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The Rockefeller Foundation's International Program on Rice Biotechnology

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Rockefeller Foundation's
International Program on Rice Biotechnology

Introduction

The goals of the Rockefeller Foundation's International Program on Rice Biotechnology are: 1) to assure that new techniques for crop genetic improvement based on advances in molecular and cellular biology are developed for rice, 2) to facilitate the transfer of these biotechnologies to rice breeding programs in the developing world for use in producing improved varieties that address priority needs, and 3) to help build the scientific research capacity necessary for continued development and application of new rice genetic improvement technologies in selected developing countries.

The Foundation's Trustees approved the program in December 1984 with the realization that a 10- to 15-year commitment of $3-5 million/yr might be required. Research at several laboratories began in 1985, and others have been added as the program has evolved and expanded. Over 50 projects are now supported with collaborative research conducted by scientists from throughout the world. Further expansion of the program in developing countries is anticipated. The program evolved from earlier Foundation work in agriculture and was designed keeping in mind principles learned from earlier programs.

Building on Solid Foundations. The International Program on Rice Biotechnology builds upon and is a continuation of the Foundation's long-term commitment to promote more effective use of science and technology to improve food production and living conditions in the developing world. As early as 1913, the Foundation's International Health Board supported research to increase agricultural productivity in China as a means of improving the nutritional status of the population.

From 1932 to 1959 the Rockefeller Foundation committed nearly $50 million to research in experimental biology. Under the direction of mathematician Warren Weaver, that program helped to bring the tools of mathematics, physics, and chemistry to the study of living organisms. This early research in biochemistry and biophysics was critical in laying the foundations for modern molecular genetics. Dr. Weaver has even been credited with coining the term "molecular biology" (Kohler, Robert E., 1976, Minerva Vol. 14, No. 3, pps. 279-306).

The Foundation's major international field research programs in agriculture began in Mexico in 1943 under the leadership of J. George Harrar. Initially, the research was diverse and expansion occurred on a country-by-country basis. As part of the Mexican program, high yielding semi-dwarf wheat varieties were developed by Norman Borlaug and colleagues. When tested in India and Pakistan, the Mexican wheats performed well and were widely adopted by farmers. Thus, it was shown that improved seed could provide an effective mechanism for delivering the benefits of science and technology across broad regions of the developing world.

To apply this same strategy, often referred to as a germplasm-based technology, to additional crops and additional countries, the Rockefeller Foundation joined with the Ford Foundation in establishing the International Rice Research Institute (IRRI) in the Philippines, the International Center for Maize and Wheat Improvement (CIMMYT) in Mexico, the International Institute for Tropical Agriculture (IITA) in Nigeria, and the International Center for Tropical Agriculture (CIAT) in Colombia. The accomplishments of these institutions have been impressive. High yielding rice and wheat varieties, for example, are now grown on over 55 million hectares - or one-third of the area planted to these cereals in the developing countries. Funding for these international agricultural research institutes and several

others is now provided by many donors and coordinated by the Consultative Group on International Agricultural Research.

Despite the success of these institutes, it became apparent in the 1970s that their research output often did not flow automatically to national programs. To assist national agricultural research programs in using institute technologies and in generating their own, the Foundation established the International Agricultural Development Service in 1975. In 1984, IADS was merged with two other organizations to form the Winrock International Institute for Agricultural Development which, now completely independent of the Foundation, continues to provide services to help strengthen national agricultural research programs.

In 1982, a major review of the Foundation's agricultural program was undertaken with the assistance of external consultants. These advisors praised past accomplishments and recommended that the Foundation's agricultural program be continued but restructured around three new thrusts. One would be a major commitment to research on the application of molecular biology to plant breeding in developing countries. This was a logical sequel for the Foundation's agricultural program, building upon previous investments in both fundamental biological research and in development of a research capacity for crop genetic improvement in the developing world. The Foundation's trustees approved these recommendations, and the staff began the process of designing the program.

Focus on Rice. In selecting a focus for a program that would apply molecular biology to plant breeding and direct the benefits to the disadvantaged in developing countries, Foundation officers sought: 1) to identify an important need that was not being addressed by others, 2) to attain a high degree of synergism amongst the various activities to be

supported, and 3) to have a strategy which would allow for eventual Foundation disengagement. Three types of options were given serious consideration. One, suggested by the external review team, would have provided support for crop-focused programs at each of several selected universities. Each university would combine molecular biology with plant breeding for its selected crop and establish linkages with the appropriate international agricultural research institute.

