

Dedication:

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It was a sunny afternoon in early autumn of 1985. I was in the middle of processing my regular plasmid preps, when a distinguished gentleman accompanied by his wife entered our lab at the Max-Planck Institute in Cologne. He wore a moustache that accented his smile and had a neatly trimmed round beard, a splendid grey suit and an attractive necktie. He asked me in formal, polite English about the availability of my boss and friend, the late Professor Jeff Schell. Upon introducing himself, he probably noticed a familiar accent in my answer because he immediately turned the conversation to Hungarian, my mother tongue. Indeed, I was astonished. George Rédei, the legendary geneticist of *Arabidopsis*, stood in front of me saying that he would spend his sabbatical with us, fulfilling the invitation of Jeff Schell. As a young undergraduate, I saw him once at a congress in Szeged (Hungary), where in 1974 he disproved Ledoux's infamous DNA transformation studies, which caused much controversy in plant science during the early 1970s. Ledoux, a well-known researcher at that time, reported in *Nature* that he accomplished genetic complementation of Rédei's thiamine auxotrophic *Arabidopsis* mutants with transducing lambda phage DNAs carrying the *thi* locus of *E. coli* (Ledoux et al. 1974). Rédei et al. (1976)

provided clear and ultimate genetic evidence that Ledoux's transformed lines were as thiamine auxotrophic as his original *Arabidopsis* mutants. Using biochemical methods, F. P. Lurquin (1976) demonstrated at the same time that Ledoux's transformations did not result in the integration of exogenous foreign DNA into either cytoplasmic or nuclear genomes of plants. This event terminated an uncertain, but luckily short, period in plant science and opened the way to the development of new powerful transformation technologies. Prominently, this included the use of transferred DNA (T-DNA) of *Agrobacterium* tumor-inducing Ti plasmids, which was pioneered by Jeff Schell, and later also became my favorite work subject.

In 1975, Rédei published an outstanding review highlighting the unique values of *Arabidopsis* as model organism for genetics. Like many other young fellows interested in plant genetics, I read this review many times. Being motivated to learn more about *Arabidopsis* and the emerging molecular genetic techniques, I often paid as much as a third of my monthly income to have papers copied in the library despite the justified criticism of my wife.

That afternoon in 1985, our discourse with George Rédei and his wife Magdi lasted until late evening. For the first time, I heard many happy and sad stories about their life before and during the 1956 uprising in Hungary, and after their immigration to the USA. To my surprise, I also learned that George's widely known genetic studies with *Arabidopsis* did not gain much support in the form of grants for nearly two decades in the USA. In fact, the bitterness over his situation led him to look for help and new ideas in Cologne. Lucky coincidence! We were just about to exploit the integration of *Agrobacterium* T-DNA into plant chromosomes to generate insertion mutations and fusions between plant genes and T-DNA encoded reporter genes. That evening I decided to shift the focus of our project from haploid *Nicotiana plumbaginifolia* to *Arabidopsis*. In retrospective, it was a wise decision. Today the *Arabidopsis* genome is sequenced and carries over half a million of T-DNA and transposon insertions. Knockout mutations can be identified in any gene, which is not essential for both female and male meiosis.

In the following days, George (64 years old in 1985!) and Magdi started to prepare media and germinated seed. In a month, the first experiments yielded *Agrobacterium*-transformed calli expressing the T-DNA encoded antibiotic resistance markers. The subsequent months, which linked us closely together, were spent on designing methods for regeneration of fertile plants from the transformed tissues, interspersed with enjoyable conversations about various subjects in genetics. From these I quickly grasped that my knowledge of genetics, which I thought was acceptable,

had some gaps and holes. Thus, as George often said, I realized that there is indeed an essential difference between knowing things and knowing about them. He taught me genetics and I explained to him molecular biology, and no disagreement disturbed this marvelous relationship until his departure. The farewell was cheered by the fact that we saw our first T-DNA tagged *Arabidopsis* plants regenerating!

During the subsequent months, we raised over 8,000 T-DNA transformed plants from tissue culture. However, as *Arabidopsis* was a novelty in the hands of our gardeners in Cologne, we collected seed from only about 900 plants. My bitterness about this failure turned to a happy smile when I received some news from George again. Upon his return to Columbia, Missouri, he equipped some of his old bookshelves with lamps and converted his air-conditioned old laboratory to a tissue culture facility. He spent his salary buying clay pots and soil, repaired his glasshouse and, despite his heavy teaching load, helped Magdi to regenerate and plant hundreds of plants every week. By the end of 1986, they obtained seed from over 3,000 T-DNA mutagenized plants, and we nearly accomplished the analysis of the first T-DNA tagged gene in the *CH42* locus of *Arabidopsis* chromosome 4. This breakthrough was accompanied by a success of *Arabidopsis* transformation and characterization of mutant genes also in other laboratories, and brought long-awaited NSF support for George. He gained permission to continue working for five more years at the University of Missouri. The success vitalized him. Full of energy and optimism, we continued hunting for new mutants and new principles.

He was 70 when he became Professor Emeritus, but he could barely accept that he had to stop all experiments in the lab. He was very bitter. It was my turn to cheer him up. Together with Jeff Schell and Nam-Hai Chua (Rockefeller University, New York), we edited a handbook entitled *Methods in Arabidopsis Research*. Then, with the help of the European Molecular Biology Organization (EMBO), we organized a training course on Advanced *Arabidopsis* Molecular Genetics in honor of George's extraordinary efforts and contributions, which led to the acceptance of *Arabidopsis* as the model plant of genetics and molecular biology during the early 1990s. Many who contributed to the start of the first international coordinated *Arabidopsis* project wrote chapters in the book and attended the course as lecturers. I was glad to see him again in the greenhouse teaching students, telling anecdotes, and discussing science with the new generation of *Arabidopsis* researchers.

