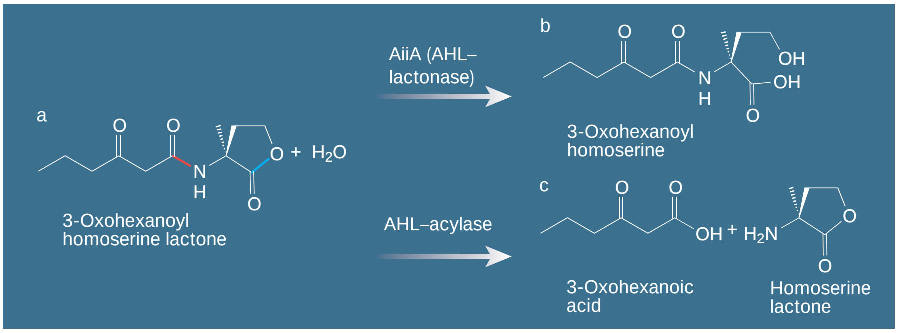

Figure 1 **Disabling soft rot: biochemical routes to the inactivation of acyl-homoserine lactone (AHL) molecules.** a, **The AHL *N*-3-oxohexanoyl-L-homoserine lactone is a quorum-sensing signal used by the *Erwinia* bacteria, which cause soft rot in certain crops, to control their ability to cause disease in plants. The bonds that can be broken by two inactivating enzymes are shown in blue and red.** b, **Dong *et al.*[1] have used the protein AiiA to hydrolyse the blue bond and generate the inactivated signal *N*-3-oxohexanoyl-L-homoserine.** c, **3-Oxohexanoic acid and L-homoserine lactone are the products of an uncharacterized AHL-acylase found in the bacterium *Variovorax paradoxus*.**

lable infection, even when challenged with comparatively low numbers of bacteria.

The result is a triumph for the approach of mining bacterial metabolic diversity for applied uses. In this case, Dong *et al.* capitalized on the discovery that many bacteria can degrade, and so inactivate, AHLs. Earlier, the same group[5] had isolated hundreds of bacterial species from soil and screened them for the ability to degrade AHLs. From this collection, a bacterium of the genus *Bacillus* was identified as being especially promising. It was from this strain that *aiiA* was cloned. As well as their exciting observations of plants expressing this gene, the authors[1] also show how the AiiA protein inactivates AHL signals: it degrades the molecule's lactone ring, so acting as an AHL-lactonase (Fig. 1).

Another soil bacterium has been identified that also degrades these signals, through an uncharacterized AHL-acylase activity[6]. Clearly, there are different mechanisms for the biodegradation of AHLs, inviting comparisons to the way in which penicillins can be inactivated.

Enzymes that degrade AHLs might be useful in controlling many other quorum-sensing bacterial populations, such as biofilms. These are dense populations of bacteria, attached to some surface, that grow to form complex, tissue-like structures; they are extremely resistant to antibiotics and have been implicated in many human diseases[7]. For example, the formation of biofilms by *Pseudomonas aeruginosa* is common in the lungs of people with cystic fibrosis. Here, quorum sensing regulates the expression of virulence factors and the development of biofilms[8]. As aerosols of mucous-degrading enzymes and other chemicals are already used to treat lung disease in cystic fibrosis patients, it might prove fruitful to add AHL-degrading enzymes to the mix.

But in the rush to develop products based on AHL-lactonases that will no doubt come, microbiologists should not lose sight of the significance of AHL-degrading enzymes to the physiology and ecology of the bacteria that produce them. There are questions to be answered, such as: do these enzymes have narrow or broad substrate specificity? And how are they regulated in the cell?

Moreover, what is the effect of signal degradation on the cells involved, and in the environment at large? No doubt bacteria have a stake in disarming the quorum-sensing systems of other species. For example, *Erwinia* regulates its synthesis of carbapenem, an antibacterial compound, through AHL-dependent mechanisms. Presumably, carbapenem keeps other bacteria away from the nutrient cache accumulated during plant infection. Those other species may use signal degradation to circumvent such a barrier. As revealed by genome sequencing, nearly identical counterparts of *aiiA* are present in several *Bacillus* species. Curiously, though, the quorum-sensing plant pathogen *Agrobacterium tumefaciens* may also have an *aiiA* relative, called *attM*, which is associated with genetic loci that encode proteins needed for this bacterium to colonize plant roots[9]. It is not yet clear why *Agrobacterium*, which makes and responds to AHL signals, might also need to degrade them.

