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Phil. Trans. R. Soc. Lond. B 1989 **324**, 525-535
doi: 10.1098/rstb.1989.0065

Phil. Trans. R. Soc. Lond. B **324**, 525–535 (1989)
Printed in Great Britain

Plant biotechnology and its application to agriculture

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The predicted expansion of plant genetic engineering has occurred since publication of the Spinks Report, but routes to profit have emerged much more slowly than the media predicted. The U.K. made a strong start in the science but its position relative to the U.S.A. has declined because of the relatively massive investment in the U.S.A. by industry and the public sector.

An impressive list of plant species have been transformed with new genes over the past few years. Of relevance to agriculture, genes have been identified, isolated, characterized, reconstructed and inserted into plants that confer tolerance to some leading herbicides, insect pests and viruses. Some field trials of the engineered plants have been carried out. Field trials of genetically engineered potato plants have been undertaken in the U.K. The conditions under which genetically engineered plants are to be released into commercial agriculture is currently a very important topic of debate.

The detection of favourable genotypes in plant breeding programmes is currently time consuming and expensive in some instances. The ability to assay genetic variation in all regions in the genome by restriction fragment length polymorphism mapping is providing promise to plant breeding programmes for identifying favourable genotypes.

Introduction

My aim in this paper is to highlight from a U.K. point of view some developments that have occurred in plant biotechnology during the past eight years since the publication of the Spinks Report. My comments are mostly limited to those aspects of plant biotechnology that relate to plant breeding and agriculture.

First, I wish to emphasize the timescale of existing plant breeding programmes, as this provides a useful perspective against which to judge progress in plant biotechnology that is orientated towards plant improvement. For many of our major crops it routinely takes ten years from the time the chosen cross is made until the progeny have been selected, evaluated and some indication of commercial success is evident. Thus any new varieties that have entered commerce in the eight years since publication of the Spinks Report originated from crosses made long before plant genetic engineering was possible.

The U.K. was one of the first countries in the world to initiate the purification of plant genes by recombinant DNA techniques. The Plant Breeding Institute at Cambridge was cloning genes from the chloroplast genome in 1977. In 1978 the Agricultural Research Council launched a Plant Genetic Manipulation Programme. It decided that the most effective place to launch its initiative was in its institutes, rather than in the universities. About 30 new positions were created and allocated mainly to the Plant Breeding Institute at Cambridge, the John Innes Institute at Norwich and Rothamsted Experimental Station at Harpenden. This was a very forward-looking initiative, taken ahead of equivalent initiatives in other countries.

The genetic engineering of plants by molecular biologists was established in 1983. In that year three programmes, one in Belgium (Herrera-Estrella *et al.* 1983), one in Monsanto (Fraley *et al.* 1983) in the U.S.A. and one in the Plant Breeding Institute in the U.K. (Bevan *et al.* 1983) produced tobacco plants containing an active gene that was constructed in the laboratory. The gene was constructed by joining a promoter and a terminator of transcription from the nopaline synthase gene of the soil bacterium *Agrobacterium tumefaciens* to the coding sequence for neomycin phosphotransferase from *Escherichia coli*. This active gene conferred on the plant cells resistance to the antibiotic kanamycin and has been used extensively since as the means of selecting transformed plant cells in culture.

Now, only five years later, plants in over 20 different species have been modified around the world by the introduction of new genes.

This progress is very impressive and illustrates well the speed of development and diversity of plant genetic engineering. It is important to note that this progress has depended on not just the means of introducing DNA into plant cells but also on recovering whole plants from those cells. This aspect of plant tissue culture is limiting the extension of gene introduction into other species. Scrutiny of table 1 shows that several major crop plants, e.g. potato, soybean, rice and

TABLE 1. SOME PLANT SPECIES TRANSFORMED WITH EXOGENOUS DNA

alfalfa	arabidopsis	asparagus
brassica	carrot	celery
cotton	cucumber	flax
lettuce	lotus	maize
pear	petunia	poplar
potato	rice	soybean
sugar beet	tobacco	tomato
white clover		

sugar beet, can now be transformed but we await success for other major crops such as wheat, barley and field beans.

