A new view of life around the root

Soil detritus — the non-living products and remains of animals, plants, and bacteria — is estimated to contain almost twice as much organic carbon as all the living organisms in and above the soil. Between 5% and 10% of this organic debris takes the form of carbohydrate.

Bacteria and fungi secrete much of this underground carbohydrate, but plant roots exude a good deal, too. Indeed, back in 1965 the Russian plant physiologist Dr S. Samtsevich announced that wheat plants release more carbohydrate into the soil from their roots than they store in the grain — although few scientists were prepared to share his conviction at the time.

Since then other scientists in various parts of the world have confirmed Dr Samtsevich's image of 'leaky' roots. Studies with radioactively 'labelled' compounds, for example, have shown that some species of forest tree send as much as three-fifths of the carbohydrate that they make down to the roots, and that much of this passes out of the roots into the soil. And if maize roots are grown out of soil in a mist chamber, they drip an exudate rich in the sugar, fucose.

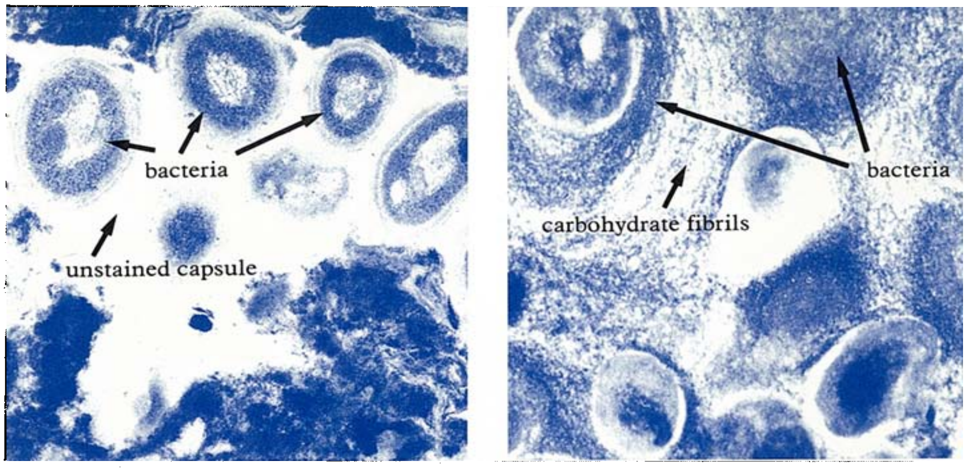
At the root surface, these carbohydrate-rich secretions form a gel. Although it was first described by a German scientist in 1883, this gel received little attention from investigators until recent years, partly because when it dries it shrinks to a very thin layer, and partly because it does not take up any of the stains generally used by electron microscopists. For similar reasons scientists have in the past had to guess the whereabouts of all the rest of the soil's carbohydrates.

Some organic matter in the soil may be as much as 1000 years old.