Studies of the complex competitive interactions among microbes will no doubt be very informative. One epic story of microbial rivalry encompasses counter-evolutionary tales of naturally occurring β-lactam antibiotics, the enzymes that degrade them (β-lactamases) and β-lactamase inhibitors, such as clavulanic acid. In a parallel to this narrative, bacteria that make AHLs may have evolved resistance to the enzymes that break the signals. Some bacteria might produce factors that bind and block the active sites of AHL-degrading enzymes. Others might have evolved enzymes that recycle the signals after hydrolysis of their lactone rings. Nature throws punches and counter-punches: it will surely be both interesting and useful to investigate and anticipate them. In the meantime, Dong *et al.*[1] have returned *Erwinia*'s first blow. In doing so, they have revealed a soft spot in soft-rot diseases, perhaps of a type to be found in other quorum-sensing pests and pathogens. ■

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Carbon cycle

The roots of the matter

F. Stuart Chapin III and Roger W. Ruess

Perhaps the most scientifically challenging phase of the terrestrial carbon cycle occurs below ground. Innovative experiments, carried out in northern Sweden, illustrate the huge influence of roots and associated fungi.

Photosynthesis by terrestrial vegetation accounts for about half of the carbon that annually cycles between Earth and the atmosphere[1]. Although above-ground plant production is relatively well documented from field measurements and globally distributed satellite observations, the quantity of carbon that plants transfer below ground is not well known. Microvideo cameras provide direct observations of the growth, longevity and decomposition of fine roots[2,3]. However, other large components of below-ground plant production, such as exudation of organic compounds by roots and transfer of carbohydrates to associated mycorrhizal fungi, are difficult to study non-destructively and have not been estimated. Estimates of the contribution of root respiration to total CO_2 efflux from soil range from 10% to 90%, with methodological uncertainties accounting for most of this variation[4].

On page 789 of this issue, Högberg and colleagues[5] present a new approach that

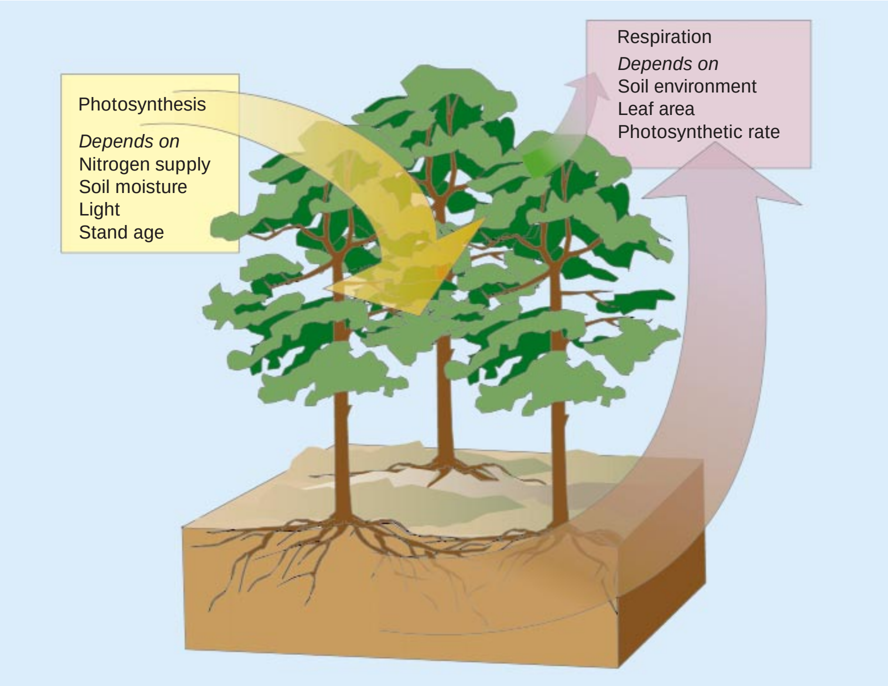

Figure 1 **The main carbon fluxes and their controls in boreal forests. The largest fluxes are carbon input from photosynthesis and carbon loss in respiration from roots, mycorrhizal fungi and other root-associated microorganisms. More minor loss is due to leaf and trunk respiration, as indicated by the small arrow. The boxes show the various factors that control the fluxes. As the results of Högberg *et al.*[5] show, events above ground are partly controlled by events below ground, and vice versa, meaning that all parts of a plant are affected by environmental change.**