A second option would have provided support for research conducted collaboratively by developed country and developing country institutions on the molecular genetics of agronomic traits uniquely important for crop production in the developing world. Resistance to maize streak virus would be an example. Under this option, Foundation support would focus on identifying and cloning genes that could instill the desired traits. Development of the techniques for gene transfer would be left to others.

The third option was to focus the Foundation's program on a single crop and to develop a fully integrated program ranging from fundamental research through to application of new techniques in breeding, and including socioeconomic evaluation.

Figure 1 and Table 1 indicate the type of assessments made in considering these options. Figure 1 presents estimates of food crop production in the developing world on a dry weight basis. The cereals account for nearly three-quarters of the production, with rice alone accounting for one-third. Of the non-cereals, cassava and sweet potato have the highest third world production. The first column in Table 1 is based on Figure 1 and indicates relative production levels. The other columns were prepared following a survey on research being conducted on each crop and required a fair amount of subjective judgement.

We believe an effective Rockefeller Foundation program could have been developed using any one of the three options considered and/or around any one or more of the crops listed in Table 1. Foundation funds are limited, however, and some focus was necessary. At the Rockefeller Foundation, this type of tough program decision is usually made by the Division Director and it was Alva A. App, then the Director for Agricultural Sciences, who recommended to the Trustees a comprehensive vertically integrated program focused on rice.

Looking at Table 1, the rationale for selecting rice can be summarized as follows. In terms of production and consumption, rice is by far the most important crop in the developing world. Moreover, projections indicate that, in the 1990s and beyond, in many developing countries growth in demand for rice will move ahead of its supply. Rice breeding programs are mature at the international centers such as IRRI and in several developing countries. There are even some who say these breeding programs are reaching a point of diminishing returns with regard to further improvements that can be made using conventional methods. Rice also turned out to be a highly neglected crop with regard to biotechnology. When we conducted the survey in 1983, we could not find a single research program in the U.S. or Europe studying the molecular genetics of rice. In the West there were only a few modest research efforts on rice tissue culture. Even in Japan there was surprisingly little research on the molecular genetics of rice, although some Japanese universities and corporations have since initiated such programs. The only category where rice did not score high was the one concerning near-term opportunities. We realized that a program focused on rice would require a considerable investment of time, effort and resources before significant results would be seen in the field. In our opinion, the other factors outweighed this concern. Moreover, there would be the option of working on other crops once the rice program had been established. Within the rice focus, a deliberate

effort, described later, was made to balance priorities among traits that would be applicable in poor production environments and traits that would contribute most to increasing production.

Wide Hybridization

As an important component of the international program on rice biotechnology, the Foundation is supporting a significant expansion of the wide hybridization program at IRRI, including the work of Foundation field staff cytogeneticist Lesley Sitch. There are 22 Oryza species, only two of which are cultivated. There are six known genomes, A-F, in the genus, including tetraploid species, as well as diploids. As indicated in Table 2, these wild Oryza species contain many desirable traits. The objectives of the wide hybridization program are to 1) transfer useful traits from wild relatives to cultivated rice, 2) generate new variability for use in rice improvement, 3) transfer wide hybridization technology to national rice improvement programs, and 4) lay the foundations for use of new molecular and cellular techniques at IRRI.

The wild species of rice, by definition, do not normally cross with cultivated rice. It is necessary to use a variety of techniques to stimulate pollination, to nurture the otherwise abortion-prone embryo through cell divisions to form a mature F_1 hybrid plant, to overcome sterility problems in the hybrids, and, finally, to produce a breeding line with desired new traits. Progress is being made in all these steps.

Numerous progeny from the second backcross of O. officinalis to O. sativa show resistance to all known biotypes of brown planthopper, as well as whitebacked planthopper. A gene for resistance to bacterial blight was transferred from O. longistaminata to IR24. Hybrids have been made with the wild species O. latifolia, O. nivara, and O. rufipogon as possible sources of

genes that would increase the yield potential of cultivated rice. O. perennis and O. rufipogon are being studied as possible new sources of cytoplasmic male sterility which could contribute to the spread of hybrid rice and help reduce the potential vulnerability of hybrid rice production which currently has a narrow genetic base of cytoplasmic male sterility.

