Cycling of nutrients from dying roots to living plants, including the role of mycorrhizas

E. I. NEWMAN and W. R. EASON
Department of Botany, University of Bristol, Bristol BS8 1UG, UK and Welsh Plant Breeding Station, Plas Gogerddan, Aberystwyth SY23 3EB, UK

Key words:  *Lolium perenne*, mycorrhiza, nitrogen, nutrient cycling, phosphorus, roots

Abstract
This paper presents information about the release of nitrogen and phosphorus from dying grass roots and the capture of phosphorus by other, living plants. We have paid particular attention to the part played by mycorrhizas in this phosphorus capture, and the possible importance of mycorrhizal links between dying and living roots.

When *Lolium perenne* plants were grown with ample nutrients and their roots then detached and buried in soil, about half the nitrogen and two-thirds of the phosphorus was lost in three weeks, but only one-fifth of the dry weight. The C:N and C:P ratios suggest that microbial growth in the roots would at first be C-limited but would become N- and P-limited within three weeks.

Rapid transfer of $^{32}$P can occur from dying roots to those of a living plant if the two root systems are intermingled. The amount transferred was substantially increased in two species-combinations that are known to form mycorrhizal links between their root systems. In contrast, in a species-combination where only the living ('receiver') plant could become mycorrhizal no significant increase of $^{32}$P transfer occurred. This evidence, although far from conclusive, suggests that mycorrhizal links between dying and living roots can contribute to nutrient cycling. This research indicates a major difference in nutrient cycling processes between perennial and annual crops.

Introduction: The role of mycorrhizas in ecosystems

Most higher plants can form mycorrhizas. Fungi closely resembling present-day vesicular-arbuscular (VA) mycorrhizas have been found in underground organs of fossils of early land plants (Wagner and Taylor, 1981), suggesting that the mycorrhizal association has been in existence almost as long as plants have been on land, and that roots and mycorrhizal fungi have evolved together. A plant root system without mycorrhizal infection is the exception rather than the norm.

Most plants of economic importance can form mycorrhizas. This includes nearly all forest trees and pasture plants. Many arable crop plants can also form mycorrhizas, though Cruciferae such as cabbage and rape are important exceptions. There has been much interest in the potential use of mycorrhizal fungi to promote crop production, particularly emphasising their role in increasing uptake of elements which are relatively immobile in soil, phosphorus, copper, zinc and perhaps others (e.g. Lambert et al., 1979). Much of the research has studied individual plants sown into bare soil in pots. This simulates the arable crop, but not the mixed-species, mixed-age plant stands that make up most non-crop vegetation. Since mycorrhizas evolved long before there were any arable crops, it is relevant to ask what role mycorrhizas play in natural and semi-natural vegetation. One clue can be found by considering where non-mycorrhizal plants occur; these must be habitats in which mycorrhizas are not essential. In disturbed habitats
non-mycorrhizal species are common, though not universal. Mobile areas of sand dunes are an example. Ernst et al. (1984) found in a Dutch dune system that many annual species, some of them grasses, had little or no mycorrhizal infection, though some of the perennial species were infected. Arable crop land is also a disturbed habitat, and this raises two questions. (1) Are mycorrhizas likely to be beneficial in arable crops, if so many species persist in natural disturbed areas without them? (2) In less disturbed vegetation, do mycorrhizas have functions other than uptake of immobile elements from soil? A mycorrhizal fungus can infect more than one plant, and thus link them together by interconnecting hyphae (Newman, 1988). This could influence relationships between the linked plants, including competition and nutrient cycling.

This paper considers nutrient cycling, especially the release of nitrogen and phosphorus from dying roots and the part played by mycorrhizal fungi in the capture of these nutrients by living plants. In the past, study of nutrient cycling has paid far more attention to above-ground parts than to roots as sources of nutrients for recycling; yet roots contain a substantial proportion of the nutrients in dying plants. It has been assumed that release of nutrients from dying plants can be studied quite separately from the subsequent capture of these nutrients by living plants. This paper will suggest that such a division may miss important features of the cycling process in perennial vegetation, including the possible role of mycorrhizal links between plants.

Loss of nutrients from ryegrass roots

This paper considers principally nutrient cycling in perennial grassland, using perennial ryegrass, Lolium perenne cv S23, as the main experimental species. Several experiments were performed to investigate the rate of loss of phosphorus, and in some experiments nitrogen, from dying roots.

Lolium perenne was grown in solution culture at 20°C in a growth room for six weeks. For ‘high-P plants’ the solution was half-strength Hoagland’s solution throughout; for ‘low-P plants’ it was the same except that phosphate was omitted for the last three weeks. The orthophosphate in the solutions was labelled with 32P, so the plants became uniformly labelled. At age 6 weeks the shoots were cut off and removed; the roots were left hanging in aerated solution which was the same as before except now not labelled with 32P, so loss of 32P from roots to solution could be determined by measurements on samples of the solution. Fig. 1 shows the amount of 32P lost during the first three weeks after the roots were detached. The rate of loss was fastest at the start and gradually declined. High-P roots lost about two-thirds of their phosphorus in 22 days, low-P roots about a quarter.

Since this experiment had shown the rate of phosphorus loss becoming quite slow by three weeks, further experiments were carried out to measure the loss of nitrogen and phosphorus during three weeks under more natural conditions. L. perenne was grown in solution culture as before, except that the solution was not labelled with 32P. Roots were then cut off the plant, some parts analysed for concentration of nitrogen and phosphorus, other parts placed in fine-mesh nylon bags which were buried at 10 cm depth in soil in pastureland. After three weeks the buried roots were recovered and analysed for nitrogen and phosphorus. Table 1 shows results from one of the experiments, conducted in May when the soil was moist and its mean temperature 11.6°C. A large proportion of not only the phosphorus but also the nitrogen in the rye-