provides an integrated estimate of the proportion of soil respiration derived from roots and their symbiotic mycorrhizae. Their experiments involved 'girdling' all trees in experimental plots of Scots pines in northern Sweden (that is, in boreal forest). In girdling, bark 1.5 m above the ground was stripped to a depth that allowed upward water flux but prevented downward transport of carbohydrates to roots and mycorrhizae. Soil respiration was measured as the rate of CO_2 accumulation in closed chambers, 24 cm in diameter, inserted into the soil surface. By comparing soil respiration in girdled plots, in which root and mycorrhizal respiration had been eliminated, with control plots where they had not, Högberg *et al.* concluded that over half of the soil respiration in the forest derived from the current year's photosynthesis.

As the authors point out, their estimate of below-ground plant respiration is conservative because root carbohydrate reserves were probably mobilized to support root function in the absence of a supply from above. The soil respiration measured in treated plots may therefore have included some respiration of tree roots, as well as the respiration of roots of understorey shrubs that were not manipulated. In addition, increased root death may have stimulated greater respiration levels of heterotrophic (decomposer) organisms than those that would naturally occur in forests. All of these sources of error would lead to an underestimate of the proportion of soil respiration accounted for by roots.

The difference between carbon released in soil respiration and that in above-ground leaf litter has been used as an index of total below-ground carbon allocation in forests[6]. These indices suggest that, relative to temperate forests, boreal vegetation allocates a higher proportion of fixed carbon to below-ground structures[7]. Högberg *et al.* now show that at least half of the soil respiration in these systems is derived from roots and mycorrhizae. Their approach minimizes artefacts associated with smaller-scale trenching experiments, which frequently alter soil moisture and the structural integrity of roots.

The ratio of plant-associated respiration derived from roots to that from their symbiotic mycorrhizae remains a mystery. Direct observations of fine roots in boreal forests point to rapid rates of growth and decomposition relative to above-ground tissues[3]. But there are few data on the proportion of plant production in this or any other terrestrial ecosystem that is allocated to mycorrhizae. Consequently, the current measures of global terrestrial production may be serious underestimates of the true values.

Högberg and colleagues' demonstration[5] of a rapid decline in soil respiration after girdling shows the tight integration of the whole-plant response to environmental changes (Fig. 1). These results are consistent with studies showing that roots and soil respiration respond to above-ground herbivory[7],

NATURE

100 YEARS AGO

Hailstorm Artillery. **In the absence of any recognised English equivalent for the expressive German term *Das Wetterschiessen*, I have thought it best in the heading of this article to avoid a literal translation of it lest it should give rise to misunderstanding. 'Weather shooting' does not refer to any haphazard or empirical attempts to foretell the weather, but to a practice which has lately come to have great vogue in Styria, Italy and elsewhere of firing off charges of gunpowder to protect the vineyards against injury from hail. So popular indeed has the practice become in some districts that there is danger of the cost of protection exceeding that of any damage likely to be caused by the hail. The idea that the weather can be affected by the discharge of gunpowder is not a new one. There have been various traditions of rain falling after, and presumably in consequence of, the cannonade of a battle… Weather shooting as now practised has, however, a more definite purpose than merely causing rain. Its object is to prevent the downpour of hail by shooting when thunder or hail clouds threaten. The recent development, which has spread very widely, is most conspicuously represented by the arrangements of Bürgermeister Stiger, of Windisch-Feistritz, in Styria, where they were originally introduced in 1896 in the form of a vine-dressers' volunteer artillery.**

From *Nature* 13 June 1901.