Postdoctoral scientists from developing countries will participate in wide hybridization research at IRRI and facilitate transfer of the technology to their home countries.

Developing A Knowledge Base And Rice Biotechnology Tools

An obvious early requirement for the Foundation's program was to support research aimed at developing for rice the various molecular and cellular biology techniques, protocols, and materials which constitute the tools of biotechnology research. In other words, it was necessary to get rice biotechnology research up to a level comparable with biotechnology research on maize, tomato, potato and other crops important in developed countries. Our strategy for this component of the program was to encourage university-based scientists in the developed world who were at the forefront of research on plant molecular and cellular biology to make a significant commitment to research on rice.

This suggestion was not always well received. Many scientists argued that work on model plants was just as important and scientifically much more promising. Others noted that the genetics of rice were so poorly understood that a common nomenclature was still lacking. At some land grant universities, faculty scientists heavily committed to work on other crops, were discouraged by administrators from working on rice, a crop that was not even grown in their state. Moreover, these same leading scientists had various other funding options.

Fortunately, through continued discussions, a sufficient number of these scientists were attracted to the idea of working on a crop plant that was a staple food for many of the world's hungry people, and of being part of a mission-oriented research program that would seek to use their research results for the benefit of those people. An initial group of laboratories joined the program in 1985. In most cases, however, it still took a year, sometimes more, to work out routine procedures, like growing rice plants and rice cell cultures, before real biotechnology research could be undertaken. Significant progress is now being made.

Genetic Maps and Markers. One of the nearer-term uses of molecular biology in plant breeding will be the development of genetic maps and markers based on cloned DNA sequences. While not genetic engineering in the strict sense of the term, use of these tools should enable greater and more efficient exploitation of both the primary gene pool in Oryza sativa and the secondary gene pool in other Oryza species. Markers will enable breeders to know when introgressions of alien chromatin have occurred and whether the genes for a particular trait are present in a progeny plant even if environmental conditions do not permit their expression. Foundation-supported projects in this area are noted below and listed in Table 3.

At Cornell University, Steven Tanksley and colleagues have recently developed and submitted for publication a saturated genetic map of rice chromosomes based on RFLP markers. An RFLP, or restriction-fragment length polymorphism, occurs in a population of rice plants when a distinctive segment of DNA present in all individuals varies slightly in sequence from individual to individual or breeding line to breeding line. By cutting total plant DNA with restriction enzymes, separating the resulting DNA fragments by length using gel electrophoresis, and then probing the gel with a radioactively

labeled cloned segment of DNA complementary in sequence to the DNA at or near the RFLP locus, it is often possible to detect differences from breeding line to breeding line in the length of the fragments containing the RFLP locus. Such differences in fragment length provide an indicator or marker of inheritance of that section of DNA and the genes located on or near it. For breeding purposes, the best markers are those that give different fragment lengths corresponding to the greatest number of different rice lines. In practice, the selection of markers is an empirical process. Many DNA clones are tested as probes and those that detect RFLPs are selected as markers because they work. Further selection and culling is based on the need to fill in gaps on the genetic map.

The Cornell RFLP map of rice now consists of 123 DNA clones obtained from Philippine variety IR36. Based on segregation analysis and use of primary trisomics provided by Gurdev Khush at IRRI, all 123 markers have been assigned to linkage groups and positioned on specific chromosomes. All 12 rice chromosomes are now marked by more than one RFLP marker, and the total number of map units exceeds that of the classical map.

Collaborative research between Cornell and IRRI will continue in order to link the RFLP markers to genes for important qualitative traits, such as resistance to certain pests and pathogens. RFLP markers should be particularly useful in following genes for traits that are not routinely expressed or easily scored, and in pyramiding genes for traits such as pest resistance. In theory, any trait that can be scored can be tagged with RFLP markers. This includes quantitative traits, and Drs. Tanksley and Khush will also attempt to use an array of markers to tag the loci of important quantitative traits, such as drought tolerance.

