Plant tumours

Wounds activate attackers

from John E. Beringer and Colin M. Lazarus

THE ability of strains of *Agrobacterium* to induce tumours on dicotyledonous plants has excited the interest of most biologists, particularly since it was discovered that tumour formation results from the inheritance of DNA (T-DNA) transferred from the bacterium to the plant, a process that depends on the function of virulence (*vir*) genes. Tumours are induced only where there is a wound on the plant and an intriguing question has been how *vir* genes are regulated so that *Agrobacterium* can recognize wounds and initiate T-DNA transfer. The answer, provided by S.E. Stachel *et al.* on page 624 of this issue, is surprisingly simple: the *vir* genes are induced by specific signal molecules, acetosyringone and α -hydroxy-acetosyringone, that are produced by wounded, but not by intact, plant cells.

This finding helps us to understand why wounds are required and demonstrates yet again how much tumour formation depends on interactions between the two partners. A series of interactions can now be recognized that are logical and all, apparently, directed towards optimizing the efficiency of the interaction from the point of view of the bacterium.

T-DNA is present as part of a large extrachromosomal molecule (plasmid) that also carries a number of *vir* genes. Like other DNA elements capable of transposition, T-DNA is bounded by identical repeats of DNA. Independent loops of T-DNA are found when *Agrobacterium* is cultured in the presence of plant cells and it is assumed that these are T-DNA intermediates in the transfer to the plant cells. Seven genes are required for T-DNA transfer. Two of them, *virA* and *G*, are expressed in vegetative cells but the other five are induced only in the presence of acetosyringone or α -hydroxy-acetosyringone.

Once it is transferred to the plant, T-DNA integrates into host DNA and the genes it carries are expressed. T-DNA encodes genes involved in the synthesis of plant hormones and for the synthesis of novel compounds (opines) that are produced only by plant cells containing T-DNA from *Agrobacterium*. Tumour formation appears to be a method evolved by *Agrobacterium* for inducing the plant to produce a large number of cells that synthesize opines, which are metabolized by *Agrobacterium* but by few other organisms.

Opines have also been shown to act as specific inducers of the transfer (*tra*) genes carried on *Agrobacterium* tumour-inducing (Ti) plasmids. It is now clear that plant metabolites induce the functioning of two distinct sets of *Agrobacterium*

genes: those for virulence and those for transfer of Ti plasmids. In both cases, DNA replication and mobilization leading to gene transfer are induced only when they are likely to be of direct value to *Agrobacterium*.

As well as answering the immediate questions of why only wounded tissue is infected by T-DNA, Stachel *et al.* may also have resolved the enigma of why strains of *Agrobacterium* carrying *Rhizobium* nodulation genes form nodules on the roots of appropriate legumes, whereas they induce tumours when inoculated on wounded tissue; presumably the close association of the bacteria and plant cells during nodule development does not lead to the induction of *vir* genes because the plant is not wounded.

This report is another example of how the study of plant-microbe interactions can yield important information on genetic regulation. Building on evidence that plant defences against pathogenic fungal attack are triggered by fragments of the host plant cell wall, K. Tran Thanh Van *et al.* (*Nature* 314, 615; 1985) have recently

shown that specific oligosaccharides can affect the developmental fate of plant cells in culture. This indicates a role for such 'oligosaccharins' in normal organogenesis. Recently J.T. Mulligan and S.R. Long (*Proc. natn. Acad. Sci. U.S.A.* 82, 6609; 1985) and L. Rossen, C.A. Schearman, A.W.B. Johnston, and J.A. Downie (*EMBO J.*, in the press) have reported that a *Rhizobium* nodulation gene is induced by root exudates in an analogous manner to *Agrobacterium vir* genes. These findings identify primary signalling molecules and raise questions concerning the transduction of signals from the cell surface to the genetic material.

What about interactions such as those of mycorrhizas and between host plants and other pathogens? Progress

in the search for similar inducers may be slow. As Stachel *et al.* have shown, finding an effect of root exudates is only the beginning of a complex isolation and characterization process. To purify the molecules responsible it is necessary to have a good assay, which in general is not an assay of a plant response. Both Mulligan and Long, and Stachel *et al.* took advantage of the extensive genetic understanding of *nod* and *vir* genes, respectively, to produce fusions of these genes with the *Escherichia coli lacZ* gene and thus could determine induction by measuring β -galactosidase activity using a simple and sensitive assay procedure.

We look forward to seeing a surge of activity in the identification of plant molecules that act as specific inducers of genes in symbiotic and pathogenic microorganisms. Perhaps, as with other aspects of plant-microbe interactions, work will be driven by studies of the genetically well-characterized bacteria *Agrobacterium* and *Rhizobium*. It is good to see that studying the biology of tumour formation can yield results that are at least as satisfying as those obtained through molecular studies of DNA. □

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The spider, *Subantarcia* sp., forms the frontispiece to the first formal presentation of the *Orsolobus* taxon of spiders, members of which are found in South America, Australia and New Zealand (Forster, R.R. & Platnick, N.I. *Bull. Am. Mus. nat. Hist.* 181, 1; 1985). The fly is the frontispiece to a taxonomic study of the ichneumon-fly genus *Banchus* in the Old World (Fitton, M.G. *Bull. Br. Mus. nat. Hist.* 51, 1; 1985).