50 YEARS AGO

Profile of Science. **Setting out unashamedly to interest those who would not touch a 'scientific' book, Ritchie Calder must be congratulated on the adventurous nature of his approach. He is aware that most people are interested in the biographical details of famous men and uses this as the way to introduce the four main subjects of the atom, radar, penicillin and vitamins. Each topic is complete in itself, and is portrayed in relation to its general scientific background; the story of penicillin, for example, is cunningly interspersed with accounts of the invention of the microscope, the discovery of germs and chemical therapeutics as well as up-to-date information about more recent investigations with antibiotics like streptomycin, chloromycetin and aureomycin… Perhaps the only criticism that can be made of his excellent impressionistic book is that occasionally the popular style becomes a little too 'hail-fellow-well-met' for those with more retiring natures.**

From *Nature* 16 June 1951.

availability of nutrients[8,9] and light[10], and other factors that govern plant carbon gain. However, roots also respond directly to the below-ground environment. For instance, root respiration increases exponentially with increases in soil temperature[11], which could explain why fine-root elongation[3,12] and root respiration[5] in boreal regions peak in mid-to-late summer, when soil temperatures are warmest. The interaction of demand for carbohydrates, as determined by the root environment, and the above-ground capacity to supply carbohydrates, as determined by photosynthesis, together govern the below-ground carbon flux and therefore root growth and respiration. Conversely, photosynthetic rate is strongly influenced both by leaf environment (light and temperature) and by soil resources (nutrients and water). This principle — that each physiological process responds to the plant's total environment — may seem obvious. In many ecosystem models, however, root respiration is often estimated as a simple function of soil temperature and total root biomass, and photosynthesis as a function of air temperature and light.

Högberg and colleagues' results, which show a high proportion of carbon allocation below ground and tight integration among all plant processes, suggest that cycling of carbon through terrestrial ecosystems is both larger in magnitude and more complex than was previously appreciated. Clearly, above-ground production is only the tip of the terrestrial carbon-cycle iceberg. ■

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Animal behaviour

Homing in on ant navigation

Mandyam V. Srinivasan

The ability of ants to travel far from their nests in search of food and to accurately chart their way back has intrigued researchers. Presenting the insects with a hilly challenge now throws light on these navigational skills.

Foraging animals have to be able to find their way to a food source and back to their home or refuge. The Saharan desert ant, *Cataglyphis fortis*, is an especially impressive navigator, unerringly traversing hundreds of metres across barren landscapes that are almost completely devoid of landmarks. That's why Wohlgemuth, Ronacher and Wehner (page 795 of this issue)[1] used trained individuals of this species to investigate one aspect of navigation: how the ants calculate the distance they have travelled in their equivalent of a car's odometer.

Saharan desert ants (Fig. 1) are long-legged, elegant creatures. In navigating, they rely on an accurate path-integration system, a mechanism that continually keeps track of where the animal is in relation to home. To perform path integration, the animal must monitor its forward motions and turns, and sum them up to establish its current position in relation to home. Mathematically, this amounts to subdividing the outbound trajectory into a number of small, straight segments, representing each segment by a vector of the appropriate length and direction, and summing these elementary vectors to obtain a 'homing' vector that specifies the distance and direction of home.

Exactly how the ant measures its forward motions and turns and puts them together is not yet clear, although there are some interesting possibilities. For instance, Müller and Wehner[2] found evidence that ants use quick and dirty approximations to compute the vector sums. Now Wohlgemuth *et al.* have illuminated an intriguing property of the ant's path-integration system that is revealed when these creatures are made to forage over undulating terrain.

In one series of experiments, ants were trained to forage at a feeding site by traversing 'hilly' terrain, simulated by a series of channels sloping alternately upward and downward in a sawtooth-like profile (see the cover of this issue). When these trained ants were tested on flat terrain, simulated by a horizontal channel, they searched for the food after they had walked a considerably shorter distance than in the training. Conversely, when ants were trained to find food at a fixed distance in flat terrain and were then tested in hilly terrain, they walked a longer distance before commencing their search. In each test, the ants searched for the food at a location that corresponded not to the actual distance walked in the training, but to the projection of this distance on the horizontal plane.

The authors conclude that these desert ants do not navigate by measuring the distance they actually walk on the undulating terrain. Rather, they project their movements onto a fictitious horizontal plane and register their position relative to the nest on this plane. The advantage of this strategy is that the location of the nest (or a bountiful supply of food) can be pinpointed accurately irrespective of the undulations of the ground. So navigation can be accurate even when the return route is different from the outbound route and has a different profile, as is commonly the case in natural foraging.

This is an attractive hypothesis. But the data do not exclude another possibility — that the ants navigate by performing path integration in all three dimensions, rather

R. WEHNER

Figure 1 **Impressive navigator — the Saharan desert ant, *Cataglyphis fortis*.**