It should be noted that the RFLP map also benefits molecular biology. It allows any cloned rice gene to be located at its correct position on rice

chromosomes. Furthermore, by providing reference points on the rice genome, RFLP markers may allow the cloning of important rice genes by putting them within reach of molecular techniques such as chromosome walking.

In this regard, Gary Kochert at the University of Georgia is conducting research which complements and will extend the molecular applications of the RFLP work at Cornell. He is conducting a systematic determination of the types of repeated sequence DNA in rice and will place these sequences on the RFLP map. Together these studies will provide considerable insight into the molecular level organization of the rice genome.

As noted above, wide hybridization is a painstaking and time-consuming process. One of the more difficult problems is detecting introgressions of alien chromatin. The small size of rice chromosomes makes this particularly difficult using traditional cytogenetic techniques. This is one of the reasons why wide hybridization for rice improvement had not been significantly exploited. Molecular biology can now help by providing species-specific probes for assessing the extent of introgression of alien chromatin in wide hybridization-derived materials and determining its location on an individual rice chromosome.

With Foundation support, a team of French scientists led by Gerard Second at the OSTROM Institute in Montpellier, and Michel Delseny at the University of Perpignan, are developing genome specific probes within the Oryza genus.

Similarly, Lynne McIntyre, now at the University of Missouri and Rudi Appels at CSIRO in Australia are developing probes for DNA of wild Oryza species based on spacer sequences. Spacer sequences are untranscribed segments of repetitive DNA which flank functional genes. The exact function of spacer sequences is unknown, but Appels and McIntyre have shown in Triticum that many tend to be species-specific and dispersed throughout the genome. Preliminary evidence suggest that this is also true in Oryza.

Perry Gustafson and colleagues at Missouri are seeking to use species-specific DNA probes to visualize alien gene introgressions under scanning electron microscopy. This in situ hybridization technique will allow determination of not only the presence of alien genetic material but also its physical location on the rice chromosomes. Gustafson's group will also explore the potential of using "DNA finger printing" as a technique for studying the genetic makeup and origin of rice plants.

Steve Tanksley's laboratory at Cornell will serve as a repository and distribution center for all rice probes and markers produced as part of the Foundation's program.

Protoplast Techniques. The genetic manipulation of individual cells is an important aspect of plant biotechnology, but it is of modest value unless whole plants can be regenerated from the cells and protoplasts. As indicated in Table 4, the Foundation is making a significant investment in research on development of rice tissue culture and protoplast techniques. The goal is to attain efficient regeneration of whole plants from protoplasts in order to use protoplasts as a vehicle for various genetic manipulations.

In 1986, E. C. Cocking's group at the University of Nottingham in England was successful. They obtained efficient regeneration of plants from protoplasts of the japonica line Taipei 309. This was one of the first reports of plant regeneration from protoplasts of any cereal. The protocol has been been extended to several other japonica lines. In March 1987, a course was held at Nottingham which provided hands-on training in the regeneration protocol for 30 scientists from most of the other laboratories in the RF network. Each of the laboratories listed in Table 4, as well as others, has now reproduced and confirmed the Nottingham results. Research continues at Nottingham and includes use of intra- and inter-specific

protoplast fusion to transfer genes and produce new genetic combinations including cybrids.

Recently, Tom Hodges's group at Purdue has obtained plant regeneration from protoplasts of indica lines IR54 and IR52 and from U.S. variety Calrose 76 which has both indica and japonica lines in its background. High yields of protoplasts are obtained from suspension cultures. When plated, these protoplasts resynthesize cell walls, divide to form small calluses, and, when transferred to regeneration media, form green embyroid-like structures which grow into small plantlets. The plants still need to mature to test fertility but they appear to be growing normally.

The focus of Hirofumi Uchimiya's research at the University of Tsukuba is on use of protoplast regeneration as a vehicle for genetic transformation. Like several other laboratories in the program, he has shown that protoplasts will take up DNA and show transient expression of foreign genes. Dr. Uchimiya has further shown that the DNA is incorporated into the genome of these rice cells, passed on to daughter cells and that genes on the foreign DNA are expressed in the resulting callus. He has been able to regenerate plants from the callus and just recently informed us that he has obtained transgenic rice plants.

