segregating membrane-bound organelles? There are several possible reasons. First, unlike the chromosomes, there is no need to divide an organelle into two exactly equivalent pieces. If one daughter receives slightly more or less membrane, then mechanisms exist to correct the imbalance[18]. Second, the mechanism is straightforward in that it inhibits a pre-existing process, though additional modifications may be needed to ensure that the vesicles contain the information needed for reassembly[10]. Third, it is general because most, if not all, vesicle-mediated pathways share the same mechanism for fusing membranes, specificity being provided by other proteins[19]. Last, it is flexible. The vesicles generated are small and easily diffusible, so they should rapidly and randomly occupy the mitotic cell cytoplasm. This means that it does not matter what shape or size the cell is, so long as the cytokinetic mechanism divides it into two daughters of equal size[3]. The molecular mechanism underlying this membrane-partitioning process is of obvious interest and the report by Tuomikoski *et al.* is a step in the right direction. □

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ECOLOGY

Answers that lie in the soil

Peter D. Moore

OUT of sight, out of mind, may be a convenient maxim for those with the inclinations of an ostrich. But it is hardly appropriate for ecologists concerned with estimating the productivity of the Earth's ecosystems, for much production occurs beneath the surface of the soil. The International Biological Programme (IBP) of the 1960s placed strong emphasis on the development of techniques for studying productivity and many data were accumulated which have subsequently been used in the assessment of the productive resources available for human support and, more recently, in developing a fuller picture of the Earth's carbon cycle. But many of these initial results are flawed by a failure to account adequately for the underground accumulation of carbon, and also for the continuous cycle of death and turnover of plant tissues above and below ground. Work by Raich and Nadelhoffer on forests[1] and by Long *et al.* on grasslands[2] now implies that some of the early results on this subject could be a serious under-estimate of the true values.

It would be wrong to suggest that the IBP pioneers were unaware of the problem of root productivity and turnover. Newbould[3] proposed that the ratio of below-ground production to below-ground biomass is proportional to that above ground and Newman[4] developed techniques for the measurement of the extent of plant roots within the soil by dissecting out sample soil volumes. Many field studies, however, neglected the subterranean part of the equation simply because of the difficulties involved in its measurement. Others estimated changes beneath the ground by subtracting the minimum from the maximum root biomass in a given year (Dahlman and Kucera in their studies of prairies[5], for example).

For forest ecosystems, there is considerable disagreement over the proportion of fixed carbon that is allocated to subterranean organs. Raich and Nadelhoffer[1] have collated and examined data derived from studies in a wide geographical range of forest ecosystems. They start by assuming steady-state conditions for their soil carbon cycle (which may itself be questionable) and derive an expression to show that the total carbon allocation to roots can be estimated by summing root detritus production and root respiration; this, in turn, is given by the soil respiration rate less the rate of above-ground litter production (which supplies soil heterotrophs with their additional source of carbon). Raich and Nadelhoffer conclude that there is a positive linear relationship between litter fall and carbon allocation to roots, but that, in proportional terms, relatively less of the fixed carbon is transported to roots in more productive forests. Ultimately, our knowledge of terrestrial carbon cycles will depend upon the precision with which such translocation can be predicted, and on more detailed evidence concerning the stability of the carbon reservoir in the soil.

Long *et al.*[2] present new results from a continuing UNEP study of four tropical grassland sites in Mexico, Kenya, Thailand and Brazil. They used 20 randomized sample plots, each 1.0m by 0.25m in size, which they cropped every month and determined the weight of living and dead tissues, both above and below ground. The root material was extracted from the soil cores using fine-mesh (2mm) sieves (no real advantage was found in using sieves of smaller aperture). They separated the live roots by staining with tetrazolium salts.

They were then able to calculate the turnover of plant matter, both above and below the soil surface, that is neglected in most standard procedures. In three of their sites they found that the traditional IBP methods had underestimated primary productivity by a factor of between two and five. On a global scale this means that there is substantially more productivity in the tropical grassland biome than has previously been realized.

These results have a bearing on both agricultural and carbon-cycling studies. In pastoralism, they imply that more energy is entering the ecosystem than had been thought. If a substantial amount of leaf material is dying and passing to detritivores, then one must conclude that the grassland is being under-used. Energy diverted to roots, however, is of no economic value to grazing animals. But even this aspect of carbon allocation has implications for global carbon-budget studies, for clearly there is a larger sink for carbon in the tropical grasslands than has previously been suspected, but only if some of the added carbon is accumulating in the soil. This does seem to be occurring in some of the grassland sites examined by Long *et al.* but much more effort needs to be expended on precise quantification of this build-up of organic matter. Equally important, the ploughing of grasslands for arable agriculture will inevitably result in the release of soil carbon back into the atmosphere. Perhaps the ostrich, with its head below the ground, was actually trying to tell us something. □

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