When visiting him three years later, having in hand our freshly printed *Cell* paper on the recognition of the essential hormonal function of brassinosteroids, he told me: "Now I see that the new generation does

*this job well and I'm too old to compete. But I think that I found something to do, which might be useful.*" George learned computing from his daughter Mari, and started a huge project based on his extraordinarily wide knowledge in genetics and other fields of biology. For 1998 he assembled over 18,000 genetic concepts and terms, 600 illustrations, and over 1,000 references to books and databases on 1,142 pages of a *Genetics Manual*, which is an extremely useful encyclopedic handbook, the first of its kind. Last, we met personally in 1996, when George as Fulbright Lecturer trained Ph.D. students at the Universities of Keszthely and Budapest in Hungary. Since then and from time-to-time, we communicated only through the Internet. I received few letters from him and I thought that he spent his well-deserved free time with his beloved granddaughters Paige, Grace, and Anne. This turned out to be only partially true. Some days ago, a sweating mailman brought a heavy parcel from him with no letter as usual, but a book inside: George P. Rédei, *Encyclopedic Dictionary of Genetics, Genomics and Proteomics*. I found his message in the Preface, where he cited the Nobel-laureate geneticist H. J. Muller: "*Must we geneticist become bacteriologists, physiological chemists and physicists, simultaneously with being zoologists and botanists? Let us hope so.*" Then he continues: "*The vision of genetics today is not less than the complete understanding of how cells and organisms are built, how they function metabolically and developmentally, and how they evolved. This requires the integration of previously separate principles based on diverse concepts and tongues.*" I fully share George's optimism and realize that he is "only" 82, yet full of energy. Therefore, I'm looking forward to see the third edition of his book, this universal treasure of genetics!

## **FROM CHILDHOOD THROUGH WAR AND STALINISM TO IMMIGRATION**

George Rédei was born in 1921 in Vienna, but he grew up in Hungary, where his father received a job as an agronomist. The large estate on which his father was employed practiced progressive agriculture involving crops, animals, and industrial processing of products. George's father read Hungarian and German professional journals and during the 1920s contributed to them on various topics, including the hybrid vigor in crosses of maize. He regularly invited scientific consultants, among them Carl Fruwirth, a polyhistor professor of Technische Hochschule in Vienna, who published a *Handbuch of Pflanzzüchtung*, the first modern handbook of plant breeding. Fruwirth, who regularly visited their home,

was a reserved old man with a long beard and was greatly admired by young George. Perhaps this was the first motivation that induced George to become a polymath.

George attended the “Benedictine Realgymnasium” (i.e., high school) in Pápa, where he graduated with an “A” average in 1939. Although his interest was attracted to the humanities, languages, literature and law, his family objected to his pursuing college studies in these fields because of economic reasons. His brother was a highly regarded young painter and illustrator. Thus, his parents felt that George had better start working on their small farm in order to secure financial means for both of them. To find some satisfaction, George performed some breeding experiments with angora rabbits and soon won blue ribbons with several of his animals at national exhibitions. In 1941, he sold his rabbits, making enough money to pay for his further education in the College of Agriculture at Magyaróvár, the alma mater of his father. The war interrupted his studies. He had to work as a lumberjack and later as a forced laborer in the hellish “cinder space” of a large coal-fired power plant. The war took away his brother, who died in a Soviet prisoners’ camp, and also his beloved parents, leaving him completely alone. When he managed to return home with great difficulties in 1945, he found an empty house, but enough grain to start farming. Thanks to his good sense of agronomy, he survived the after-war famine and managed to make enough money to finish college.

In 1948, George was classified “kulak,” his farm was confiscated and merged into a cooperative (i.e., the Hungarian version of a Russian “kolhoz”). Accidentally, he learned that the National Institute of Plant Breeding launched a special course to prepare students for a research career in civil service. When he decided to make a trip to Budapest, he found that there was no longer a vacant training spot available. Fortunately, the Chief of the sponsoring agency, the Research Division of the Ministry of Agriculture, was willing to interview him and gave him permission to enroll without stipend. When telling me this story, George added a remark to characterize conditions of life in Stalinistic Hungary: *“I was extremely lucky to acknowledge the acceptance, because on the next day my benefactor was arrested by the state security police on the basis of a false accusation and thrown into jail for several years without any court procedure.”*

George completed the course with the highest grade among his peers and was offered a job with a regular stipend of “excellence” that was almost equal to a monthly salary. One of the greatest influences in George’s life was his acquaintance with Professor Barna Györffy, an excellent geneticist, during the course. As George recalls: *“He has been*

*the most knowledgeable person I have ever met. He was also the kindest person. It was the most fortunate event in my professional life when Professor Györfy accepted me as a graduate student in 1953 in the Institute of Genetics of National Academy of Sciences in Budapest.*” Until 1953, George was employed as research assistant at an experimental station. During the days, he worked in the nurseries under the guidance of an eminent plant breeder, Vilmos Teichmann, who was a student of Erich von Tschermak-Seysenegg, one of the rediscoverers of Mendelian laws. In the evenings, he turned into an accountant and a payroll clerk. Although he disliked it, he did his job very well, which caught the attention of his supervisors. Against his will, soon he was promoted to be a Program Director of Plant Breeding and Genetics in the Ministry of Agriculture with the expectation that he would follow the official doctrines of Lysenkoist genetics. To keep his brain trained, during the weekends he worked as a translator of English, German and French journal articles, and took a day off weekly to escape and read science in the library.

Although the power of Hungarian dictator Rákosi had weakened by 1953, George had to carefully select his first research subjects, because modern genetics was banned in Hungary as in the Soviet Union, and Lysenko’s opponents were effectively persecuted. His first research efforts were concerned with the inheritance of fruit weight in tomato. He observed that the average of segregating  $F_2$  displayed a geometric mean of parents and constructed a heuristic model, assuming multiplicative effects of alleles and additivity of contributions of loci examined. In his first paper, he showed that this model explained remarkably well his experimental data in about two dozen crosses (Rédei 1949). As a practical breeder at that time, he was advised to work on wheat-rye hybrids and, to his surprise, succeeded in creating some hybrids with *Triticum turgidum*. These initial breeding studies were continued by his good friend, Dr. Árpád Kiss, an exceptionally skilled research worker, who later produced hundreds of agronomically useful hexaploid and octaploid *Triticale* lines (Kiss and Rédei 1952; Bona and Kiss 2002). George was interested in practical and theoretical aspects of heterosis, which proved to be important in maize production. Outcrossing in rye was considered not advantageous (Roemer and Rudorf 1939; Kress 1951), but George demonstrated in 60 combinations of 17 diploid rye cultivars that the best hybrids surpassed the parentals by up to 35% (Rédei et al. 1954).

