MICHAEL DENIS GALE
25 August 1943—18 July 2009
Michael (Mike) Gale was an internationally well-known crop geneticist with a career devoted mostly to wheat genetics. However, he also studied rice, maize, pearl millet and fox millet for the benefit of agriculture in developing countries. He brought new knowledge and techniques into plant breeding that made a difference to crop improvement worldwide. Noteworthy is his team’s leadership in (i) defining the genetic basis of dwarfism in wheat, the major genetic innovation underlying the previously achieved ‘green revolution’ in wheat production; (ii) expanding knowledge of ‘pre-harvest sprouting’, which occurs in many wheat varieties growing in temperate climates, which reduces their flour quality and value; (iii) developing the first comprehensive genetic maps of wheat based on isozymic and DNA-based molecular markers; and (iv) developing the comparative genetics of grasses based on the conserved order of genes on chromosome segments, consistent with the evolution of the species from a common ancestor. These discoveries had a major impact in plant genetics. His team also provided the worldwide cereal geneticists and breeding communities with technologies and genetic markers that accelerated the development of cereal genetics and facilitated more efficient plant breeding. He made major and influential contributions to international agricultural research, particularly targeted at developing countries, through his participation on international and national committees, including those of the Consultative Group for International Agricultural Research. His contribution helped to drive the international research agenda for crop genetics, plant breeding and plant science generally.

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Michael Gale was born in Wolverhampton to Sidney Gale and Helen Mary Gale (née Johnson) on 25 August 1943. While World War II continued he lived in Lechlade in Gloucestershire, but after the war the family home was a farm in Drimpton, near Beaminster in Dorset. The Gales were considered ‘leaders’ in the rural village and his mother was, according to Mike, the strength of the family. Mike described his life as a child as very stable and well supported. He attended the village primary school until seven years old but from 1950 he attended Bincombe Preparatory School in Somerset as a boarder, and then West Buckland School (1954–1961) near Barnstaple, Devon, again as a boarder. These boarding schools enhanced his enthusiasm for competitive sports, particularly racquet sports. They probably also enabled the development of his excellent social skills. Mike had a younger brother, Richard, and a sister, Patricia. He met Susan Rosbotham when they were students at the University of Birmingham in the 1960s, and they married in 1979 when he was 36 years old. They had two daughters, Hazel and Tess.

Mike’s early interests in biology must have originated on the family farm and grew significantly in the sixth form, kindled by an exceptional teacher, but Mike readily admitted that he failed the botany A-level first time around, possibly trying to fit too many things into his school life. Nevertheless, his love of botany stimulated his applications to universities, and he became an undergraduate in the botany department of the University of Birmingham in 1962. The degree course exposed him to genetics, and he veered from botany to genetics for the third year of his undergraduate degree by switching to the genetics department, led by Professor Kenneth Mather FRS. There he learned aspects of cytogenetics, and quantitative and population genetics, often linked to crop improvement, and emerged with a 2:1 degree in 1965. This switch from botany to genetics would turn out to be of extraordinary significance for the rest of his career.

One wonders whether Mike’s career choices of botany, then agriculture and plant breeding, stemmed from being brought up in a farming environment. He recounted that his father had said that he would not leave Mike the farm when he died because the work was very physical and farming was uncertain, and he had given Mike the opportunity of a good education instead.

Postgraduate studies

With the subjects of botany and genetics firmly established in his experience, Mike moved from Birmingham in 1965 to do a PhD in the Department of Agricultural Botany at the University College of Wales at Aberystwyth, with Professor Hubert Rees (FRS 1976; known as Hugh) as his supervisor. To his surprise, Mike had won an Agricultural Research Council studentship and passed a 10-minute interview with Professor Rees in the bar of the Bellevue Hotel in Aberystwyth to gain support for his PhD position. Birmingham to Aberystwyth, and the other way, was a common path for students graduating in genetics, as Hugh Rees had been a staff member at the University of Birmingham with Kenneth Mather and Professor John Jinks (FRS 1970) prior to going to Aberystwyth. Each department recommended the other’s promising students for PhD opportunities.

‘Cytogenetical and biometrical studies in the Gramineae’ was the title of Mike’s PhD thesis project. He investigated genetic variation that influenced chiasma frequency, cytologically
scoring the numbers of crossovers in meiotic chromosomes in five subspecies of the genus *Hordeum* (barley). He also developed a series of barley lines in which each chromosome was substituted by a homologue from another variety using translocation stocks. Field trials conducted with these lines enabled the genetic control of characters, such as plant height, to be assigned to the substituted chromosomes. Mike was slow in writing up his research work and departed for a job in Cambridge prior to finishing his thesis, which was completed only following pressure from his new employers at the Plant Breeding Institute (PBI) in Cambridge and a short sabbatical back in Aberystwyth. The thesis was examined in 1969 by John Thoday FRS, professor of genetics at the University of Cambridge. Mike’s PhD study addressed many of the sorts of questions that he would address throughout his research career, namely the genetic mapping of traits in cereal crops.