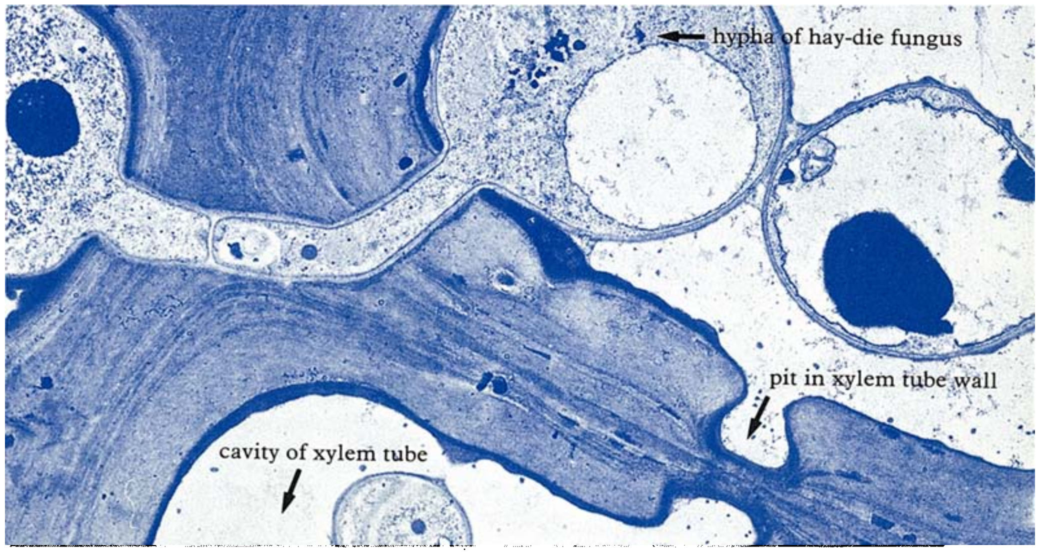
Now Dr Ralph Foster of the CSIRO Division of Soils has pinpointed these carbohydrates, using staining techniques developed by cytologists for the study of cellular tissues. With an electron microscope he found that some of the carbohydrates form fibrous strands extending across pores, less than 1 μm (one thousandth of a millimetre) wide, between soil particles. The fibres entangle small stacks of clay particles, and occur commonly in pasture topsoil.

Other soil carbohydrates are exposed in Dr Foster's electron micrographs as granular gels filling the minute crevices between stacks of clay particles.

Both the fibrous and the gel carbohydrates clearly help to bind soil particles together, producing a soil texture more favourable for plant growth. Dr Foster's observations also help to explain why very