In 1953, George was instructed by the Ministry to reproduce the reports of T. D. Lysenko, who claimed that spring planting stably converts winter wheat into a new cultivar, which does not need vernalization anymore. The results showed that only 2 of 387 winter wheat

cultivars responded to this type of selection with an annually decreasing extent. Both of these cultivars originated from crosses between winter and spring wheats many years before. Therefore, it became obvious that commercial wheat cultivars are genetically not pure lines and thus the Lysenkoist theory failed under exact tests (Rédei, Györfy, Makó and Váróczy 1953). At the request of I. E. Glushchenko, George agreed to a Russian translation and publication of his paper in the *Izvestiya Akademii Nauk SSSR*. Upon back-translation of the Russian article, it turned out that the editor, Gluschenko, altered the text to fit to the Lysenkoist ideology.

After joining Professor Györfy, George continued his studies on the hybridization of distantly related species. With the aid of embryo culture, he could raise hybrids from crosses between *Triticum durum* and rye (Rédei 1955). As such distant crosses led to endosperm degeneration, he started cytological and physiological studies on embryo and karyopsis development (Rédei and Rédei 1955a). For the first time, he obtained mature wheat plants by a combination of ovary and embryo cultures (Rédei and Rédei 1955b, 1955c). He also made considerable attempts to identify growth factors critical for endosperm development (Rédei 1955c). Some earlier reports indicated that the milky maize endosperm (Nétien and Beauchesne 1953) and coconut milk (Schantz and Steward 1952) contain some growth promoting substances. Therefore, George and his wife Magdi, who worked as a technician in the same institute, started to search for growth promoting substances by fractionation of maize, wheat and barley endosperms, as well as carrot tissue cultures (Györfy et al. 1955). Their ultimate goal was to proceed from single cells to regeneration of fertile plants *in vitro*, in order to do genetics with plant somatic cells. Roger J. Gautheret (1959) cited these early research efforts at length in the 2nd edition of his plant tissue culture monograph. Even upon discovery of kinetin by Folke Skoog (Miller 1961), G. Doby (1965) referred to George's thesis and publications in his plant biochemistry book as pioneering achievements in tissue culture research.

In 1955, George completed his thesis work and started to look for a new experimental tool that would facilitate research in classical and biochemical genetics. He read some papers of F. Laibach, who successfully regenerated flax from embryo cultures, and thereby also became familiar with Laibach's cytological studies on a weed called *Arabidopsis* (at that time *Stenophragma thalianum*). Laibach favored this plant for genetic and developmental studies because he observed that *Arabidopsis* has only a few chromosomes ( $n=5$ ), a short life cycle, high seed yield, and can be easily crossed and cultivated in Petri dishes and test tubes. Prof. Laibach's collaborator, Erna Reinholz (1947), at the University of

Frankfurt also succeeded in inducing mutations by X-radiation in *Arabidopsis*. Given these advantages, George recognized that *Arabidopsis* is an ideally suited model plant for genetic studies. With the help of Prof. Györfy, he obtained seed samples from Friedrich Laibach in 1956 and had just initiated some radiation experiments, when an uprising broke out in the country. At that time, he worked at the Agricultural Research Institute in Martonvásár, close to Budapest. When the Russian tanks circled the capital in November, many of the staff decided to depart to a sugarbeet-breeding institute at Sopronhorpács, in the vicinity of the Austrian border. After the last dramatic call for international help by the prime minister, Imre Nagy, was broadcasted, George and others decided to cross the border. They lived in a refugee camp for a couple of months until January 1957, when George got permission to immigrate to the USA and work on a temporary basis as an assistant professor at the University of Missouri. As he was passing through the agricultural safety check, he honestly declared that he carried in his pocket a vial with *Arabidopsis* seeds. Fortunately, the officer never heard about this unimportant plant and did not find it in the list of prohibited materials.

### **ARABIDOPSIS: A STRANGER IN THE NEXUS OF PLANT GENETICS IN COLUMBIA, MISSOURI**

At the University of Missouri, Dean John H. Longwell assigned the former laboratory space of Barbara McClintock to George and generously permitted him to conduct research in any field of genetics of his choice. George continued his experiments from the point where he had finished in Hungary. Radiation mutagenesis offered a possibility to gain insight into the nature of the gene as anticipated by Timoféeff-Ressovsky, Zimmer and Delbrück (1935). Now, in addition to chemical mutagens, which became popular at that time (Westergaard 1957), radiomimetic agents and carbonyl compounds discovered by Auerbach and Robson (1944) and Rapoport (1946), respectively, were all within his reach. Next to his door were located L. J. Stadler's old X-ray machine and greenhouse. With his appointment, he received an annual salary of \$5,000 and a research budget of \$300 to equip the lab and cover all operating expenses for a year. In a storage area, he found a few pieces of glassware and test tube racks, and some clay pots in the greenhouse. He began to work within days. Once, he told me the following story from those days: "*Shortly after my appointment, a new department chairman arrived. Everybody forgot to introduce me to him, as I looked very busy. About four months later the chairman, Emmett Pinnell, came over to my*



Fig. 1.1. George P. Rédei and Barbara McClintock in 1978.

