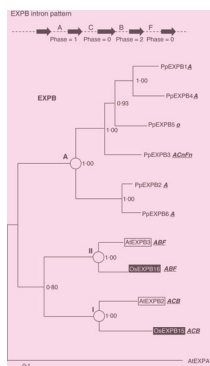


Can they fix it? Yes they can!

Fixation of nitrogen by *Rhizobium* and *Bradyrhizobium* in symbiotic associations with legumes and by *Frankia* endosymbionts of *Alnus* and *Casuarina* is a well-known phenomenon. However, these symbiotic bacteria represent only a small proportion of N-fixing prokaryotes. There are many free-living, soil-dwelling bacteria that fix N and there is evidence that plants may benefit from this if the bacteria are located in the rhizosphere. This is especially true of mycorrhizal systems in which uptake of nitrogenous compounds is enhanced. Furthermore it is now clear that

N-fixing bacteria may live *inside* tuberculate ectomycorrhizae. These are mycorrhizae in which tight clusters of mycorrhizal root tips are enclosed by a hyphal sheath to form a tubercle. **Paul *et al.* (British Columbia, Canada and Uppsala, Sweden, pp. 1101–1109)** have previously shown that N-fixing bacteria of the species *Paenibacillus vinicolor* and *Methylobacterium mesophilicum* live inside the tuberculate ectomycorrhizae formed by *Suillus tomentosus* on roots of *Pinus contorta*. They have now investigated the nitrogenase (N-fixing) activity (as measured by the acetylene reduction assay) in these mycorrhizae. In all three study sites in British Columbia, roots with tuberculate ectomycorrhizae exhibited significant nitrogenase activity, with roots from younger stands showing higher activity than roots from older stands. There was some seasonal variation with activities in summer being much higher than those in spring. This result surprised the authors: they expected a spring-time peak, followed by a decline of activity in the dry summer. Non-mycorrhizal roots and roots with non-tuberculate mycorrhizae did not exhibit nitrogenase activity. Thus, only the structures within which the bacteria were living were active in N-fixation. The authors regard this system as a truly symbiotic relationship dependent on a particular mycorrhizal morphology. Further, although the nitrogenase activity is only approx. 10 % of that observed in the *Frankia*–*Alnus* symbiosis, it is clear that it contributes significantly to the N economy of *P. contorta*, especially in nutrient-poor soils.



Model moss provides family portrait

Professor David Cove first introduced me to the moss *Physcomitrella patens*, enthusing about its potential as a 'model'. His enthusiasm was not misplaced, as is evident from the paper by **Carey and Cosgrove (Pennsylvania State University, USA, pp. 1131–1141)**. Cosgrove's group is well-known for work on expansins, non-enzyme proteins involved in rapid cell wall expansion in angiosperms. Expansin genes exist as a super-family comprised of four families, EXPA, EXPB, EXLA and EXLB, of which EXPA and EXPB encode the 'classic' expansins that weaken linkages between cellulose microfibrils. In order to understand further the evolution of the expansin super-family the authors have focussed on *Physcomitrella* as a less-complex land plant. The data show clearly that *Physcomitrella* possesses EXPA and EXPB families of expansin genes but not the EXLA or EXLB families. There are 27 genes in the EXPA family (one more than *Arabidopsis* but one less than *Populus*) and seven in the EXPB family (one more than

Arabidopsis and four more than *Populus*). Therefore, the individual genes, many of which show cell-specific expression patterns in angiosperms, have arisen at least 400 million years ago, before the increase in the range of cell types associated with the evolutionary route from simple to complex land plants. Further analysis of gene structure places the EXPA family into six groups (the latter two, E and F, each consisting of one gene). Groups D, E and F are more similar to angiosperm expansins than groups A, B and C. This analysis, taken with other data, suggests that the common ancestor of *Physcomitrella* and angiosperms had at least two EXPA genes that gave rise to the A, B, C and to the D, E, F lineages. EXPB genes by contrast fall into one group (there are two in *Arabidopsis*), which appears to be a sister group (i.e. derived from a common ancestor) to those in angiosperms.



Little green apples

As I write this, the apple trees in my garden are in full bloom; I look forward to a good harvest in the late summer and on through the autumn. However, between now and then, many of the fruit that initially set will fall off, a phenomenon known as the ‘June drop’. This is, in effect, a self-thinning activity that ensures an economical allocation of resources to fruit and seed production.

There is a distinct hierarchy in this process. The central flower in a cluster of five opens first (and is thus usually pollinated first) and it is the fruit forming from this flower that is most likely to be conserved. Commercial growers of apples often encourage fruitlet abscission by spraying the trees with hormone solutions, as described by **Dal Cin *et al.* (Padova and Trento, Italy, pp. 1195–1202)**. In common with many abscission events in flowering plants, ethylene is involved. In both a ‘conventional’ variety, ‘Golden Delicious’ and in a ‘spur variety’, ‘Red Delicious’, there was increased transcription of the gene encoding ACC-oxidase, the last enzyme in the ethylene biosynthesis pathway. In ‘Red Delicious’ this occurred in all fruitlets but in ‘Golden Delicious’ it was confined to lateral fruitlets. However, in both varieties, increased ethylene production occurred only in lateral fruitlets (implying a further level of control in ‘Red Delicious’). Even though ethylene is clearly involved, one of the hormones used by growers to promote fruitlet abscission is the cytokinin benzylaminopurine (BA): application of BA causes an increase in transcription of the ACC-oxidase gene and ethylene output. However, only in ‘Golden Delicious’ was fruitlet abscission stimulated. Despite this, data from measurement of shoot growth suggest that BA stimulates fruit drop in ‘Golden Delicious’ by promoting vegetative growth at the expense of reproduction. A spur type such as ‘Red Delicious’ does not respond because shoot growth is regulated in a different way.



The gall of the *Lotus* eaters

One of the lesser-known aspects of plant pathology is the parasitism of plants by nematodes, estimated to cause annual yield losses worth \$100 000 000. Interactions between parasite and host cause various modifications to plant morphology/anatomy; here we focus on parasitism by ‘root-knot nematodes’. In this type of plant–nematode interaction, infection leads to the formation of giant cells adjacent to the vascular cylinder, surrounded by a gall or root-knot, as described by **Poch *et al.* (Harpenden, UK, pp. 1223–1229)**. Formation of the giant cells triggers, in some way, the development of the nematodes from juvenile to adult female forms, which feed on nutrients from the giant cells. Intriguingly, the cells are only maintained if the nematode continues

feeding. Thus, there is a two-way interaction between the plant and its parasite. The authors are interested in the extent to which these interactions vary in relation to the success of the parasite; they have investigated this in a range of ecotypes, 60 in all, of the legume *Lotus japonicus*. Plants were inoculated with equal numbers of stage-2 juveniles of *Meloidogyne incognita*, all hatched from the same egg mass. Plants were scored for gall (root-knot) formation and for nematode egg production 6 weeks after inoculation. There was an over 100-fold range in susceptibility, with some ecotypes sustaining very few galls and others several hundred. Further, the number of nematode egg masses was highly correlated with the number of galls formed ($r = 0.794$), indicating the necessity of gall formation for nematode reproduction (although in four ecotypes the two processes were not tightly linked). Interestingly, neither gall formation nor egg production showed a plateau when ecotypes were arranged in rank order. This suggests that there may be even more susceptible ecotypes. At the other end of the scale, the highly resistant ecotypes are likely to provide a genetic resource for plant breeding.

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