Mike got, or created, much out of his time in Aberystwyth, and was a well-known character in the pubs of the town. Aberystwyth is a small town and isolated—quite a contrast to cosmopolitan Birmingham. The ‘small town’ nature of Aberystwyth and the absence of many sporting opportunities was why Mike started playing golf there, a passion for the rest of his life. Alongside his busy research programme, he also managed to fit in, as students do, late-night poker sessions, which initiated another life-long competitive hobby.

**His career path**

There was much contact between the Welsh Plant Breeding Institute, Aberystwyth University and the PBI at Cambridge in those days because all three specialized in cereal/grass cytogenetics, genetics and breeding. With Mike’s experience in cereal cytogenetics and field trials he was a natural candidate to fill a vacancy in the Department of Cytogenetics at the PBI in Cambridge in 1968. This department, led by Ralph Riley FRS, had become well-known internationally for discoveries in wheat cytogenetics and in particular the discovery and potential exploitation of the genetics of chromosome pairing and crossing over at meiosis to introduce genes from related wild species into wheat. Riley, supported by Douglas Bell FRS, the director of the PBI, had made the case to the Agricultural Research Council to substantially expand the Cytogenetics department to exploit the special wheat aneuploid stocks and germplasm developed there, in order to define the genetic basis of many agriculturally important traits. The authors of this memoir were also part of the ‘Riley Expansion’ of the Cytogenetics department (figure 1). RBF arrived at the PBI in 1969, and JWS in 1973.

The PBI and its successor, the John Innes Centre (JIC) in Norwich, was to be Mike’s single institution of employment until his death. The PBI moved to the site of the John Innes Institute in Norwich in 1990 and became formally integrated with it in 1994 because the UK government of the day had sold the plant breeding, but not the science, departments of the PBI to Unilever in 1987. The privatization of the plant breeding of the PBI has been a point of controversy over the years and it is relevant to reflect on it again in this memoir, given how much of the career of Michael Gale linked discovery science with applied plant breeding because they were co-located in the PBI in Cambridge.

Upon joining the PBI, Mike rapidly became engaged in learning what specialist wheat germplasm was available for genetic experiments, working with the teams of Colin Law and Ralph Riley. Given the interests of Ralph Riley, it is not surprising that one of Mike’s first
papers to be published there (1971) featured the mapping of the gene on chromosome 5B that regulated homoeologous meiotic chromosome pairing in wheat.

Mike’s outgoing personality quickly established him as a PBI celebrity. He contributed greatly both scientifically and socially to the whole of the PBI. It was Mike and the fellow new arrivals that changed the culture and scientific outlook to a more progressive vision of what a scientific institute should be, even though it remained hamstrung by civil service methodologies and procedures for some years.

The retrospective of Mike’s research career within the PBI and JIC reveals a natural progression. It started with the mapping of cytogenetic and other traits using wheat aneuploid and specially constructed stocks already available at the PBI, followed by a focus on discovering the genetic control of plant height and dwarfism. This was followed by biochemical and genetic analyses of the trait of precocious germination before the seed was harvested (known as ‘pre-harvest sprouting’, a highly detrimental trait for farmers), and also of seed weight development. In all such studies there were never enough genetic markers for detailed genetic mapping, and so the next phase of his career was to adopt and develop isozyme- and DNA-based technologies to produce much more detailed maps of wheat
chromosomes and compare them with similar maps of other cereals and grasses. By comparing genetic maps developed with common genetic markers, his team, in collaboration with that of PBI/JIC colleague Graham Moore, was able to reveal the extent of the conservation of gene order (gene synteny) in chromosomal segments during divergence of grass species from their common ancestor. This story gained wide appreciation across the plant scientific community and was a major reason that he and Graham Moore were awarded the Darwin Medal of the Royal Society in 1998.

Mike subsequently created a unit in the JIC known as the Comparative Genetics Unit to advance the creation of as many markers as possible to enable genes for agriculturally important traits to be mapped with greater precision, and in elite breeding populations. This was initially in wheat and related Gramineae, but was expanded to other crops, such as pearl millet and foxtail millet, as the team’s skills became established and international collaborations flourished.