Genetic Transformation. The genetic transformation of rice through the introduction of alien or modified genes is one of the principal technological goals of the program. In addition to the protoplast work described above, support is being provided for research on a variety of other techniques, as indicated in Table 5. At the annual meeting of the Foundation's program, held at IRRI this past January, significant progress was reported.

At the University of Ghent, Marc Van Montagu's group has shown that Agrobacterium vectors bind to rice cells and that rice induces the "virulence"

functions of the Ti plasmid that are required for T-DNA transfer. At the University of Leiden, Rob Schilperoort and colleagues obtain numerous roots at a wound site on rice seedlings when the wound is infected with Agrobacterium rhizomes, suggesting that T-DNA transfer has occurred. Both results suggest that Agrobacterium should be able to serve as a vector for gene transfer to rice, but this is yet to be confirmed.

At Stanford University, Virginia Walbot's lab has demonstrated the utility of electroporation for introducing DNA into protoplasts, as have several other labs. Using electroporation, she is also introducing DNA and obtaining foreign gene expression in rice mitochondria. Genetic transformation of mitochondria could be highly useful to breeders since it would enable them to move foreign genes in or out of a line by making a simple sexual cross.

At Cornell University, Ray Wu's laboratory is experimenting with both protoplast uptake of DNA and use of a particle gun to deliver DNA to intact cells. Like Dr. Uchimiya, Dr. Wu recently reported that he has obtained transgenic rice via plant regeneration from transformed protoplasts. Thus, it appears that genetic transformation of rice has been demonstrated in at least two labs, but much refinement of the protoplast technique and further development of other techniques will be required before rice genetic engineering becomes a routine process.

Cloning and Characterizing Rice Genes. The application of genetic engineering to rice genetic improvement will involve the introduction of novel genes and/or the modification of existing rice genes and genetic systems. To engineer a desired genetic change will require understanding of the genes and gene products responsible for important biochemical and physiological functions. Moreover, the engineered genes will need to be expressed properly, in the right organelle, cell type, and tissue; at the right stage of plant

development; and with appropriate response to various environmental stimuli. Identifying genes responsible for important traits and understanding the regulation of their expression in rice is a substantial research task. Listed in Table 6 are relevant research projects currently being supported as part of the Foundation's program.

At Rockefeller University, Nam-Hai Chua and colleagues are studying genes regulated by the plant hormone abscisic acid and by light. The ABA work may lead to a better understanding of mechanisms behind drought tolerance and other traits that appear to be correlated with high levels of ABA synthesis.

At Washington State University, research by Gyn An on nitrate reductase genes and Tom Okita on ADP glucose pyrophosphorylase genes may lead to identification of genetic strategies for improving the efficiency of nitrogen utilization and starch biosynthesis, respectively.

Genes for rice storage proteins are being cloned and characterized by Dr. Okita at Washington State, and by Dr. Tanaka in Kyoto, Japan. The major rice storage proteins, the glutelins, are encoded by at least three gene subfamilies, and the prolamines are encoded by at least two subfamilies. Current research is directed at determining how these genes are regulated at transcription and translation, and the molecular signals responsible for intracellular sorting and packaging of the proteins. The goal is to enhance the nutritional value of rice by increasing total protein and/or improving the digestibility of storage protein bodies. Up to 30 percent of the storage proteins have been shown to be packaged in indigestible forms in rice.

Research led by Alice Cheung at Yale University on genes for carotenoid biosynthesis in rice is also aimed at improving the nutritional value of rice, in this case by making rice grain a new source of pro-vitamin A compounds such as Beta-carotene. The genes for carotenoid synthesis are present in rice, as in all photosynthetic plants, but are expressed in photosynthetic tissue and

not in the endosperm. Through genetic engineering it may be possible to modify the regulation of these genes such that carotenoid biosynthesis occurs in the endosperm of rice, as it does in the case of yellow maize.

One of the likely applications of research on the waxy gene of rice, which is being conducted by Susan Wessler at the University of Georgia, will be the identification of regulatory sequences which provide for high level expression of genes in rice endosperm. Dr. Wessler is also using the waxy gene to study possible indigenous as well as introduced transposable elements in rice. The identification or introduction of a transposable element would provide a powerful tool for tagging and isolating important rice genes.