The U.K.'s profile in international plant genetic engineering was more striking in 1983 than it is now. Although we were one of the first to produce an engineered tobacco plant, none of the other species in table 1 was first transformed in the U.K. Why have we slipped relative to our competitors? Our science in the plant biotechnology area has not deteriorated, but the subject has exploded in the U.S.A. and grown very substantially in other countries of Western Europe and more recently in Japan. Industrial investment in the U.S.A., in the large multinationals as well as in smaller 'boutiques', has been extraordinary. North American industry has done much to develop the fundamental science. Industrial Laboratories were the first to transform approximately 14 out of the first 22 plant species to be genetically engineered. U.K. industry has been more cautious and has done much less to develop the fundamental science. However, during the last eight years ICI and Unilever have entered the seeds business, spurred on, no doubt, by the possibility of future opportunities that will be derived in part from biotechnology research. Whether industrial investment in plant genetic engineering during 1980 to 1988 will turn out to have been 'the right amount at the right time' for each company remains to be seen. What is clear in 1988 is that North American industry and one or two specific companies in Europe have increased the fundamental knowledge base substantially and have sought to win major patent positions.

With the scale of investment in the private and the public sector being expanded so much

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more extensively overseas than in the U.K., it is inevitable that our overall strength relative to that in the U.S.A. looks less impressive now than in the early 1980s.

Developments in the techniques of introducing new genes into plants

DNA can be introduced into plant cells by several means. When the cell wall is removed and protoplasts are produced, DNA can be introduced very easily by disrupting the membranes with polyethyleneglycol (Werr & Lorz 1986). Alternatively the membrane can be disrupted by electric pulses (Fromm *et al.* 1986). Such DNA can find its way to the nucleus and be incorporated into the chromosomes. In some species, the protoplasts can regenerate a wall, divide to form a callus and be induced to differentiate into a whole plant. Tobacco does this readily and this is the reason why this species has been the favourite of the plant genetic engineer in the past five years. Tobacco, along with many other plant species, is susceptible to the pathogenic bacterium, *Agrobacterium tumefaciens*. It was discovered in 1977 (Chilton *et al.* 1977) that this bacterium causes crown gall tumours by transferring a specific segment of one of its plasmids into the chromosomes of plant cells. This extraordinary process of gene transfer was rapidly seen as a useful means for researchers to introduce genes into plants. The bacterial genes in the special plasmid segment causing the tumour were to be replaced with genes of value to the scientist, farmer or end-product user. Thus since 1980 we have seen the proliferation of some outstanding bacterial genetics on *Agrobacterium* and *E. coli* to design new vectors for the easy transfer of genes into plant cells via *Agrobacterium*. One series of vectors, in use in many laboratories around the world, was designed and constructed in the U.K. by Michael Bevan at Cambridge (Bevan 1984). From a historical perspective it is interesting to note that bacterial genetics has contributed enormously to the development of plant science in the past decade.

Because the regeneration of whole plants from single transformed cells is difficult in many species, other approaches that attempt to introduce DNA into the cells of organized structures such as meristems and embryos are being attempted. Microinjection of DNA into many cells of oil-seed rape embryos has proved successful. Recently, much interest has been aroused in the shooting of DNA-coated tungsten particles through cell walls and cell layers to transform cells. Cellular activity of genes shot into maize, onion, wheat, rice and soybean cells has been reported, so the method holds considerable promise (Klein *et al.* 1987; Wang *et al.* 1988). Particle acceleration by electric discharge has also been used to introduce DNA-coated gold particles into meristems of immature soybean seeds (McCabe *et al.* 1988). Transformed plants were produced. This method may therefore also emerge to be extremely useful for introducing genes into plants not easily regenerated from single cells.

The introduction of herbicide, insect and virus resistance into plants by genetic engineering

I have selected three examples of genes which have been isolated, characterized, reconstructed and introduced into crop plants to confer properties of direct agricultural interest to illustrate that substantial progress has been made in a relatively short time.