Mike had many leadership and administrative roles at the PBI and JIC as his seniority and research successes increased. He became head of the Cereals Research Department of the Cambridge Laboratory in 1988, succeeding Dr Colin Law when Colin took the position of head of the Cambridge Laboratory—the name given in 1987 to the part of the PBI that was not privatized. After the Cambridge Laboratory relocated in 1990 to the John Innes Institute site, close to the University of East Anglia in Norwich, and then Colin Law retired in 1992, Mike assumed the position of head of the Cambridge Laboratory. When the Cambridge Laboratory became formally assimilated into the new JIC in 1994, he became the associate director of the Centre. In this role he oversaw many aspects of the internal science of the Centre and also took on many duties associated with running of the site, together with Professor Barry Smith, head of the Nitrogen Fixation Laboratory, which had also been assimilated into the JIC, from the University of Sussex. When the director of the JIC (RBF) resigned in 1998, Mike was appointed caretaker director in 1999 until Professor Christopher Lamb (FRS 2008) was appointed as the new director of the Centre in 2000. Mike then returned, full-time, to research and his increasing international commitments.

In 2003 at age 60, Mike retired from having a formal full-time position in the JIC, as was required by the Biotechnology and Biological Sciences Research Council Staff Code at the time. This was celebrated with a symposium attended by friends and colleagues from many parts of the world (figure 2). He became a John Innes Foundation Emeritus Fellow, and Professorial Fellow in the School of Biological Sciences, University of East Anglia, until his death in 2009. He remained in what had then become the Crop Genetics Department (started in 2001 under JWS), always having an open door for colleagues and students at JIC seeking his advice.

His career path was thus a logical and highly successful one, built around the wish to find and exploit the genetic basis of important traits, using the best approaches of the day, as they emerged from other areas of biology. Much of the remainder of this memoir describes this path in more detail. The directional singularity of this path contrasts with those of many other scientists who deliberately change their field of interest and places of employment over their research lifetime. What was especially significant about Mike’s career was his drive and abilities to link his research progress to international and national agricultural bodies and other world-leading research groups—activities that stimulated transfer of his team’s outputs to others and made him an international leader.
DWARFISM IN WHEAT

The stature of a wheat plant is critical for its productivity, and hence unravelling its genetic control is very important for wheat improvement. At the PBI, Colin Law’s team had opened up genetic studies into the trait of height when Mike arrived. It was an obvious topic to be studied in the PBI because the cereal breeding teams had made a major change to their breeding programmes by incorporating the now famous dwarfing genes, derived from Japanese sources, that had been so instrumental in generating the higher wheat yields of the ‘green revolution’ in Mexico, India and Pakistan by the Nobel Laureate Norman Borlaug (ForMemRS 1987). It was judged that, to get full exploitation of the dwarfing trait, much more knowledge about the primary genetics and biochemistry/physiology of height was required. Mike took on these challenges soon after joining the PBI, and over the next 10 years his team, including his technician Geraldine Marshall (now Heath), became world leaders in the genetics of dwarfism in wheat. He learned some of the physiology by spending time back in Aberystwyth at the laboratory of Philip Wareing (FRS 1969), a world expert in the chemistry of plant plant hormones.

By 1973 Mike and Colin Law had (i) shown that one primary dwarfing gene, *Gai3*, was genetically partially dominant and lay on chromosome 4A, and (ii) confirmed that numerous dwarf and semi-dwarf wheats did not respond as seedlings to the addition of the hormone gibberellic acid (GA) to the growth medium, unlike normal wheats which etiolated in response to added GA (1)*. The dwarf types were insensitive to exogenously applied GA (2) (figure 3). This provided an assay that enabled dwarf and non-dwarf seedlings to be distinguished a few

* Numbers in this form refer to the bibliography at the end of the text.
days after seed germination *in vitro*. This assay became a routine feature of Mike’s research for many years and, following publication, became the predominant test used worldwide for wheat breeders to select for dwarf and semi-dwarf segregants in their breeding populations at the seedling stage (4). This still allows large logistical savings in breeding programmes, worldwide, in terms of land and numbers of plants to be assessed in the field.

Extensive screening of aneuploids and other lines, short and tall, led to the discovery and mapping of several other loci that altered the height of wheat plants (1) (figure 4). Mike and the team named them *Rht* (reduced height) loci. The one initially called *Gai2* and later *Rht2* was mapped on chromosome 4D, and was, and still is, the major dwarfing allele used in breeding UK semi-dwarf wheats (3). It had been introduced originally from the Japanese variety Norin 10, which contained two dwarfing alleles, *Rht1* and *Rht2*. Mike’s team also characterized the dwarfing alleles in several other major breeding programmes around the world, bringing genetic clarity for the first time to the basis of the dwarf phenotypes in those programmes.