Diagnostic Tools and the Study of Host-Pathogen Interaction. Bacterial blight and blast are two important diseases of rice worldwide. Cultivar resistance is often short-lived due to changes in the pathogens. As indicated in Table 7, support is being provided for collaborative research with IRRI conducted by Jan Leach at Kansas State University and Sally Leong at the University of Wisconsin on the pathogens causing bacterial blight and blast, respectively. Near-term goals are to 1) study the genetics of these pathogens and their ability to overcome resistance, 2) identify race-specific genes and develop probes for rapid race diagnosis, and 3) better understand the molecular mechanisms controlling pathogenesis. The long-term goal is to use the knowledge generated to produce more durable resistance in rice.

Novel Genes for Rice Improvement. Genetic engineering should make it possible to incorporate essentially any gene from any source into rice. Identifying alien genes which can instill useful traits in rice is an exciting and expanding aspect of the rice biotechnology program and of plant genetic engineering in general. Relevant research projects currently funded by the Foundation are listed in Table 8.

An exciting recent accomplishment in plant genetic engineering was the demonstration by several groups of resistance or tolerance to viral infection in transgenic plants containing viral genes. It should now be possible for many plant virus pathogens to identify candidate viral genes which, when introduced into a plant's genome, can instill this new type of "cross protection." With Foundation support, scientists led by Roger Hull at the John Innes Institute and Roger Beachy at Washington University are collaborating with IRRI to characterize the rice tungro viruses at the molecular level in order to identify candidate genes for resistance to tungro infection. Similar research on other rice viruses will soon be initiated.

It has now also been demonstrated that transgenic plants expressing toxin genes from Bacillus thuringensis insecticides are resistant to insect feeding. There are hundreds of B.t. strains, and each toxin is specific to particular insect pests, with the Lepotoptera species being the most susceptible. The Entomology Department at IRRI has initiated a research program to screen B.t. strains for toxicity to the yellow stem borer and other insect pests of rice. Once toxic strains are identified, they will collaborate with molecular biologists to isolate the genes for transfer to rice.

Two projects are currently being supported aimed at identifying genes from other cereals which may be useful if incorporated into rice. One, led by Gerald Reeck at Kansas State University, seeks to isolate genes from wheat which code for inhibitors of digestive enzymes of both the wheat and rice weevils, whose larva infest stored grain. The goal is to isolate wheat genes which provide a good source of genetic resistance to weevils and transfer them to rice which lacks a good source of resistance to very similar weevils.

The research program at Iowa State University, led by Don Robertson, is aimed at isolating the Y1 gene from maize using transposon tagging. The Y1

locus of maize is thought to code for a regulatory element which allows carotenoid biosynthesis in the endosperm of yellow maize. The goal is to use the Y1 gene, or knowledge concerning its function, to turn on carotenoid biosynthesis in the endosperm of rice.

The Foundation seeks to identify and support additional research aimed at identifying and isolating other novel genes with potential to instill useful traits in rice.

Setting Priorities and Analysing Impacts

Shortly after the International Program on Rice Biotechnology was initiated in 1985, the Foundation began an in-house assessment of the agronomic traits that should receive priority.

The process of setting priorities consisted of first listing all the potential problems that affect rice which could be addressed using biotechnology. For each problem, estimates of importance were made using several criteria. One consideration was the recognition that the benefits of new production technologies go not only to producers through reductions in the cost of producing rice, but also to consumers through reductions in the price of purchased rice. Only producers who adopt a new technology can benefit from it through lower costs, so the particular type of technological innovation is important. For these reasons, biotechnologies that could solve rice problems using little or no capital investment or purchased inputs and which affected a large mass of Third World rice farmers have higher priority than biotechnologies requiring purchased inputs or which could only be adopted by a few farmers.

Another consideration was the expected probability that a production technology to solve each problem could be successfully developed using biotechnology approaches. Stated another way, this criteria is the estimated

length of time it would take to develop a technology to solve each problem. These first two considerations primarily reflect producer's interests.

A third consideration is the quantity of additional rice that would be produced due to a given biotechnology. This primarily reflects consumers' interests. If public policies, such as price supports, which can prevent efficiency gains of technological change from benefiting consumers are not implemented, all consumers gain in proportion to the quantity of rice they consume. From the consumer's viewpoint, the most important aspect of a potential biotechnology is the additional rice it will produce and the resulting price reduction.