*lab. I had to admit not knowing who he was! He actually enjoyed my response and quipped: ‘I must be a damn good chairman if you do not know about me even after 4–5 months.’ And he was! He had been always most helpful whenever I needed him, but never imposed any burden on me. Although very few people occupied the building, I found a very vibrant research activity. I remain indebted to Ernie and Lotti Sears for the intellectual atmosphere secured around them during the years and until their death.”*

George’s primary aim was to induce auxotrophic mutations in *Arabidopsis*, although several of his colleagues warned him that he might follow a mirage. After screening over 2,000 irradiated single families, he found some interesting mutations, but none of them responded to complete nutrition. The July temperature was merciless in the greenhouse. Thus, on his wife’s urging, he took a week of vacation in the Rockies. Upon return, anticipating the worst, he rushed to look at his plants growing in test tubes on minimal medium. One of the families segregated several bleaching plants, but with an odd ratio, which was puzzling. When planting the same family on various vitamins, he observed that thiamin restored normal growth of the bleaching mutants. Further analysis revealed that the auxotrophs were deficient in the synthesis of 2,5-dimethyl-4-amino pyrimidine. Within weeks, he solved the rest of the

puzzle. The pyrimidine auxotrophy locus was closely linked to an unusual female gametophytic factor mutation, which caused approximately 1:1 segregation (Rédei 1960). Within a year, he identified a mutation that caused auxotrophy for 4-methyl-5- $\beta$ -hydroxyethyl thiazole, another precursor of Vitamin B<sub>1</sub> (Rédei 1962a). By 1963, he characterized five additional thiamin auxotrophs and submitted a manuscript to the *American Journal of Botany* (Rédei 1965b). As George remembers: “*This paper was lost in the editorial office and its publication was delayed by two years. One of the reviewers commented that there are numerous auxotrophic mutations in higher plants. Upon my request of naming at least one of them, the Editor informed me that the reviewer made a mistake, as he confused Arabidopsis with Neurospora. Actually, even 40 years later, these and other, subsequently identified thiamin mutants of Arabidopsis are the only obligate auxotrophs in angiosperms except tomato.*”

### **EXPLOITING ARABIDOPSIS MUTANTS TO UNCOVER NOVEL GENE FUNCTIONS AND GENETIC PRINCIPLES**

In 1965, Steve Li joined Rédei’s laboratory. By 1967 they had accumulated over 60 thiamin auxotrophs, but failed to find auxotrophy in any other metabolic pathway suggesting a functional redundancy of corresponding genes (Li et al. 1967). The thiamin mutants occurred at several loci and ranged from a few leaky mutants to obligate auxotrophs (Rédei 1965b; Li and Rédei 1969e). They provided very useful tools for the study of reversion (Rédei 2003), estimation of mutation rate (Li and Rédei 1969c; Rédei and Li 1969b), the first direct observation of glucose effect in a higher plant (Li and Rédei 1969d), as well as for the study of allelic complementation (Li and Rédei 1969b), and analysis of overdominance (Li and Rédei 1969a; Rédei 1962b).

Li and Rédei continued to characterize the female gametophyte factor *GF1*. The *gf1* mutation showed linkage with the pyrimidine (*py1*) mutation. By that time, George identified five mutations in the same linkage group. This was the first reported case, when linkage was used in *Arabidopsis* for genetic analysis. The segregation ratio for *py1* in crosses with wild type was 12923:4290, but in crosses with the *gf1* mutant it was 5726:5968. All other linked markers in the same chromosome displayed distorted ratios according to their map distance from the *GF1* locus, yielding the first ever constructed *Arabidopsis* chromosomal linkage map with the *gf1-er1-py1-as1-su1* markers. It was expected that the fruits, in which the segregation of *gf1* mutation was

examined, should show 50% seed set due to total absence of female transmission. By examining over 400 fruits with more than 12,400 seeds, however, George found that the total seed set exceeded 60%. This appeared an impossible outcome for Mendelian segregation. Sectioning the ovules revealed twin megaspores and embryo sacs in some of the plants, suggesting that the higher than 50% seed set must have been brought about by megaspore selection. The megaspore tetrads with wild type *GF1* constitution in the basal position were preferentially selected to contribute to the formation of the egg (Rédei 1965a,c).

During the early 1960s, George identified some X-ray mutants that displayed late onset of flowering and altered photoperiodic responses. Some of the mutants produced 20 times higher dry weight and 10-fold higher seed yield than the wild type. All late flowering mutants (*gi1*, *gi2*, *ld1* and *co1*) were recessive under long-day conditions, but *co1* was unusual, as it displayed a change of dominance under short day. As late flowering ecotypes of *Arabidopsis* are predominant in natural ecological conditions, George performed a population genetic analysis to test their selective value under laboratory conditions. In segregating families started with F<sub>1</sub> hybrids of wild type and late flowering mutants, the wild type was practically eliminated (i.e., about 99% of the survivors were mutants) within about ten generation cycles. The estimated selective advantage of three independent late-flowering mutations was 1.3, 2, or >2, respectively. This was a very unusual finding for any mutation, particularly for X-ray induced mutations (Rédei 1962c). Consequently, George became interested to determine the nature of genetic change in these mutants. He could not detect larger deletions by cytological analysis, and the transmission of mutant alleles appeared perfectly normal (Rédei and Steinitz-Sears 1961). However, he observed that 8-azadenine (Hirono and Rédei 1966b) and 5-bromodeoxycytidine or 5-bromodeoxyuridine dramatically promoted the onset of flowering in some late-flowering mutants under short days (Hirono and Rédei 1966c). *Arabidopsis* is not an obligate long-day plant, but the onset of flowering is much delayed under short-day conditions. By characterizing the physiology of flowering response, George found that flowering readily took place in about 7 weeks in complete darkness in glucose supplemented liquid medium. After 9 weeks of culture in total darkness, some plants even developed fruits with seeds, which however failed to germinate.

The time to develop flower primordia is usually characterized by the number of rosette leaves. According to George's observations, the late-flowering mutants did not significantly differ from the wild type. This observation on the *ld1/ld1* homozygote was particularly surprising because this mutant never developed flower primordia under short days

(i.e. 9 hours daily illumination). Therefore, George concluded that light is not the epigenetic factor required for the synthesis of flower-inducing substance. Rather, he proposed that prolonged cycles of daily illumination are conducive to the inactivation or breakdown of an inhibitory protein or metabolite synthesized under short-day conditions. As the response of wild type and late-flowering mutants in dark cultures were similar, he argued that an early step of epigenesis, leading to initiation of flowering, is probably controlled by the length of illumination, and not by locus-specific florigens.