The PBI team then generated near-isogenic lines for most of the major dwarfing genes then known in wheat, and these enabled the effects of the alleles on many traits to be assessed and compared in field-grown plants. They found the presence of GA-insensitive dwarfing alleles resulted in smaller grains with lower protein content (10). Therefore, the increased yields of the UK semi-dwarf varieties must have been due to the production of more grains per plant. Such results were important for understanding the agronomic basis of the higher yields of the UK’s dwarf wheats. Genetic analyses showed that there were other genes that affected the height of wheat plants besides the *Rht* genes, and different combinations of these combined with the major dwarfing genes enabled preferred heights to be defined. ‘Tall dwarfs’, a term coined by Colin Law, became the frequently heard catchphrase in the labs of Mike, JWS and Law to describe what sort of plant was required to gain highest yields. Most of this work was summarized in an influential review paper in 1985 (6).
Pre-harvest sprouting and grain development

Sprouting of wheat grains in the ear in the field before harvest (figure 5) is a major problem facing all cereal farmers in temperate regions of the world where the weather at harvest is unpredictable and often wet. This topic was a natural successor for Mike’s interests in the genetics of dwarfism since he had observed the different growth rates of dwarf and tall seedlings after seed germination and noted that some dwarf lines were more resistant to pre-harvest sprouting. Furthermore, from the mid 1970s, Mike and his team had studied the plethora of enzymes induced after seed germination. Many of these enzymes are catabolic and responsible for the release of sugars and amino acids from the macromolecules stored in
the endosperm of the seeds. These supplies of sugars and amino acids support early growth of the seedling before soil-borne nutrients and photosynthesis become available. Induction of these enzymes is under the control of hormones including GA. Mike and his team showed that there were significant differences in the induction kinetics of these enzymes between dwarf and tall wheat seedlings. For example, alpha-amylase production by the aleurone layers of the dwarf seeds was much less than in tall varieties. Such observations also provided another simple assay to distinguish dwarf and tall wheat lines. When embryos were allowed to grow in combination with different endosperms it was concluded that, for many dwarf lines, it was the endosperm that was the source of the GA insensitivity.

Grain maturation is usually programmed genetically to be completely separated from germination, often with dormancy factors also aiding the physiological separation. When the developmental disorder of pre-harvest sprouting occurs, the two phases occur more-or-less simultaneously. Mike wrote a major review of the genetics of pre-harvest sprouting in 1989 (7), but relatively little specific knowledge of the genes involved was available. During the 1990s Mike, and his colleague John Flintham, studied the genetic basis of pre-harvest sprouting (23) using populations segregating for the syndrome. Subsequently, they extended the analyses using comparative genetics (22). They discovered that many genetic loci were involved, residing on most chromosomes. This complexity was expected given the plethora of the controls regulating seed maturation, desiccation, dormancy and germination. Some loci programming resistance to the syndrome were identified, subsequently aided by discoveries in maize, rice and *Arabidopsis* where similar phenotypes had been identified and related to specific genes.

Mike became a leader and organizer of international meetings on pre-harvest sprouting and galvanized the community into international cooperation. This again illustrated Mike’s social skills in being able to mobilize people from different countries, cultures and backgrounds into cooperation around a common research problem. In recent years the international wheat
research community has made substantial progress in identifying specific gene variants affecting pre-harvest sprouting as the techniques of precise molecular marker mapping have progressed, something to which Mike’s team made a major contribution (see below).

Studies on grain development are obviously important in any cereal, and Mike and colleagues took further advantage of specialized wheat genetic stocks available at the PBI and JIC to explore grain development through measurement of DNA and starch grain accumulation in grain endosperms of single chromosome substitution lines, where each chromosome was in turn substituted by the homologous chromosome of another variety, seeking to keep the genetic background of the recipient line constant. This enabled them to locate genetic variation on specific chromosomes. Such studies drew on Mike’s understanding of quantitative genetics and ways to exploit advanced cytologically derived stocks—topics he studied initially during his PhD programme.

The above examples in which his team developed the genetic understanding of important grain traits, and generated tools for improved variety production, illustrate Mike’s commitment to bringing scientific discovery into practice, a hallmark of what the PBI was all about. Not only did his results and breakthroughs reach the academic community, they were also appreciated by farmers who sought understanding and approaches for improving their cereal productivity and on-farm product stability. This appreciation resulted in the award to Mike of the gold medal for research of the Royal Agricultural Society of England in 1994 and the Rank Prize for Nutrition in 1997.