(*a*) *Herbicide resistance*

Considerable progress in the engineering of selective herbicide resistance has occurred over the past few years because knowledge of the mode of action of the herbicides enabled target

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genes to be identified rapidly (Comai & Stalker 1986). The Monsanto herbicide, Roundup, inhibits the shikimate pathway enzyme, 5-enolpyruvylshikimate-3-phosphate synthase (EPSPS) involved in aromatic amino acid biosynthesis (Amrhein *et al.* 1980; Mousdale & Coggins 1984). A mutant petunia gene was isolated by the Monsanto team which encodes an EPSPS protein that still retains its enzymic activity but is 6000-fold less sensitive to glyphosate inhibition than the wild-type petunia EPSPS. When this gene, activated by a strong promoter from cauliflower mosaic virus, was inserted into tobacco and tomato plants it conferred resistance to high levels of glyphosate. Recent field trials of the tomato plants confirmed that resistance is inherited and does not have deleterious side effects on yield (R. Fraley, personal communication). However, because the herbicide is rapidly transported to meristematic zones, the levels of mutant EPSPS present in the engineered plants seems unable to produce complete tolerance to the herbicide in these parts of the plants.

The sulphonylurea herbicides of Dupont and also the imidazolinone herbicides of American Cyanamid inhibit the enzyme acetolactate synthase (ALS), which catalyses a step in the biosynthetic pathway of isoleucine, leucine and valine (Chaleff & Mauvais 1984; Shaner *et al.* 1984). Plants resistant to these herbicides have mutant *ALS* genes. Insertion of such genes from tobacco and *Arabidopsis* into tobacco or tomato plants by the Dupont team has produced plants resistant to high levels of sulphonylurea herbicides. Field tests have confirmed the value of the phenotype under agricultural conditions (B. Mazur, personal communication).

The antibiotic bialophos is a product of *Streptomyces*. It is a tripeptide composed of two L-alanine residues and an analogue of glutamic acid known as phosphinothricin (PPT). In plants and bacteria, intracellular peptidases remove the alanine residues and release PPT, which is an inhibitor of glutamine synthase (Thompson *et al.* 1987). Inhibition of glutamine synthase by PPT causes rapid accummulation of ammonia, which leads to death of the plant cells. Bialophos is produced commercially from *S. hygroscopicus* and PPT is synthesized commercially (Basta, Hoechst A. G., F.R.G.). The gene of *S. hygroscopicus* that confers resistance to bialophos has been cloned, put under the control of a strong promoter for plant cells and introduced into a range of plant species in the company Plant Genetic Systems in Belgium (De Block *et al.* 1987). The gene product, phosphothricin acetyltransferase, acetylates the free NH_2 group of PPT thereby inactivating the herbicide and making the plants resistant to high levels of the herbicide. Potato plants containing the phosphinothricin acetylase gene have been evaluated in field trials and been shown to display high levels of resistance to PPT without any yield loss (W. De Greef, Plant Genetic Systems, personal communication).

More sophisticated versions of all these genes conferring resistance to the herbicides are being constructed to provide higher levels of resistance to each herbicide in the appropriate parts of the plants.

Why has resistance to broad-spectrum herbicides been engineered so rapidly? Is it the most important attribute the farmer would like to have engineered into their crops? Although herbicide resistance is a desirable character for many crops, a major reason for the emphasis on engineering for herbicide resistance is that it is the agrochemical companies, the manufacturers of these herbicides, that have had most money to spend on genetic engineering. These companies have perceived that if money can be gained by selling a herbicide, even more money can be gained if many more crops are resistant to it. One of the problems of the seeds business is that in the major commodity crops profits on sales of seed are relatively low. This limits the returns that are possible on genetically engineered seeds. However, if additional

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revenues can be gained by selling seed and chemicals, then the investment with plant genetic engineering may be recouped more easily.

(*b*) *Insect resistance*

The larvae of several major insect pests are controlled in agriculture in some countries by the spraying of spore preparations of *Bacillus thuringiensis* (Dulmage 1980). The insecticidal activity is caused by crystals containing toxins in the spores. Different strains of *B. thuringiensis* produce different toxins, which are active against different lepidopteran, dipteran or coleopteran insect species. The crystals dissolve in the larval gut, and the proteins are released and proteolytically cleaved to yield smaller toxic fragments (Lilley *et al.* 1980). The genes encoding these toxic proteins have been cloned from many different strains, put under the control of plant promoters and inserted into various plant species via *Agrobacterium tumefaciens* (see, for example, Fischoff *et al.* (1987) for tomato and Vaeck *et al.* (1987) for tobacco). Some of the plants produced express the protein in their leaves to levels that kill larvae when the leaves are eaten. Death occurs within a few days and leaf damage is thereby highly restricted. In field trials done by Monsanto, under conditions where control tomato plants were completely defoliated by tobacco hornworm, transgenic tomato plants suffered little agronomic damage. Applications of egg masses of *Heliothus zea* (tomato fruitworm) caused fruit damage of 17–23% on control plants but only 4–9% on the transgenic plants containing the *B. thuringiensis* gene (R. Fraley, Monsanto, personal communication).