George tried to exploit his observation that halogenated nucleoside analogs dramatically shortened the time required to induce onset of flowering in all late-flowering mutants, but not in *ld1*, which did not respond to these analogs under short days. He performed extensive biochemical genetic studies with radioactive bromodeoxyuridine (BrDU) by fractionating methanol-acetone water extracts from wild type and mutants using thin layer and radioscanning gas chromatography. Although he failed to detect differential metabolism of BrDU in the late-flowering mutants, he found that BrDU could replace about 18–26% of thymidine residues in the DNA without causing a substantial mutagenic effect. Upon feeding the plants with BrDU and both  $^{14}\text{C}$ -arginine and  $^{14}\text{C}$ -valine, he found an increased incorporation of radioactive carbon into a non-histone protein fraction (Rédei et al. 1974). Based on our current knowledge, of course, the limitations of these experiments are evident. However, one should consider that these studies were pursued in the early 1970s before the birth of molecular biology. Nonetheless, the granting agencies did not appreciate George's excursions to biochemical genetics. As he recalls: "*In retrospect, I have no doubt that we were on the right track. The information on eukaryotic transcription factors was very limited at that time. The 1975 edition of the classic biochemistry book from L. Stryer did not even mention this term. In 1969 the NSF terminated the support of my research based on the recommendation of the Genetics Panel, which was convinced that it is not worthwhile to develop Arabidopsis because prokaryotes are more likely to contribute significantly to new knowledge. During the following decades I relied on the \$1,800 annual combined research and teaching support of the University of Missouri.*"

## STUDIES ON VARIEGATION

By 1964, George identified several *chlorina* (*ch*) mutations, which resulted in reduced chlorophyll b production (Hirono and Rédei 1963b;

Rédei and Hirono 1964). One of these *ch* mutations was mapped to chromosome 4 in a close distance from another mutation, which caused dwarfism with dark green leaf color. X-irradiation of plants heterozygous for these and other linked markers revealed the presence of single and twin spots on the leaves. In a few cases, seed-bearing shoots could be obtained from the mutant sectors, facilitating classical genetic tests on the sectors. This was of considerable interest because evidence for mitotic recombination did not exist in plants at that time, except for a single case suggesting somatic translocation in maize (Jones 1938). Using the *ch* and dwarf mutations in linkage with proper flanking markers, George demonstrated that during premeiotic recombination the genetic exchange generally, but not always, involved a reduced transmission of chromosome strands participating in the exchange (Hirono and Rédei 1965b). Thus, *Arabidopsis* was the first higher plant with verified X-ray-induced premeiotic recombination (Hirono and Rédei 1965a).

In the early 1960s, George also studied a recessive mutation, *immutant* (*im*), which caused an extremely high variegation depending on the intensity and duration of illumination (Rédei 1963b). Initially, he assumed that this phenotype was attributed to an active transposable element. However, this hypothesis turned out to be invalid because the progeny of green and white sectors were not different. When predominantly white mutant lines were grown in test tubes on 6-azauracil-containing medium, the chlorophyll and carotenoid contents of leaves increased. Exposure of seeds or plants to X-irradiation also conspicuously increased the extent of green sectors (Rédei 1967b). The white-green variegation persisted through mitotic divisions, but vanished after meiosis (Rédei 1967h). As expected, electron microscopic studies showed that chloroplasts in white cells lacked grana stacks of thylakoid membranes, but also the green sectors displayed abnormal thylakoid differentiation (Chung et al. 1974; Rédei 1975a). Further studies detected increased ribonuclease activity in the nuclear and chloroplast fractions of variegated leaf tissues, but not in plants that were grown in vitro in the presence of 6-azauracil (Rédei 1967a,b). In analogy with the 6-azauracil effect on the hereditary human syndrome orotic acidurias (Pinsky and Kroth 1967), George observed that 6-azauracil elevated the orotidine-5'-monophosphate decarboxylase activity in the variegated *im* leaves (Chung and Rédei 1974). Today, we know that *IM1* encodes a chloroplast homolog of mitochondrial alternative oxidase, which likely serves as a redox component in phytoene desaturation (Aluru et al. 2001; Joët et al. 2002). How *IM1* participates in the compensation of photooxidative damage is an intriguing question, which still awaits explanation, as does George's 35-year-old observations on the compensatory effect of 6-azauracil (Rédei 2003a).

## PLASTID MUTATOR

Inspired by Barbara McClintock's work on transposable elements, George aimed to activate silent transposons by chemical and X-ray mutagenesis, and thus continued to analyze several other variegated *Arabidopsis* mutants. In maize, Rhoades (1943) described an intriguing nuclear mutation, *iojap*, which causes variegation by affecting chloroplast differentiation. Röbbelen (1966) found a similar mutation (*am*) in *Arabidopsis*, which as *iojap* was characterized by alterations in chloroplasts development. It was conceivable that mutation of a nuclear gene could result in either activation of a transposable element or defective DNA repair in the chloroplasts. As transposable elements were already well studied in prokaryotes and chloroplast was considered of prokaryotic origin (Thorsness and Weber 1996; Millen et al. 2001; Traven et al. 2001), this assumption appeared to be worth testing.

By screening for variegated mutants, George isolated three independent mutant alleles of a gene in chromosome 3, which he named *CHM*, chloroplast mutator (Rédei 1973e). He described the first instance of testing allelism between mutations affecting chloroplast biogenesis. The classical allelism test is based on non-complementation/complementation of recessive nuclear mutations. However, as the *chm* mutation affected an organellar (i.e., plastid) phenotype, the conventional cross did not provide an unambiguous answer. Therefore, George combined one of the alleles, *chm2*, with an unlinked *as1* mutation affecting leaf shape and then crossed *chm2*, *as1* plants with wild type. The resulting  $F_1$  was then crossed with plants, which carried the second allele, *chm1*, in linkage with the *gl1* mutation blocking leaf trichome differentiation. In case the two independent *chm* mutations would have been non-allelic, the testcross progeny would not have displayed variegation. However, half of the testcross progeny was variegated, indicating allelism of *chm1* and *chm2* mutations. The *chm* mutation resulted in inhibition of chloroplast biogenesis at various stages, yielding white leaf sectors (Rédei and Plurad 1973). George demonstrated that after removal of the nuclear *chm* mutation and several cycles of selfing, homoplastidic mutants could be sorted out, which synthesized very low amounts of chlorophyll, but could be propagated on sugar-supplemented media. Despite intensive efforts, George could not detect rearrangements and point mutations of chloroplast DNA in the homoplastidic *chm* mutants. Today we know that the *CHM* gene encodes an *Arabidopsis* homolog of *E. coli* MutS protein that is involved in mismatch repair and recombination in bacteria. Remarkably, chloroplast defects of *chm* lines show co-inheritance with specific rearrangements in the mitochondrial DNA, which highlights a

yet-unknown aspect of coordinated regulation of chloroplast and mitochondrial biogenesis in higher plants (Martinez-Zapater et al. 1992; Abdelnoor et al. 2003).