**MARKERS FOR GENETIC MAPPING IN CEREALS**

Advances in plant genetics have always relied on the development of new tools to enhance the genetic dissection of traits. In particular, cereal genetics had been hamstrung since its origin by the lack of genetic markers to enable fine mapping of the genes determining interesting and agriculturally important traits, most of which are specified by many genes. In wheat, this was compounded by it being a triploid species with a large DNA content, the genome consisting of over 16 billion base pairs. In the next phase of Mike’s research career he set about redressing the shortage of convenient genetic markers. This was possible because of the developments in biochemistry and molecular biology in the 1980s.

**Using isozymes**

It was widely established by 1980 that gel electrophoresis and isoelectric focusing gels could enable separation of isozymes and reveal variants that differ in size or electric charge. Such techniques were therefore in widespread use. Mike’s familiarity with the enzymes activated during grain germination made it obvious that there was value to be gained from studying the genetic variation in these enzymes using these techniques. His team, including Charles Ainsworth and various PhD students, applied the techniques during the 1980s to many enzymes (5) and thereby accumulated a large number of variant genetic markers mapped to chromosomes. The many papers describing such variation were not especially impactful as individual papers, but taken together they moved wheat/cereal genetics from being cytogenetically- to biochemically-based, and provided geneticists and breeders around the world with many new kinds of mapped chromosomal markers. This was a substantial contribution.
Using restriction fragment polymorphisms

A collaboration between RBF and JWS in the PBI during the early 1980s had illustrated the use of restriction endonucleases for mapping genetic variation in wheat through restriction fragment length polymorphisms (RFLPs), which had already been extensively used to construct genetic maps in other species. Mike recognized the potential value of RFLP markers as a natural progression from his work on isozymes. To have hands-on experience, he and his family left Cambridge in 1985 for a six-month study leave at the laboratory of Rudi Appels in CSIRO, Canberra, Australia, to learn some of the techniques required to develop this field. Following his return to PBI, Mike attracted an Australian, Peter Sharp, to the PBI to help launch large-scale RFLP mapping. The lab rapidly expanded, including Shiaoman Chao and Katrien Devos, who would turn out to be long-term collaborators. In 1989, Mike’s group published the first two of a large number of papers showing maps for each homoeologous set of wheat chromosomes, based on RFLPs (8, 9). The mapping was facilitated by the plethora of cytogenetic stocks in the PBI and showed for the first time the extent of the genome relationships between the homoeologous chromosomes, each derived from a different ancestral species but combined into the triploid bread wheat genome. Further, the group were able to accurately describe the reciprocal translocations involving chromosome arms 2BS and 6BS and chromosomes 4A, 5A and 7B, which had stabilized in the evolutionary history of wheat since it arose as a triploid species around 10000 years ago (11). Since the markers that the group developed could also be used for mapping in related Gramineae species such as rye and barley (12), the extent of conservation of synteny and the many translocations between chromosomes that had occurred during species evolution from a common ancestor were revealed. This added up to a substantial body of work during the 1990s. By 1995, over 2000 loci had been mapped in wheat by worldwide studies.

At the time, it was an expensive and time-consuming task to develop and implement the many molecular markers needed for good genome coverage. So, to accelerate the process, Mike became a leader in creating an international consortium, which became known as the International Triticeae Mapping Initiative to distribute the work across a network of cooperating laboratories. The field also became intensively competitive, particularly with groups in the USA, which Mike relished, as it played to his strengths, having honed his competitive skills in tennis, squash and golf!

Using microsatellites

RFLPs were very useful, but they had technical limitations, particularly for rapid, widespread use. They involved using radioactive isotopes, and the technology was relatively expensive. Mike and colleagues therefore looked at the newer techniques of molecular genetic analysis that were cheaper to develop and apply. They adopted ‘microsatellite DNAs’ as sources of variation as markers, where variation results from different numbers of copies of repeats in a chromosomal array. He raised financial support from the major European wheat breeding companies to generate a large cereal mapping programme based on satellite DNA markers. The companies benefitted exclusively for commercial applications, but information on the DNA primers used to amplify the fragments containing variation in numbers of repeats was distributed for research purposes to over 200 labs around the world in the late 1990s (16). This was a special contribution to genetic mapping in wheat. Mike’s team also used other marker systems, such as randomly amplified polymorphic DNA (RAPD) and amplified fragment
length polymorphisms (AFLPs), in various projects along the way to gain experience of the best systems to use to dissect the genetic basis of phenotypic traits in cereals.