A different gene has been used to confer insect resistance on plants by the group in the Botany Department at the University of Durham, supported by the Agricultural Genetics Company. They recognized that the level of a trypsin inhibitor, a naturally occurring protein in seeds of cowpea (*Vigna unginculata*), correlated with field resistance to the bruchid beetle (*Callosobruchus maculata*). The gene for this protein was isolated, given a strong plant promoter and transferred into tobacco via *Agrobacterium tumefaciens*. The gene product, expressed in the leaves, caused the death of *Heliothus*, *Manduca* and *Spodoplera* larvae thereby reducing leaf damage by the larvae considerably. The cowpea trypsin inhibitor is apparently not toxic to humans so it may provide a useful route for protecting many plants used as human foods against insect devastation.

(*c*) *Virus resistance*

A remarkable series of plants has recently been created by introducing active copies of genes encoding the coat protein of pathogenic viruses. The plants show considerable resistance to the viruses from which the coat-protein genes were obtained (Nelson *et al.* 1988). The idea for the experiments came from old observations (McKinney 1929) that plants infected with a mild virus often showed reduced symptoms after infection by a more virulent, related strain. The most likely explanation for this is that the coat protein of the mild strain prevents particles of the severe-challenge virus from uncoating after they have entered the plant cell.

In a field test of transgenic tomatoes containing the coat protein gene of a common strain of tobacco virus (TMV), no more than 5% of the plants innoculated with TMV showed systemic disease symptoms compared with 99% of the control plants (Nelson *et al.* 1988). Lack of disease symptoms was correlated with a lack of virus accummulation. Fruit yield was unaffected by viral infection in the transgenic plants but reduced by 26–35% in the control plants. The phenomenon of protection by insertion of a virus coat protein gene into plants appears to be

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a general one as tolerance to numerous viruses has now been produced by this approach (see table 2).

Another route to creating virus tolerant plants by inserting viral genes is possible where the viruses have additional small RNA molecules or satellites in their genomes. Viruses with satellites can sometimes be used to protect plants against more virulent strains lacking a satellite. For example, in China, a cucumber mosaic virus (CMV) isolate containing a benign natural satellite has been used to protect valuable tomato and pepper plants against severe strains of CMV.

TABLE 2. VIRUS RESISTANCES CREATED BY INSERTIONS OF COAT PROTEIN GENES OR SATELLITE RNA

coat protein	satellite RNA
tobacco mosaic virus	cucumber mosaic virus
alfalfa mosaic virus	tobacco ringspot virus
tobacco rattle virus	
cucumber mosaic virus	
potato virus X	
potato virus Y	

At the Plant Breeding Institute at Cambridge, in collaboration with the Scottish Crops Research Institute, a dimeric copy of the CMV satellite has been introduced into tobacco plants such that the gene was expressed as an RNA. Upon infection with CMV or a closely related virus, tomato aspermy virus, the RNA was recognized, amplified and interacted somehow with the virus to reduce markedly the severity of the infection (Harrison *et al.* 1987). Similar experiments have been done with a gene derived from the satellite of tobacco ringspot virus (Gerlach *et al.* 1987).

The three examples of plant genetic engineering for agriculture that I have noted are the products of some outstanding science and have exploited methods of gene isolation, gene construction, transformation and plant tissue culture. The results strongly suggest that plants with resistances to herbicides, insects and viruses will enter agriculture in the next decade or so providing regulatory authorities allow their dissemination (see below).

MOLECULAR BIOLOGY TO HELP THE PRACTICE OF PLANT BREEDING

The process of plant breeding is laborious and expensive. Many of the desirable plant phenotypes are determined by combinations of genes, and to improve varieties in a conventional crossing programme and keep all the desirable combinations of genes intact means that large populations of progeny have to be surveyed. Because of this, the practice of plant breeding could be made more efficient by any simple techniques that allow the presence of specific genes to be inferred and that avoid assay of a complex phenotype in the field. Techniques that assay genes closely linked to the desirable genes are in this category. Electrophoretic analyses of enzymes or grain proteins are consequently being used more and more to help breeders select progeny of predictable phenotype. However, the variation in these proteins is often too limited and there are too few to cover the genome. In contrast, at the DNA level, polymorphisms in base sequence within a species are extraordinarily numerous.