## FRUCTOSE EFFECT

During his studies of chlorophyll deficient mutants (i.e., many of which could only be maintained on sugar-containing media), George observed that wild type *Arabidopsis*, *Hylandra*, and *Cardaminopsis* plants showed retarded growth on media containing 3% fructose (Rédei 1974e). As he was aware of hereditary fructose intolerance in humans (Froesch 1972), which was dramatically revealed by increased application of fructose as low caloric value sweetener, he made a short excursion to study the observed fructose effect. He found that fructose underwent substantial degradation during autoclaving, and that plants grown on autoclaved fructose media exhibited reduced amounts of chlorophylls, carotenoids, phospholipids, pyruvic and glutaric acid. By monitoring the activity of various enzymes involved in fructose metabolism, he found a significant reduction in the condensation reaction of fructose-1,6 diphosphate aldolase. He showed that fructose-1-phosphate aldolase, which is defective in human hereditary fructose intolerance, had no detectable activity in the studied crucifers, but the observed growth defect correlated with a suppressed synthesis of fructose-1-6 diphosphate aldolase in plants grown on autoclaved fructose media (Rédei 1973f,g, 1974e).

## MUTAGENESIS STUDIES

When choosing *Arabidopsis* as a genetic model, George realized that this plant is a better organism for studies of the mutation process in the diploid germ line than the majority of plant species. The major advantage of *Arabidopsis* is that it has a short life cycle and small size, which facilitates screening of very large populations. Being a good geneticist whose research budget was severely limited, George paid particular attention to developing procedures that yielded the largest number of independent mutations at the lowest cost. Therefore, he worked out a simple mathematical procedure to optimize the size of  $M_1$  and  $M_2$  populations in mutation experiments. He showed that theoretically it was most effective if only a single offspring was tested in  $M_2$  from each cell of the germline. This was seemingly a controversial idea, because if a recessive mutation segregates in a Mendelian manner, only 0.25% of the

tested sample would display the sought-after phenotype. By contrast, testing 24  $M_2$  progeny would increase the probability of detection of a recessive mutation to 0.999. Although this logic is of course correct, with simple mathematics George showed that examining a large number of offspring in the segregating  $M_2$  generation is actually deceptive under experimental conditions. He argued that the frequency of induced mutation at a particular gene is low (e.g.,  $\sim 10^{-3}$ ), thus only a small fraction of  $M_1$  individuals will carry the mutation desired. He stressed therefore that it is most important to treat with mutagen as large a number of germline cells as required by the expected rate of mutation and the expected rate of recovery of that mutation. Because in each germline cell only one mutation per gene is expected, and a second one is unlikely to occur more frequently than the product of the two independent mutation events (e.g., at the above assumed frequency at  $\sim 10^{-6}$ ), it is best to use a large  $M_1$  and examine only a single individual per each cell of the germline in the  $M_2$ . Since the production cost of a plant in the  $M_1$  and  $M_2$  generations may not be identical, he worked out the principles of how to make decisions in planning the optimal size of  $M_1$  and  $M_2$  in mutation experiments (Rédei 1974h, 1981; Rédei et al. 1984b; Rédei and Koncz 1992). Till today, plant researchers follow these guidelines to ensure the efficiency of low-cost mutant selection and screening experiments. George demonstrated that these procedures can suitably be applied not only for induction of genetic variations to obtain chromosomal markers and mutations for plant breeding purposes, but also for screening of T-DNA knockout mutations (Feldmann and Marks 1987), and testing chemical, physical, and environmental mutagens (Rédei et al. 1984b). In a test series, he studied 42 compounds, including mutagens, carcinogens and genetically inactive chemicals. The efficacy of mutagenic tests with *Arabidopsis* was compared with other prokaryotic and eukaryotic mutagen assays conducted within an international project by 62 laboratories. The outcome indicated a remarkable performance in the sensitivity and accuracy of the *Arabidopsis* test (Rédei et al. 1984c).

Based on the principle of fluctuation test developed by Luria & Delbrück (1943), which is generally credited as one of the most important contributions of bacterial genetics (Stent and Calendar 1978), George worked out a modified fluctuation test for *Arabidopsis*. In this mutagen test, George used random sampling of an average of 2 progeny per  $M_1$  plants yielding several hundred  $M_2$ s, which along with wild type controls were planted in hundreds of small pots in the greenhouse. The distribution of low-frequency-induced and spontaneous mutations observed in the individual pots was evaluated by fitting to the Poisson and expanded negative binomial distributions. The latter procedure

proved to be better, as the negative binomial reflected a joint outcome of separate Poisson series. The detection of mutations depended on the occurrence of mutations, sampling of the mutant cell progeny, the collection of seed output of  $M_1$  plants, and other random events. The difference between control and mutagen-treated series was ascertained by the log-likelihood method. The application of the fluctuation test permitted the determination of extremely low mutation frequencies with an unprecedented precision at high statistical significance (Rédei et al. 1984b; Acedo and Rédei 1984; Rédei and Koncz 1992). In addition, using half of the probability of Hardy–Weinberg distribution in the populations, George was able to estimate the frequency of undetected mutations (Rédei and Koncz 1992). Based on accurate calculation of induced mutation rates (i.e., either per locus or per genome), George estimated in 1982 that the *Arabidopsis* genome encodes 27,813 genes (Rédei 1982c). Sequencing the genome 18 years later suggested that *Arabidopsis* has 25,498 protein coding genes (*Arabidopsis* Genome Initiative 2000). However, reannotation of the genome by April 2003 ([ftp://ftp.tigr.org/pub/data/a\\_thaliana/ath1/Arabidopsis\\_release.v4.0.README](ftp://ftp.tigr.org/pub/data/a_thaliana/ath1/Arabidopsis_release.v4.0.README)) revealed that *Arabidopsis* contains 27,170 protein-coding genes, only a few hundred less than George estimated by measuring the mutation rates.