GENETIC SYNTENY, GRASS EVOLUTION AND COMPARATIVE GENETICS

Mike’s group at JIC was one of several major international groups generating genetic maps of grass species. The emphasis of his group was cereals, notably wheat, rye and barley. The group also cooperated with others studying rice, maize and sugarcane. The pooling of gene mapping results across the grasses started to reveal the extent of conservation of large segments of chromosomes across the Gramineae with respect to the order of genes. This conservation was independent of the amount of DNA the chromosomes contained, or of recombination rates between genes and physical distances along the chromosomes, since, for example, a rice cell has 38 times less DNA than a wheat cell. The problem was how to put all of this information into an easily digestible and visible format for the wider audience of the cereal and plant science communities to appreciate and use. At JIC, Graham Moore had suggested the idea of breaking genomes and their chromosomes into chromosomal ‘Lego’ blocks to look for syntenic blocks going across species, after having watched his young son playing with that child’s toy. Moore suggested that such ‘Lego’ blocks might be revealed most simply by aligning all the mapping information with the smallest genome, that of rice. Exploiting rice genome data obtained from Nori Kurata and colleagues in Japan (13), comparative data from Mike’s group on wheat, and data on maize from Tim Helentjaris’s group in the USA, did reveal a set of ‘Lego’ syntenic blocks. Moreover, by stacking these blocks into a single ‘ancestral’ structure, and by cleaving the structure in different places, all chromosomes found in the different cereals could be reconstructed (15).

Further progress was then made during a small round-table discussion of JIC scientists (which JWS attended) with visiting scientist Francesco Salamini, then a director at the Max Plank Institute for Plant Breeding in Cologne. Salamini produced a hand-written drawing of an attempt to create a framework of cereal genome synteny by circularizing the single ‘ancestral’ Lego stack and placing the different chromosomes of separate cereal genomes into a series of concentric circles with rice at the centre. From these discussions, Mike and Moore realized that by combining the Lego block and concentric circle ideas they could create a coherent diagram that revealed the full synteny between different cereal genomes using a series of concentric circles, code coloured for the different syntenic blocks, with rice at the centre as the reference genome. This was facilitated by further data then available from Mike’s group on millet, data on sugarcane from the USA, and on sorghum and sugarcane from France. In 1995 this genetic synteny enabled Moore, Mike and other colleagues to present in a seminal paper (14) the pieces of chromosomes of grasses aligned around a circle, beautifully illustrating their evolution from common ancestral chromosomes (see figure 6). The circular representation in figure 6 is now known universally in the plant science community as ‘Crop Circles’. It provokes the conclusion that despite the 60 million years since the ancestors of rice and the other grass species diverged, fewer than 30 chromosomal ‘Lego blocks’ are now required to reconstruct all the diverged plant genomes when the small blocks are joined together in different orders. It also suggested the idea that there might have been a single ancestral cereal chromosome.
Figure 6. Gale and Devos ‘Crop Circles’. Colinear segments of grass chromosome marker maps arranged as circles and aligned to show evolutionary relationships between the chromosome segments (‘Lego blocks’). Loci controlling analogous traits in the different species are found to map at similar radii of the concentric circles. Rice, the smallest genome, resides at the centre of the nested circles. (Photograph provided by the John Innes Centre.)

The comparative maps were subsequently updated over the following decade by Mike and Katrien Devos in prominent publications (17, 18, 20) illustrating the major value of comparative mapping to the genetics research communities, revealing the synteny not only of genetic markers, but also of genes controlling important and useful traits. Knowledge of where an important gene function mapped in one species indicated the position where a homologous gene function is likely to reside in other species (see figure 6). Similarly, mutations mapped in one species predict where functionally equivalent mutations are likely to map in other species. The comparative maps also revealed the many rearrangements and translocations that had occurred during evolution, coupled to centromere and telomere positional changes. With the completion of the rice and other cereal genome DNA sequences, the extent of the conservation and divergence has become clearer; there is some loss of synteny in places owing to small, local rearrangements, and where duplicated genes and paralogues have been moved to new locations during evolution (20).

Synteny is not a new concept, having been demonstrated in many groups of species, plant and animal, from the early days of genetics. However, the work on cereals and grasses, stimulated greatly by the work of Mike, Moore and Devos, had an important impact in plant science because it provided the basis for the plant scientific communities to integrate genetic
knowledge across species boundaries, including those separating the major crops species. Also, the recognition that rice, with its small genome, can be used to help identify and clone orthologues from larger genomes, such as wheat, by ‘genome walking’ was useful until the full genome sequences of the relevant genomes became available.