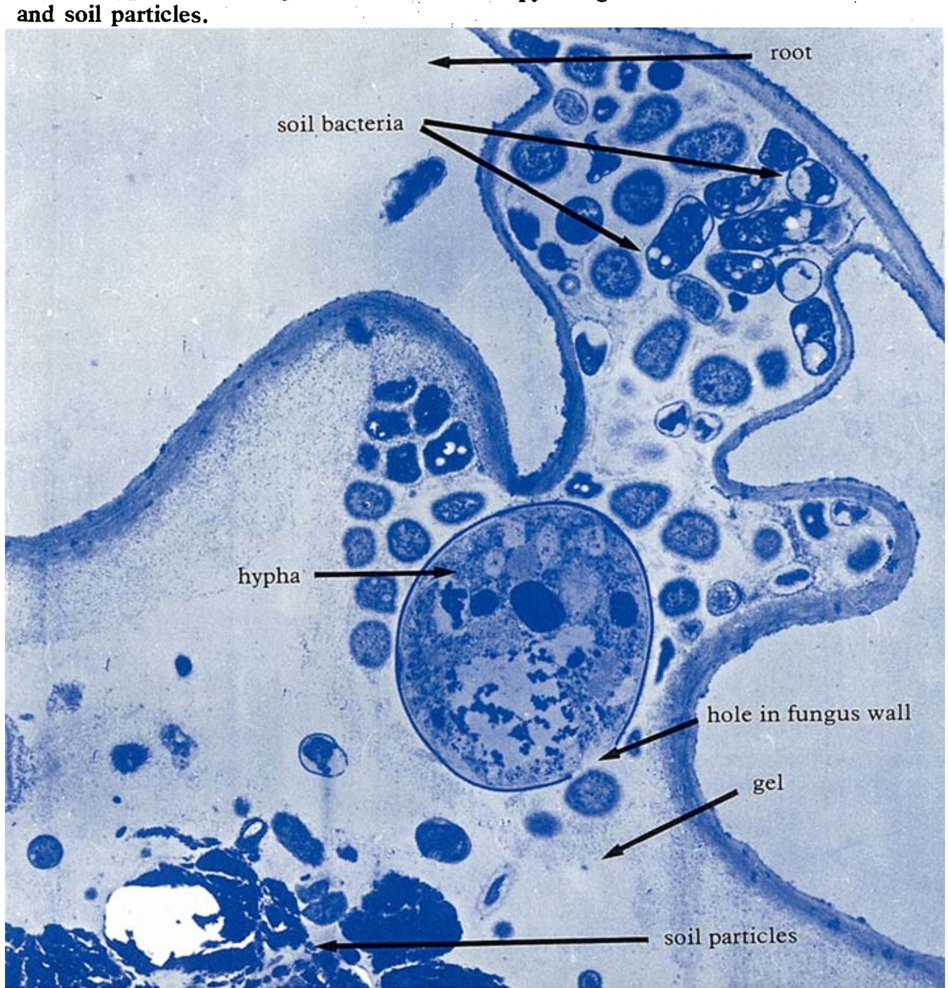


Soil bacteria under the electron microscope. With traditional techniques (left), their common capsule appears blank. Using stains for carbohydrates, Dr Foster has revealed fibrils of polysaccharide in the capsule (right).



Hay-die moving in: this cross-section through the xylem (woody, water-conducting tissue) of a wheat root shows hyphae of the disease fungus partially blocking the xylem tubes.

Scope for future biological control? Bacteria have bored a hole in the wall of this hay-die hypha. Both fungus and bacteria occupy the gel between the root surface and soil particles.



Almost the entire root cortex breaks down, digested by micro-organisms.

small amounts (as little as 0·2%) of carbohydrate produced by micro-organisms bind particles strikingly well when they are added to clay.

Meal for bacteria

All this carbohydrate makes a potential meal for bacteria in the soil, yet carbon-dating studies show that some organic matter in the soil may be as much as 1000 years old. Some of these compounds resist attack by becoming chemically associated with substances that bacteria cannot metabolize, but others escape bacterial attention because they occur in crevices, as little as 0·03 μm in diameter, that are simply too small for bacteria to enter. Most soil bacteria measure at least 0·3 μm across.

Scientists cannot yet say which type of protection, chemical or physical, lasts longer, because chemical analysis of organic compounds cannot — so far — be combined with electron microscopy. As Dr Foster puts it, 'you can either see where a substance is but not know what it is, or you can know what it is but cannot tell where it came from'.

Root gel oozes into the soil, eventually extending more than 50μm from the surface of the root. Dr Foster's electron micrographs show that at first the gel immediately next to the root forms a more or less uniform layer 5μm or more thick. Outside this lies a layer containing shorter molecules and colonized by micro-organisms. A maize plant, whose total root length must be measured in kilometres, is estimated to produce a large enough area of gel to cover a tennis court.

Micro-organisms convert root gel into their own forms of carbohydrate, such as the polysaccharide (high-molecular-weight carbohydrate) capsules that surround many soil bacteria. Fungi in the rhizosphere (the miniature ecosystem round the root) secrete a gel that is chemically more stable than root or bacterial gel, and that may therefore contribute to soil stability in forests, where mycorrhizal fungi — fungi intimately associated with roots — abound.

Some micro-organisms release antibiotics, which may help to keep other organisms — including some causing root diseases — at bay. A number of species fix atmospheric nitrogen into nitrogenous compounds that higher plants can absorb and make use of. This 'non-symbiotic' fixation plays a particular role in tropical and subtropical grasslands, and Professor Denis Carr and his colleagues at the Australian National University have shown that even in Australian alpine grasslands the bacteria living on grass roots may fix more nitrogen than do the symbiotic bacteria of legumes in the same habitat.

Bacteria around a plant's root can influence both the root's form and its physiology. Studies in the Division by Dr Glyn Bowen and Dr Albert Rovira have shown that the anatomy of the root, its length, the frequency of side roots (in the family Proteaceae and other species with proteoid roots), and the number of root hairs are influenced by bacteria in the rhizosphere. And, since soil nutrients must cross the gel to reach the root, the gel's microbial inhabitants, by picking out certain substances, can affect the plant's diet, even causing deficiency of some nutrients.