As only a few biological assays are available for detection of aneuploidy caused by environmental factors, George worked out a genetic test to detect chromosome disjunction. He took advantage of recessive mutations characteristic in the Neatby's virescent gene *v1* in the short arm of chromosome 3B of hexaploid wheat. E. R. Sears has earlier identified a centromere defect in this stock leading to nondisjunction. The *v1* allele is a recessive suppressor of pigmentation and displays hemizygous ineffective condition. The homozygotes express cream color, the hemizygotes are normal green, and the trisomics are white. On this basis, both losses and duplications of a locus at that critical chromosomal location are easily detectable. The appearance of single or twin sectors indicate the recovery of one or both products of nondisjunction, as well as deletions or duplications, in response to mutagenic treatments (Rédei and Sandhu 1998).

## GENETIC TRANSFORMATION

In the absence of grants, George had only \$3,500 of research support from the Missouri Agricultural Experiment Station during the early 1980s, which was obviously insufficient to perform modern research. In 1983, Jeff Schell, the Director of the Max-Planck Institute (Cologne), visited his

laboratory and invited him to Germany. In 1985, he spent six months in Cologne establishing with us the *Agrobacterium*-mediated transformation and T-DNA insertion mutagenesis techniques, which provided a simple tool for isolation and functional characterization of mutagenized *Arabidopsis* genes (Rédei et al. 1988). In 1989, we showed that the T-DNA is preferentially integrated into potentially transcribed chromosomal loci of transformed plants, indicating that it is a very efficient mutagen (Koncz et al. 1989a). In 1990, we published the first characterized T-DNA insertion mutation in the *CH-42* locus that encodes the ATP-binding subunit of protophorphyrin IX Mg<sup>2+</sup>-chelatase involved in chlorophyll biosynthesis. George has located the T-DNA tagged gene, which he named *CS*, to chromosome 4 by trisomic analysis and allelism test with the X-ray-induced *ch42* mutation. Subsequent mapping involved scoring over 80,000 seeds in F2 fruits to identify the yellow *cs* progeny, which provided a resolution of about 10 to 25 kb in terms of physical distance (Koncz et al. 1990a).

Our further experiments concentrated on the study of T-DNA integration mechanism. Sequence analysis of T-DNA junctions and genomic target sites indicated that the T-DNA is integrated into plants' chromosomes by illegitimate recombination. The T-DNA recombination model suggested that the VirD2 protein, which is covalently attached to the 5'-end of single-stranded T-DNA intermediate (i.e., the integrating T-strand), plays a chief role in the recognition of chromosomal target sequences (Mayerhofer et al. 1991; Koncz et al. 1994). Although it took some time to explain this observation, recently we could demonstrate that the VirD2 protein interacts with the TATA-box binding TBP protein and with a protein kinase (CAK2) component of the RNA polymerase II associated TFIIF general transcription factor complex. As these proteins are involved in transcription-coupled DNA repair, the interaction of VirD2 with TBP and TFIIF well correlates with the observed frequent integration of T-DNA into transcribed chromosomal domains (Bakó et al. 2003).

Subsequently, we searched with George for insertion mutations causing so-called genetic dwarfism, which is characterized by cell elongation defects that cannot be corrected by any known plant hormone. We have found a beautiful dwarf mutant that showed constitutive photomorphogenesis in the dark (i.e., except for chlorophyll biosynthesis, the mutant developed as light-grown plants in the dark). The analysis of T-DNA tagged *cpd* (*CONSTITUTIVE PHOTOMORPHOGENESIS AND DWARF*) locus revealed that the gene encoded a cytochrome P450 enzyme, which showed remarkable homology to animal steroid hydroxylases. As it was known for a while, primarily from the work of Japan-

ese scientists, that crucifers and other plants produce growth-promoting steroids, called brassinosteroids, we performed some chemical complementation experiments. These studies showed that the *CPD* gene encoded P450 enzyme, CYP90A1, is a steroid C23-hydroxylase, which is essential for conversion of cathasterone to teasterone in the biosynthesis pathways of brassinosteroids (Szekeres et al. 1996). These results indicated that brassinosteroids are essential plant hormones and opened a new research field aiming at the study of regulatory functions of plant steroid hormones.

As we were primarily interested in regulatory mutants that affect multiple qualitative and quantitative traits, we started to characterize a T-DNA-tagged gene that we called *PRL1* (*PLEIOTROPIC REGULATORY LOCUS 1*). The *prl1* mutant displayed many alterations in normal metabolism, development, hormonal regulation and gene expression, which all were caused by inactivation of a nuclear regulatory protein carrying seven WD-40 (tryptophan-asparagine) repeats (Németh et al. 1998). From the breeders' point of view, it was highly interesting to learn why this single gene mutation causes altered leaf development, overproduction of chlorophyll and anthocyanins, increased production of free glucose, fructose and sucrose, and accumulation of starch, as well as hypersensitivity to cold stress and plant hormones auxin, cytokinin, ethylene and abscisic acid. A key to understand the regulatory function of PRL1 derived from the observation that many stress-regulated genes, which are either positively or negatively modulated by glucose repression, showed highly increased expression in the *prl1* knockout mutant. PRL1 was found to interact with several important signaling proteins, among them with AMP-activated protein kinases (AMPKs) that play a central and conserved role in the regulation of glucose repression and stress responses in eukaryotes (Bhalerao et al. 1999). PRL1 turned out to be an inhibitor of plant AMPKs, which were found in so-called transcription co-activator complexes. In these co-activator complexes, AMPKs interact with histone arginine methylases, which are also PRL1-binding regulatory proteins. In addition to modulating transcription, PRL1 also affects another function of AMPKs. In plants, the AMPK kinases occur in stable association with the 26S proteasome and SCF (Skp1-cullin-F-box) E3 ubiquitin ligases that control ubiquitination dependent proteasomal degradation of important regulatory factors (Farrás et al. 2001). By inhibiting the functions of AMPKs, PRL1 plays a role in the regulation of stability of several transcription factors involved in hormonal and metabolic signaling.