As noted earlier, Mike set up the Comparative Genetics Unit in the JIC to map mutations, quantitative trait locus and genes that controlled important traits, taking advantage of the aligned chromosome maps and cross-species synteny. Before the developments in comparative genetics, Mike was known predominantly in the cereal genetics communities. After comparative genetics was recognized as a new powerful genetic tool in plant biology, he became much more widely known. In this regard it is noteworthy that his major honours appeared soon after publication of the comparative genome papers.

While most of Mike’s work had focused on wheat and its close relatives, other species of importance for tropical and semi-tropical countries became a focus from the early 1990s until he closed his lab in the mid 2000s when greater administrative and international responsibilities had begun to dominate his time. There was a three-pronged driver for this change from wheat to species of importance to developing countries. First was Mike’s greater involvement with the Rockefeller Foundation and the Consultative Group for International Agricultural Research (CGIAR; https://www.cgiar.org) and its associated research institutes. Secondly, Mike became closely involved with the Plant Sciences Programme set up by the UK Government Department for International Development (DfID) for research cooperation between the UK and developing countries. Under the auspices of the DfID programme, Mike set up a series of collaborations with the international agricultural centres, especially the International Crops Research Institute for the Semi-Arid Tropics, which focused on crops important for subsistence farmers. Thirdly, Mike had nurtured and expanded cooperation with research groups of the Chinese Academy of Agricultural Sciences and the Chinese Academy of Sciences. Through contacts with all these organizations, Mike’s group began work on the important tropical cereals, pearl millet, foxtail millet and green millet (19, 21, 24). Katrien Devos was instrumental in driving forward these activities until she left JIC in 2003 to become a professor at the University of Georgia, USA. The well-established skills in molecular genetic comparative mapping enabled the team to rapidly generate genetic maps for these species and compare them with related species. The research programmes attracted students from overseas. Mike supervised more than 15 graduate students, many of whom were from China or other developing countries in Asia, the Indian sub-continent and Africa.

Leadership in international and national science

Up until the late 1980s, Mike had focused on wheat and had become well-known within the international wheat community for his work in dwarfism, pre-harvest sprouting and mapping wheat chromosomes with enzyme markers. Meanwhile, the agricultural research communities worldwide had started to look towards molecular biology/biotechnology and its potential contributions to agriculture. One of the first significant roles that Mike was awarded was membership of the Scientific Advisory Committee for the influential Rockefeller Foundation’s Rice Biotechnology Program (1989–1999). Genomics with relevance to agriculture developed as a specific area, and Mike became a founding member of the Organizing Committee of the Plant and Animal Genome Conference (1992–2009), and a founding member of the
International Grass Genome Initiative (1994–2003). Soon after the story broke of the extensive synteny among grass genomes, including rice, Mike was elected as a Foreign Fellow of the Chinese Academy of Engineering (1998). This was followed by becoming a member of the Board of Trustees of the International Rice Research Institute in the Philippines (2000–2004). This is a CGIAR sponsored institute, and in 2000 Mike also chaired a review commissioned by the Technical Advisory Committee of the CGIAR into rice ‘Plant Breeding Methodologies’. Here, Mike’s broad knowledge of the newer technologies underpinning plant breeding was being recognized and exploited beyond wheat into the other major global crop, rice. He subsequently became a member of the CGIAR Genetic Resources Policy Committee (2004 until his death) and a member of the top CGIAR science committee, the CGIAR’s Science Council (2004 until his death). Such appointments to influential committees illustrate the major contributions Mike made to policy and strategy for international and national agricultural research, and was still making until his untimely death.

These latter activities amounted to almost a full-time position and obviously involved much overseas travel. Fortunately, Mike liked travelling and being with people, and cheerfully put up with the many discomforts to be found in rural and remote parts of the world while visiting farmers and agricultural research institutes. This was also because Mike had an iron constitution and rarely got sick from digestive problems, unlike many of his fellow travellers and colleagues. He put this down to being brought up on a farm with its own water supply, subsequently shown years later to be contaminated with chicken slurry! His wife, Sue, increasingly accompanied him on his trips in the later years, and they neatly combined business with pleasure, so that when the dense business of meetings and site visits was over, Sue would join Mike for short side trips to interesting and exotic locations.

In the UK, Mike served as a member of the Overseas Development Administration Management Group for plant breeding and physiology (1990–1995) and, following the major societal issues surrounding the use of transgenic genetically modified organisms, he served on the Health and Safety Executive’s Advisory Committee on Genetic Manipulation (1996–2000) and the Nuffield Council’s Bioethics Working Party on the Genetic Modification of Plants (2002–2003). The UK’s DfID also used Mike’s experience in their Renewable Natural Resources Research Programme Evaluation Steering Group. He was clearly one of the few scientists with great experience in genetics to provide broad and expert advice at senior levels in UK agriculture. His election to the Fellowship of the Royal Society came in 1996, two honorary doctorates in 2005 and he held an honorary research professorship of the Institute of Crop Germplasm Resources, Academia Sinica, Beijing, China, from 1992 until 2009.