Trees can send much of the carbohydrate they make down to their roots.

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Like a customs post on an international frontier, the root surface selectively controls the passage of commodities, especially ions, in and out of the root. In fact, as much as nine-tenths of these 'ion-exchange' properties of the root may be those of the gel and its organisms. For example, an examination of different varieties of wheat has shown that those that can tolerate high levels of aluminium in the soil are those with the most copious gel; the gel protects the root against aluminium toxicity.

Dr Foster is investigating the biochemical activity, not of individual bacteria, but of the whole community. Bacteria cultured in the laboratory can switch their enzymes on and off, and so test tube experiments do not tell us just what the bacteria are actually up to in the soil.

Remarkable shapes

The identity of most of the gel bacteria remains a mystery, too. Those closest to the root surface, in the region called the rhizoplane, prove particularly difficult to extract from the soil and grow in the laboratory. Some rhizoplane bacteria show remarkable shapes — lobed or like stars — in electron micrographs of soil sections. The bacteria of the gel 'outback' have simpler shapes.

Scientists have not yet succeeded in culturing many of the oddly shaped rhizoplane bacteria, possibly because nobody has yet added the right ingredients to the nutrient agar on which laboratory bacteria grow. Being right next to the root, the rhizoplane bacteria get 'first bite' at any amino acids, vitamins, or other complex compounds being secreted by the root, and perhaps some of these compounds are essential to their diet.

Dr Foster's interest in the rhizosphere was stimulated more than 20 years ago in England, when he was filming the growth of root hairs. He found that the living contents of some epidermal and cortical cells simply disappeared. More recently, his electron microscope studies have thrown light on how this happens.

The cells appear to die randomly at first. Bacteria, actinomycetes, and fungi then invade the cells, possibly because the root's defence mechanisms have stopped operating. Eventually (in wheat plants, at the flowering stage) almost the entire cortex breaks down, digested by soil micro-organisms. The stele remains intact, and the plants are perfectly healthy.

These electron microscope investigations have resolved another matter, too. For some years botanists have debated the nature of the root surface, some describing a cuticle lying over the epidermis like that over a leaf, some talking of a gel, and some finding fibrils extending from the root into the soil. Dr Foster has shown that all three ideas are right: the root surface simply changes as the cells grow older.

The tip of the root is covered by a cap of cells that secrete a mucilage. This lubricates the tip as it penetrates the soil. Mucilage also makes up a large part of the outer layer of the walls of root surface cells behind the tip.

At first, this mucilage is enclosed by a fine cuticle, but as the root forces its way through the soil the cuticle is ruptured and the mucilage escapes into the nearby soil. When the epidermal cells die, gel secretion stops, and soil micro-organisms begin to attack the root surface and expose the fibrils that form the inner layers of the cell walls.

The micro-organisms of the rhizosphere together make up a minute but complex ecosystem. Some bacteria, like *Bdellovibrio*, prey on others; some are attacked by bacteriophage viruses. A few electron microscope pictures show tiny holes in fungal hyphae, and these are almost certainly the result of bacterial attack. Already scientists are asking themselves whether this ecosystem could be deliberately modified to achieve biological control, for example of the wheat fungal disease known as take-all or hay-die.

Meanwhile Dr Foster, Dr Rovira, and Mr Trevor Cock, also of the Division, are preparing an 'Atlas of Rhizosphere Ultrastructure', which will include not only their own electron micrographs but also scanning electron microscope pictures taken by Dr Richard Campbell of Bristol University.

John Seymour

More about the topic

The ultrastructure and histochemistry of the rhizosphere. R. C. Foster. *New Phytologist*, 1981, **89**, 263–73.

Polysaccharides in soil fabrics. R. C. Foster. *Science*, 1981, **214**, 665–7.