retallack 1981). However, there is also some evidence that these early soils were biologically active and were associated with microbial communities. Golubic & Campbell (1979) have compared the mid Precambrian microfossil, *Eosynechnococcus moorei* Hofmann with the extant cyanobacterium *Gloeothece coerulea* Geitler, which is a subaerial form. They have suggested that prokaryotic communities may have colonized the land surface as long ago as the early Precambrian. Organic-rich palaeosols are known from Blind River Formation of Ontario (Campbell 1979) which is 2.4 Ga old.

It has been suggested that as many forms of cyanobacteria inhabit intertidal settings, and are adapted to daily alternations of wetting and drying and salinity variations, they are pre-adapted for life in terrestrial settings (Campbell 1979). Intertidal microbial forms are well documented from the Precambrian and Schopf (1968) has compared the late Precambrian intertidal form *Cephalophytarion grande* to the living *Microcoleus vaginatus*, which occurs in recent subaerial algal crusts (Campbell 1979). It is possible that the land surface was initially colonized by such pre-adapted intertidal forms early in the Precambrian. By the late Silurian–early Devonian a variety of algal remains are known, in association with the earliest vascular plants, and some of these algae may have been subaerial forms (Edwards 1980). Evidence also exists of other types of early land plants (Niklas & Smocovitis 1983).

Some guide to these primitive subaerial communities may be found by comparisons with living forms. Several types of microbial communities such as algal crusts and lichens exist today. Algal crusts have been described from a variety of terrestrial environments but their occurrence is most striking in desert areas. Cyanobacterial communities (desert crusts, algal crusts, desert stromatolites, cryptogamic earths) are well known from the semi-arid and arid areas of the southwestern United States and Israel (Campbell 1979; Friedmann *et al.* 1967; Krumbein & Giele 1979). They are composed of a variety of microorganisms including filamentous and coccoid cyanobacteria, and chlorophytes. Campbell (1979) has described in detail one such crust community which is dominated by two species of *Microcoleus*; one is normally a fresh water form, while the other is normally marine. The occurrence of these communities in deserts is clear proof of the ability of the cyanobacteria to colonize successfully even harsh environments, and it seems likely that similar forms occupied comparable habitats in pre-late Silurian times (Edwards *et al.* 1979).

It has been speculated that lichens or bryophytes may have colonized the land surface long before the vascular plants (Retallack 1981). The vast majority of lichen-forming fungi belong to the Ascomycetes whose geological range is uncertain. Tiffney & Barghoorn (1974) suggest a pre-Carboniferous appearance for the Ascomycetes but Pirozynski (1976) has favoured a Mesozioc origin. However, Gray (this symposium) has identified fossils attributable to the Ascomycete fungi from the Ludlow of Sweden. Lichens may have existed on the pre-late Silurian land surface. Furthermore, Kobluk *et al.* (1977) have suggested that a probably algal, lichen or moss cover existed on a karstic surface developed at the Silurian-Devonian (Gedinnian) disconformity in Ontario but detailed evidence is lacking.

If some form of organic soil cover did exist in the pre-late Silurian, with what types of soils would they have been associated? It is likely that such microbial covers would have existed on a variety of soils but it is difficult to study any modern analogues because such microbial soils are limited in occurrence to areas unsuitable for vascular plants. The variety of microbial soils today is presumably much smaller than in the pre-late Silurian. The nearest possible analogues which are well documented are those developed under lichens or moss cushions. These have been especially studied in association with limestone soils and have been termed protorendzinas (Kubiena 1970). They are characterized by a community of microarthropods (mites and springtails). Such animals have a geological record at least as far back as Siegenian (Rolfe, this symposium) and probably earlier. Such soils are now seen only in settings in which higher plants are not prominent and would not represent the spectrum possible in the past. These soils show little mixing of the mineral and organic matter in the soil and the resulting humus is thin. Effective mixing of these components with resulting thick humus formation is achieved in modern soils by such organisms as myriapods and earthworms. Unequivocal representatives of the former are known from the uppermost Silurian (Rolfe, this symposium). It is possible that the early vascular plants colonized a land surface with an existing biologically active soil with a humus cover of sorts. By early Carboniferous times a variety of humus types can be recognized identical to moders and mulls (Wright 1984).