Finally, desired traits that have been relatively difficult to introduce using conventional approaches were given higher priority than traits easy to introduce with conventional approaches.

A system of "weights" associated with each problem or technology were provided so that problems affecting the most deserving farmers could be given greater priority and technologies with positive environmental impacts could be given greater priority. The weights are, of course, arbitrary, but they can be used to illustrate the effect different configurations of research priorities are likely to have on consumers and on various categories of producers.

Technologies addressing problems in upland conditions were given "equity weights" of 3, those for deep water and rain-fed lowland conditions, weights of 2; and those for irrigated conditions, weights of 1. It was assumed that $0.2 million would be invested on each problem annually. A social rate of time preference was used to discount the expected weighted costs and benefits of solving each problem from the year of expected solution to the present.

Problems effectively addressed by conventional approaches were assigned "biotechnology potential" scores of 0.5. Problems for which the likely

effectiveness of biotechnology is unknown were given scores of 1. Problems for which conventional approaches have been ineffective even with heavy investments were given scores of 2, as were problems for which there are indications that biotechnology may offer especially effective approaches. An aggregate biotechnology potential score was derived by multiplying the score of conventional approaches by the score for biotechnological approaches.

Table 9 shows four alternative priority listings for the 68 problems included in the analysis ranked according to (1) current value of rice lost to each problem or not produced because of each unmet opportunity for raising potential productivity, (2) current value of output lost, adjusted by equity weights; (3) the equity-weighted value of output lost, discounted to its Net Present Value; (4) the equity-weighted NPV multiplied by the biotechnology potential score for each.

Data in the table are in million dollars, representing increases in productivity that are distributed among classes of producers and consumers in complex patterns. Zero or negative values at the bottom of the first ranking mean that those problems were each estimated to result in increased production valued at less than the discounted NPV of $0.2 million annual research costs. Comparing the ranking between columns gives an idea of the effect that applying the specified weights and biotechnology potential scores has on the rankings.

The results of this analysis indicate that the problems that are widespread and highly yield-limiting in any of the agro-ecologies and for which there is a reasonable chance that biotechnology can provide a solution should be addressed using biotechnology. Among the insect pests, the highest priorities include gall midge, brown planthopper, yellow stemborer, leaf folder, storage insects, striped stemborer and rice hispa. Among the

diseases, the highest priorities include tungro virus, ragged stunt virus, blast (if at the same time a greater degree of upland drought tolerance can be introduced), sheath blight and bacterial blight. Among physical environmental conditions, the highest priorities are submergence tolerance to flash floods, tolerance to waterlogged conditions or chronic stagnant water of 1-3 feet depth, upland drought tolerance, lowland drought at anthesis and cold temperature at the seedling stage. Among the opportunities for raising potential productivity are greater lodging resistance, cytoplasmic male sterility, greater seedling vigor and apomixis. Additional problems that are highly ranked despite the lack of any apparent genetically determined means of control are weeds and birds. Both are especially important in Africa, as well as in other areas where upland rice is important.

The results of this analysis are being used as a general guide for allocating the Rockefeller Foundation's resources addressed to identifying genes for rice improvement (Table 10), but the allocation decisions are tempered by the recognition of the following weaknesses in the analysis:

- The estimates of area and yield lost to each problem for Latin America, the Middle East and North Africa are purely nominal; estimates of experts familiar with those areas must be obtained, as well as better data for the other regions.

- The estimates of success with conventional approaches and the potential for biotechnological solutions need further improvement, and, in fact, the latter will change as researchers discover new ways to use the evolving tools.

- The use of arbitrary weights to reflect environmental and equity considerations leaves much to be desired. At the least, additional experiments on the model to discover the effect of alternative sets of weights will be conducted.

- Alternative approaches to incorporating the equity and environmental dimensions will be sought, as well as practical alternative ways to reflect the fact of diminishing returns to research on individual problems.

It is not always easy to predict the impact of technological change, as illustrated by the "unintended consequences" that have been identified with

the Green Revolution. A part of the rice biotechnology project is directed at generating a more complete understanding of the consequences of technical change. This includes a series of research projects in China, India, Indonesia, Bangladesh, the Philippines, Thailand and Nepal (Table 11) that compare areas where semi-dwarf rice varieties and fertilizer have been widely adopted with areas in similar socioeconomic conditions where the new technology has not spread widely. Emphasis is on the differential impact of the technical change on the factors of production including careful examination of differences in labor migration, wage rate changes, land rental and sales, capital and input use.