These latter polymorphisms can be detected by using restriction enzymes, which cut only at

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sites with specific sequences, followed by electrophoresis to characterize the different lengths of DNA fragments produced (Beckmann & Soller 1986). Where the polymorphism involves insertion or deletion of DNA between two conserved restriction sites then electrophoresis will also detect the differences in DNA fragments produced. In most applications, it is necessary to detect the fragments in question by Southern blotting and hybridization to a radioactive probe DNA. Thus the technical requirements to reveal the polymorphisms are isolation of DNA, treatment with a restriction endonuclease, electrophoresis, Southern blotting, hybridization and autoradiography. This approach has the potential to make major contributions to plant-breeding practice and the assay of genetic variation, especially if the technology can be automated and reduced in cost. The major companies already in plant breeding have recognized this and are now investing substantially in the production of sets of DNA probes that can be used to characterize genetic variation in all regions of the genomes of the major crops species. The availability of such probes and methods is also enabling many new genes to be recognized and mapped rapidly, even those involved in polygenically determined traits (Paterson *et al.* 1988). The growth of this topic is a major new development of the application of the methodology of molecular biology to plant breeding and has been very catalytic in increasing the interest of plant breeders in the potential of molecular biology for plant breeding. These methods are also very useful for identifying variants in commercial seed lots and for proving ownership of germ plasm in courts of law.

Other opportunities for plant breeders and related industries are emerging from molecular biology. For example, kits to screen for the presence of pathogens, relying on detection of the foreign nucleic acids or pathogen proteins, have already been incorporated into plant breeding programmes and quarantine laboratories (Baulcombe *et al.* 1984).

Release of genetically engineered plants into agriculture and horticulture

The future of many aspects of plant biotechnology in agriculture depends on being able to release transgenic plants to the farmer. If this is not possible then industries will see little purpose in the development of transformed plants, and this in turn will depress public-sector research. In the last few years the scientific community, industry and the general public have started to debate whether and/or under what conditions genetically engineered organisms should be released into the environment. In the USA the release of the 'ice-minus' bacterium without all the necessary permits was a major news item for many months and Jeremy Rifkin, who is fighting against the release of all genetically engineered organisms, has become well known in society. Two 'releases' of plants have taken place in the U.K. under the guidelines of the Advisory Committee for Genetic Manipulation (ACGM); both releases were of potatoes. At Rothamsted Experimental Station at Harpenden potatoes that were the product of fusing protoplasts from two sexually incompatible species were grown. At the Plant Breeding Institute at Cambridge, potatoes that had two active genes introduced into them via *Agrobacterium tumefaciens* were evaluated in a field trial (figure 1). These releases have helped ACGM and the scientific community to gain experience in the issues involved. Some of these issues are as follows:

1. Will the genes be passed to other crops or wild plants? If so, does it matter?
2. Would the genes be spread amongst wild populations of plants?