To identify T-DNA mutagenized genes on a large scale, in 1999 we started to sequence the junctions of T-DNA tags isolated from George's

mutant population. We surveyed 1000 T-DNA insertions regarding their chromosomal locations. The data showed that only 4.7% of the insertions landed in interspersed, centromeric, telomeric regions, and rDNA repeats. By contrast, open reading frames contained 35.4 % of the inserts, and of these 62.2% landed in exons and 37.8% in introns. In accordance with our previous observations, we found preferential integration of the T-DNA in 5' and 3' regulatory domains of genes. In summary, almost half of the T-DNA insertions caused knockouts in *Arabidopsis* (Szabados et al. 2002). To reach our ultimate goal, we completed a saturation T-DNA mutagenesis by generating 92,600 transgenic plants that carry over 220,000 insertions in the *Arabidopsis* genome. This collection now allows the identification of a gene mutation with an estimated probability of 0.77 (Rios et al. 2002), which was one of our ultimate goals when we started the T-DNA mutagenesis project with George in 1985.

#### **AFTER “RETIREMENT”**

In 1991, George retired and donated approximately 6,700 mutant stocks and genetic constructs to the *Arabidopsis* Resource Center at Ohio State University. The Columbia wild type and Landsberg erecta (Ler) stocks from his laboratory are the most widely used standard types for research. The former became the first higher plant with completed genome sequence.

Besides experimental genetics, George has always been interested in the history of the emergence of genetic ideas and their experimental foundations. As he said: “*I always felt that I need some familiarity with the developmental course of genetics as a whole and not only with the history of research of my objects, to be able to make decisions regarding my goals. Scientific research is distinguished from crafts by the originality of its approaches and ideas. Good science does not repeat its facts, but aims at the unexplored. Historical retrospect guides the research workers toward new horizons.*” In 1973, George composed an annotated list of 477 papers on genetics that, according to his judgment, have made the most important contributions to the development of the field (Rédei 1974a). As he recalls the fate of this manuscript: “*Two journals rejected it by editorial comments that such a paper would not be of interest to the readers. Eventually, I submitted it to Professor Hans Stubbe, who himself was a highly regarded historian of genetics. He accepted it for Biologisches Zentralblatt, which did not have a particularly high impact factor (i.e. 0.224). Yet, after it appeared in print, I received more*

than 400 requests for reprints, indicating that not all editorial judgments are perfect.”

Recently, in two invited papers George has surveyed some of the historical oddities of genetics along with some of the current developments (Rédei 2002) and controversies, as well as the future potential of long-term selection for quantitative traits (Rédei 2003b). His first comprehensive review on biology and genetics of *Arabidopsis* appeared in print in 1970 (Rédei, 1970c) and this was followed by updated reviews (Rédei 1975a,c,d). The latter paper in *Annual Review of Genetics* attracted to *Arabidopsis* a new generation of research workers, who made major contributions to the field (Pennisi 2000). The major historical papers on genetics of *Arabidopsis* were summarized in Rédei (1992c), whereas a comparative review on the historical development of *Arabidopsis* genetics within the context of relevant milestones of genetics was published in 1994 (Koncz and Rédei 1994). He has also written tributes to L. J. Stadler (Rédei 1971a), A. Sturtevant (Rédei 1971d), B. Györfy (Rédei 1986) and E. R. Sears (Rédei 1992) analyzing the impact of their contributions to genetics.

## TEACHER AND EDITOR

George is not only an excellent geneticist but, as I also experienced, a warm-hearted, precise and honest teacher. Through his career at the University of Missouri, he always provided detailed lecture notes to students in all classes he taught. He taught formal one-semester courses of Basic Plant Genetics, Analytical Genetics, Genetic Engineering, Evolution of Genetic Concepts, Plant Cell and Tissue Culture, and Genetic Bases of Physiological Responses. He lectured for three years in a graduate-level course at the ELTE University of Budapest, and was a Fulbright Lecturer for a semester in Keszthely, Hungary. His book *Basic Plant Genetics* (1,191 pages) was published in five editions, each time revised and updated. His textbook *Genetics* (736+36 pages) was translated into Hungarian and Chinese, and during the past decades has been used by over 50,000 students worldwide. In 1998, he published his *Genetics Manual. Current Theory, Concepts and Terms* (1,141 pages). *The Encyclopedic Dictionary of Genetics, Genomics, and Proteomics* (1,392 pages), one of the most comprehensive books of its kind, appeared in print in 2003. For four years, George was the founder and editor of the Hungarian plant-breeding journal *Növénytermelés*, and served as co-editor of the now defunct *Arabidopsis* Information Service, the first and only journal of *Arabidopsis* researchers during the pioneering time. In 1969, George

initiated with Gordon Kimber the annual Stadler Genetics Symposia, and then organized its meetings and edited its proceedings for 15 years in Columbia, Missouri.

## IMPACT

For nearly twenty years, George Rédei was almost alone in the USA to appreciate the extraordinary value of his beloved genetic model organism *Arabidopsis*. Today more than 12,000 people work in the field of *Arabidopsis* research, contributing to progress in plant biology, genetics, breeding and biotechnology (Somerville and Koornneef 2002). By 2003, more than twice as many molecular genetics papers were recorded in Medline using *Arabidopsis* rather than maize, another higher plant with a much longer tradition in genetics. In one of his papers (Rédei 1992c) about science history, George says: “*History has a meaning only in shaping the future.*” This is exactly what he achieved through the history of his scientific career. And the use of *Arabidopsis* in plant genetics will continue to provide tribute to his pioneering contributions. Personally, I remain ever indebted for his help as friend, teacher, and mentor.

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