THE FRIEND TO MANY WHO PLAYED AND WORKED HARD TO MAKE A DIFFERENCE

Mike was charming and engaging in personal relationships; his interest in people shone through positively. He was very much an all-round person—good at individual sports such as squash, tennis and particularly golf, although he abhorred team sports! His competitive spirit was obvious if you engaged him in sports activities or around the poker table, playing backgammon or other board games.

All his commitments to external activities meant a large and varied workload, which sometimes meant that deadlines were missed. However, Mike attracted around him a dedicated
team of assistants and colleagues, willing to pick up the tasks and to share the load. Indeed, one of Mike’s overwhelming personal characteristics was his ability to recognize scientific and administrative talent and thereby surround himself throughout his career with capable, dedicated and hard-working people, who were able to implement and expand on his ideas, enthusiasm, foresight and eye for the opportunities that new technologies offered to plant genetics.

As a husband to Sue and a father to Hazel and Tess (figure 7), Mike is remembered as a happy, warm, hard-working and incredibly funny man. He was the life and soul of the occasion, and his family will always remember how people would immediately warm to him and seek out his company. Mike and Sue were great party givers for large numbers of people whom he gathered as friends from around the world. He was particularly good with PhD students and visiting scientists, not only training them thoroughly scientifically, but also nurturing their social skills and looking after their families, thereby making life-long friends and dedicated collaborators in the process. Mike was a heavy smoker until late on in his life, and he enjoyed beer and nice wine, and large American style steaks. He lived life to the full. His untimely death at the Latitude Music Festival in Suffolk, England, in 2009, when he had played golf in the morning and listened to music in the afternoon, meant he was still enjoying himself when the end came.

**HONOURS AND AWARDS**

1992  Honorary Research Professor, Institute of Crop Germplasm Resources, Academia Sinica, Beijing, China
1994  Research Medal, Royal Agricultural Society
1996  Fellow of the Royal Society
1997  Rank Prize for Nutrition
1998  Foreign Fellow of the Chinese Academy of Engineering
1998  Royal Society Darwin Medal, jointly with Professor Graham Moore
2005  Honorary DSc, Norwegian University of Life Sciences
2005  Honorary DSc, University of Birmingham

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The authors thank current and former colleagues of Mike for their anecdotes and memories of their discussions with Mike. Further thoughts and memories are taken from Mike Gale’s personal computer archives held by JWS. The portrait photograph was taken in 1996 by Prudence Cuming Associates and is © The Royal Society.

AUTHOR PROFILE

Richard B. Flavell DSc CBE FRS

Richard Flavell is a molecular geneticist whose career has been focused on plant chromosomes and the application of molecular genetics to crop plants. Significant areas of output include the families of repetitive sequences found in plant genomes, the cloning of the first plant genes, organization of plant mitochondrial genomes, genetic transformation of plants, epigenetics, post-transcription mRNA turnover, and large-scale discovery of plant gene sequences. He developed his career in the UK alongside Michael Gale and they were colleagues at the Plant Breeding Institute, Cambridge, and John Innes Centre, with Flavell ending up as director of the John Innes Centre and Michael as associate director. In 1998, Flavell went to the USA to become chief scientific officer of a start-up agricultural genomics company, Ceres. Since then he has served as chief scientist of two other start-up companies in the USA and is also chair of the International Wheat Yield Partnership (iwyp.org).

John W. Snape PhD

John Snape is a crop geneticist whose career has focused on understanding the genetic control of agriculturally important traits in wheat, and the development of biotechnologies such as doubled haploid and transformation technologies for crop improvement applications, first at the Plant Breeding Institute in Cambridge, and subsequently at the John Innes Centre in Norwich. He joined the Plant Breeding Institute in 1973 alongside Mike Gale and RBF as a fellow project leader, and had numerous collaborations and joint publications with them. In 1990, he moved to Norwich following the privatization of the Plant Breeding Institute and continued his research at the John Innes Centre. He became head of the Department of Cereals Research in 1992, succeeding Mike, and
founded the new Crop Genetics Department in 2001. He retired from full-time duties at the John Innes Centre in 2010, but continued as an emeritus fellow doing post-grad teaching, and, as Mike had done, focused on advising national and international organizations in the public and private sector on research policy and strategy for major crops, particularly wheat and maize, as chair of the Board of Trustees of CIMMYT, the International Maize and Wheat Improvement Center, Mexico.

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