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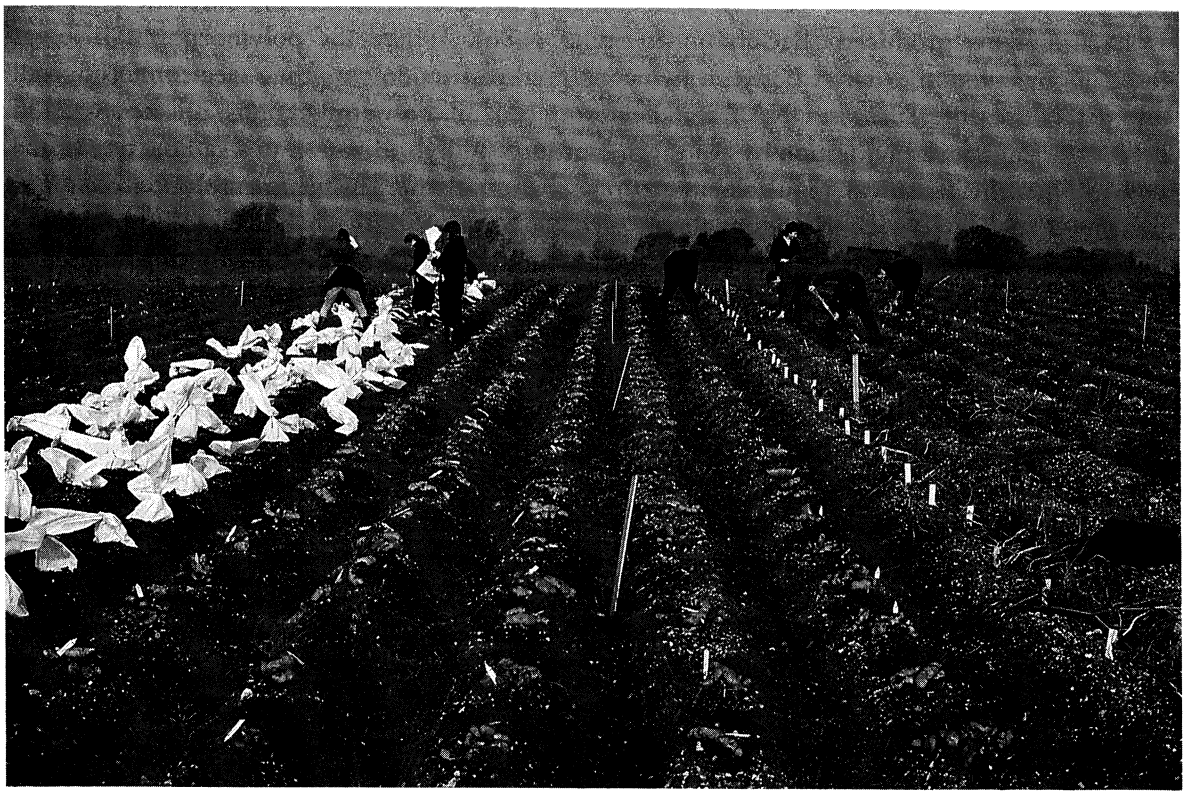

FIGURE 1. Tubers being harvested from the first U.K. field trial of genetically engineered potatoes, Cambridge 1987.

3. Can the plants enter food chains or be adequately protected from being eaten by people, insects, animals, etc?

4. If they were eaten, would there be any serious consequences?

The answers to virtually all questions of this type cannot be no or never. Risk assessment must therefore be used, and consequently it is necessary for the scientific community, ACGM and other bodies to gather the experience and knowledge to assess the risks and make decisions accordingly. Where there is a good case for making the release, there will be insufficient risk to veto the proposals. Clearly for the time being the situation will need to be managed on a case-by-case basis. The setting up of the correct bodies, legislation and education of the general public to consider and allow releases where appropriate are extremely important if plant genetic engineering is to have a future in agriculture.

However, whether a plant should be released into the environment or not is not the whole issue. Plants are in the food chains of a multitude of organisms, including humans. If virus-resistant, insect-resistant or herbicide-resistant plants are created for the farmer by expressing new proteins in the leaves or elsewhere, will the plant material be acceptable to the food industry? Gaining evidence to satisfy the appropriate decision-making bodies might be time consuming and expensive. Would it be worth the effort and cost? Futhermore, if a food company has spent vast sums of money and effort to develop a reputation for supplying safe food to the consumer, would it want to jeopardize its reputation by marketing a food product made from 'genetically engineered plants' especially if it were required to put it on the packet

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and the genetic engineering was only to help the farmer. These are the sorts of questions that are now being addressed internationally, and finding answers that are acceptable to all concerned will take a lot of debate and discussion. Within Europe it is very important that the different countries develop common guidelines, providing they are the correct ones. It will be a nonsense if one country allows the release of plants that are forbidden by another because release is release and pollen and seed dispersal mechanisms, not to mention plant breeders, do not recognise political boundaries. At present Germany has a five year moratorium on releases and they are forbidden in Denmark. In Holland, France and the U.K. field trials of genetically engineered plants have taken place.

While the debate about the release of genetically engineered plants gathers momentum there is a strong movement that says the processes by which the plant was created is irrelevant. It is the properties of the plant product that provide the criteria on which the release of a plant should be evaluated. This raises the much wider question of whether existing plant releases into agriculture should be scrutinized similarly to genetically engineered plants.