One of the most important effects of an organically active soil cover is in the biochemical weathering of the mineral matter. Soluble organic compounds such as citric and oxalic acids and some phenolic compounds are very important in the hydrolysis of rock-forming minerals. The role of lichens in weathering is well known and the fungal component is able to produce chelating acids such as oxalic acid (Wilson & Jones 1983). Indeed, such fungally produced oxalic acid is believed to be a major factor in mineral decomposition in modern soils. Biochemical weathering may also have been an important process in soil formation in the Lower Palaeozoic and earlier.

Vascular plants play an important role in stabilizing the land surface and their appearance is likely to have had a major influence on sedimentation (Schumm 1968). However, microbial mats are well known for the ability to bind sediment in marine, and terrestrial settings (Campbell 1979) and they may have played an important role in the Lower Palaeozoic and earlier. The absence of root systems binding the deeper parts of the soil must have meant that they were not as resistant to erosion as modern vascular plant communities.

Although inconclusive, there is some evidence that a biologically active soil cover did exist long before the late Silurian. These primitive soil communities were probably composed of cyanobacteria, fungi, chlorophytes, etc. By the late Silurian these soils probably contained a fauna of myriapods and micro-arthropods. Conditions must thus have existed for such processes as biochemical weathering and humus formation, as in modern soils. There is now a real need for studies of pre-late Silurian soils to ascertain whether such processes occurred. The early vascular plants may have colonized not a barren land surface but one with a biological history already long established.

REFERENCES

Campbell, S. E. 1979 Soil stabilization by a prokaryotic desert crust: implications for Precambrian land biota. *Origins of Life* **9**, 335–348.

Edwards, D. 1980 Early land Floras. In *The terrestrial environment and the origin of land vertebrates* (ed. A. L. Panchen), pp. 55–85. London: Academic Press.

Edwards, D., Bassett, M. G. & Rogerson, C. W. 1979 The earliest vascular land plants: continuing the search for proof. *Lethaia* **12**, 313–324.

Friedmann, I., Lipkin, Y. & Ocampo-Paus, R. 1967 Desert Algae of the Negev (Israel). *Phycologia* **6**, 185–200.

Golubic, S. & Campbell, S. E. 1979 Analogous microbial forms in Recent subaerial habitats and in Precambrian cherts: *Gloeothece coerulea* Geitler and *Eosynechococcus moorei* Hofmann. *Precambrian Res.* **8**, 201-217.

Kobluk, D. R., Pemberton, S. G., Karolyi, M. & Risk, M. J., 1977 The Silurian-Devonian disconformity in southern Ontario. *Bull. Can. Petrol. Geol.* **25**, 1157–1186.

Krumbein, W. E. & Giele, C., 1979 Calcification in a coccoid cyanobacterium associated with the formation of desert stromatolites. *Sedimentology* **26**, 593–604.

Kubiena, W. L. 1970 *Micromorphological features of soil geography*. New Jersey; Rutgers University Press, 254 pages.

Niklas, K. J. & Smocovitis, V. 1983 Evidence for a conducting strand in early Silurian (Llandoverian) plants: implications for the evolution of the land plants. *Paleobiology* **9**, 126–137.

Pirozynski, K. A. 1976 Fossil fungi. *Ann. Rev. Phytopath.* **14**, 237–246.

Retallack, G. J. 1981 Fossil soils: indicators of ancient terrestrial environments. In *Paleobotany, paleoecology and evolution* (ed. K. J. Niklas), vol. 1, pp. 55–102. New York: Praeger Publishers.

Schopf, J. W. 1968 Microflora of the Bitter Springs Formation, late Precambrian, central Australia. *J. Paleontol.* **42**, 651–668.

Schumm, S. A. 1968 Speculations concerning the paleohydrologic control of terrestrial sedimentation. *Bull. Geol. Soc. Am.* **79**, 1573–1588.

Tiffney, B. H. & Barghoorn, E. S. 1974 The fossil record of the fungi. *Occas. Pap. Farlow Herb. Cryptogam. Bot. Harv.* **7**, 1–42.

Wilson, M. J. & Jones, D. 1983 Lichen weathering of minerals: implications for pedogenesis. In *Residual deposits* (ed. R. C. L. Wilson), *Geol. Soc. Spec. Publ.* **11**, pp. 5–12, Oxford: Blackwells.

Wright, V. P. 1984 The ecology of early Carboniferous paleosols. In *European Dinantian environments* (ed. A. E. Adams, J. Miller & V. P. Wright). Cheshire: Shiva Press. (In the press.)