Public sector research and its interactions with industry

During the past three years a consortium of 11 industries, together with the Department of Trade and Industry, has been funding a programme of research, the 'Plant Gene Tool Kit', in several U.K. institutions. This kind of new initiative has been useful to both sides, both in furthering research knowledge, training people and understanding how to associate with partners in these kinds of ventures.

In 1983 AFRC signed a research and marketing agreement with the new government inspired company, the Agricultural Genetics Company (AGC), which was set up to develop and market research in plant genetic engineering and the associated sciences. AGC has the rights to much of the AFRC plant biotechnology carried out in the institutes. AGC is putting money into the AFRC research laboratories and this is very welcome, but relations between the Research Council scientists and AGC have not always been harmonious. Other industries resent AGC's position and have complained bitterly that they do not have access to AFRC science; or, perhaps more accurately, they are unwilling to gain access to it on AGC's terms. It is important that the means of transfer of technology from AFRC institutes and universities to industry runs smoothly because the competition is moving very rapidly and if our transfer is inefficient, we will lose the international races and not recover.

While discussing technology transfer and relations with industry in the period since the Spinks report, it is relevant to note that the British Government has sold to Unilever part of the Plant Breeding Institute at Cambridge because it was profitable in plant breeding and because it was in competition with other private breeding companies. Whatever the long-term merit of this decision it certainly cleaved an institution that was capable of technology transfer of basic plant science into plant breeding and inspired many fundamental scientists, myself included, to do this. Technology transfer of this type is frequently quoted as one of the U.K.'s weaknesses. The sale of the Plant Breeding Institute certainly looks odd in this light. In the eyes of our competitors all over the world who are struggling to create organizations, whether private or public, that have the capabilities in fundamental and applied plant science, it was an extraordinary decision. If the motivation was to ensure that all U.K. plant biotechnology companies have access to the science centre of the Plant Breeding Institute and AFRC in

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addition to the breeders of the Plant Breeding Institute then it is vital that they now use this expertise and this is where the role of AGC in facilitating access is very important.

I have two more consequences of current U.K. plant science policy to relate. The sale of the Plant Breeding Institute and the severe cutbacks of funds to AFRC have created much uncertainty. One of the strongest groups in plant biotechnology, that of the former Plant Breeding Institute, which was not in the part sold to Unilever, now has to move from Cambridge to the John Innes Institute, Norwich, with all the difficulties that entails for keeping staff and attracting the top-class postdoctoral and graduate students during the move. Other institutes with good plant biotechnology programmes are also under threat as a result of reduced funding by AFRC. The positive side of the Cambridge team moving to the John Innes Institute is that the combination of the plant science programmes of the two teams, together with the Sainsbury Laboratory, a large venture funded by the Gatsby Charitable Foundation, will create one of the largest groups of plant biotechnologists in Europe. Close by the John Innes Institute is the AFRC Institute of Food Research and the University of East Anglia who also have many researchers involved in aspects of plant biotechnology.

The second aspect of current U.K. policy is the 'near-to-market' research that the government is stopping, especially by large cuts to AFRC via the Ministry of Agriculture, Fisheries and Food. What is 'near-to-market' research? How will the cuts affect plant biotechnology? Are we in danger of losing technology transfer if the state gets out of 'near-to-market' research in plant biotechnology? These are questions that need to be addressed urgently if we are to keep competitive programmes in plant biotechnology with a better record of application through industry. I make these comments without the intention of saying whether the policies are right or wrong, but the issues are very relevant in any description of the current state of the U.K.'s plant biotechnology.

In summary, I believe that plant biotechnology has developed very rapidly and impressively and has made a very large impact on plant science. Commercial returns will emerge much more slowly than originally predicted by many popular articles in the press. However, many companies around the world have made major commitments, including some in the U.K. The massive investment made in the U.S.A. in public and private institutions since 1980 has reduced the competitive position of the U.K. relative to its position in 1980. Also, U.K. policies of reduced support for agriculture have produced uncertainties that are influencing the future of plant biotechnology in the U.K. Nevertheless, much excellent science is being done and the opportunities are expanding to reach many more corners of plant research and agriculture. The change in plant science has been revolutionary and all in the timeframe of analysing the progeny of a single cross in a breeding programme, looking for the new variety of the next decade.

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PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

FIGURE 1. Tubers being harvested from the first U.K. field trial of genetically engineered potatoes, Cambridge 1987.

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