Preliminary analysis indicates that in a number of countries labor has migrated from non-adopting to adopting areas, and agricultural wage rates have increased in the same proportion in both adopting and non-adopting areas. Because similar analysis is being conducted in a number of countries, it should be possible to determine the interaction of technological change with socioeconomic conditions. Researchers will be challenged to consider what agronomic traits might be incorporated in rice to have the optimal socioeconomic impact.

Building Capacity in Developing Countries

Initially, a major portion of the Foundation funding committed to the rice biotechnology program was used to support research in advanced laboratories to assure development of the knowledge base and technologies required for the genetic engineering of rice. Progress has been made in gaining that knowledge, and a greater portion of the funds will now be used to facilitate transfer and use of new rice improvement technologies in the developing world and to help build the scientific capacity for further development of rice biotechnology in selected developing countries. This includes support for research and a major commitment to training.

A substantial effort has been and continues to be made by the International Rice Research Institute in the Philippines to develop and maintain a productive network of rice researchers throughout the world. IRRI scientists constitute a key central component of the Foundation's rice biotechnology program by collaborating in both applied and basic research. The work of IRRI helps to assure that research supported by the Foundation is relevant to priority needs of developing countries, and that the results and benefits of the research reach those countries. CIAT plays a similar role in Latin America and IITA in Africa.

Since 1985, the Foundation has been providing support to rice breeding programs at the institutions listed in Table 12 for research on the use and improvement of biotechnologies such as anther culture that can be applied today. With completion of the RFLP map, an important new research technology will soon be available, and plans are currently underway for appropriate workshops and facilities to permit its transfer to the developing world. We are also in the process of identifying several more national rice research institutions which will be invited to join the program.

Last year, the Foundation initiated discussions with officials in China and India concerning opportunities for a significant expansion of Foundation support for rice biotechnology research in those countries. It will include research and training on the knowledge-generating and technology development aspects of the program, as well as applications in rice breeding. We believe that Chinese and Indian scientists will make important contributions to all aspects of the program, and we anticipate that the resulting national rice biotechnology programs will, over time, assume more and more responsibility for future development and refinement of rice biotechnologies.

Arrangements for implementing this new phase of the Foundation's program are proceeding most rapidly in China. The Foundation has signed a Memorandum

of Understanding with the China National Center for Biotechnology Development (CNCBD) of the State Science and Technology Commission for a cooperative program entitled "Biotechnology Development for Rice Improvement." CNCBD, which has national responsibility for structuring, promoting, and supporting biotechnology initiatives in China; does not itself conduct research but rather works through existing Chinese research institutions to accomplish its goals. Last year, a call for proposals from Chinese scientists with competitive evaluation by international professional peer review led to the selection of 23 research proposals at 15 institutions (Table 13) as the initial group participating in the Chinese component of the program. CNCBD and the Foundation share research funding and oversight responsibilities. Participating institutions are eligible to nominate their best young scientists for Rockefeller Foundation predoctoral, postdoctoral and career development fellowships.

In India, officials of the Department of Biotechnology in the Ministry of Science and Technology and of the Indian Council of Agricultural Research have expressed enthusiasm for Foundation assistance in establishing a similar coordinated national program on rice biotechnology. Discussions are currently underway concerning the details.

Management

The scientific design and management of the Foundation's International Program on Rice Biotechnology are currently based on professional input from the following people. Peer review of research proposals and evaluation of progress routinely involve advice from consultants, scientists already receiving support and many other scientists who provide valuable assistance on an ad hoc basis.

Advisory Committee

Ralph Riley, Chairman, Cambridge, U.K.
Lloyd Evans, CSIRO, Australia
Emil Javier, ISNAR, The Netherlands
Fowden Maxwell, Texas A&M, U.S.A.
M. S. Swaminathan, India

Foundation officers

Robert W. Herdt, Director, Agricultural Sciences
John O'Toole, Senior Scientist responsible for South Asia
Lesley Sitch, Associate Cytogeneticist seconded to IRRI
Gary H. Toenniessen, Associate Director

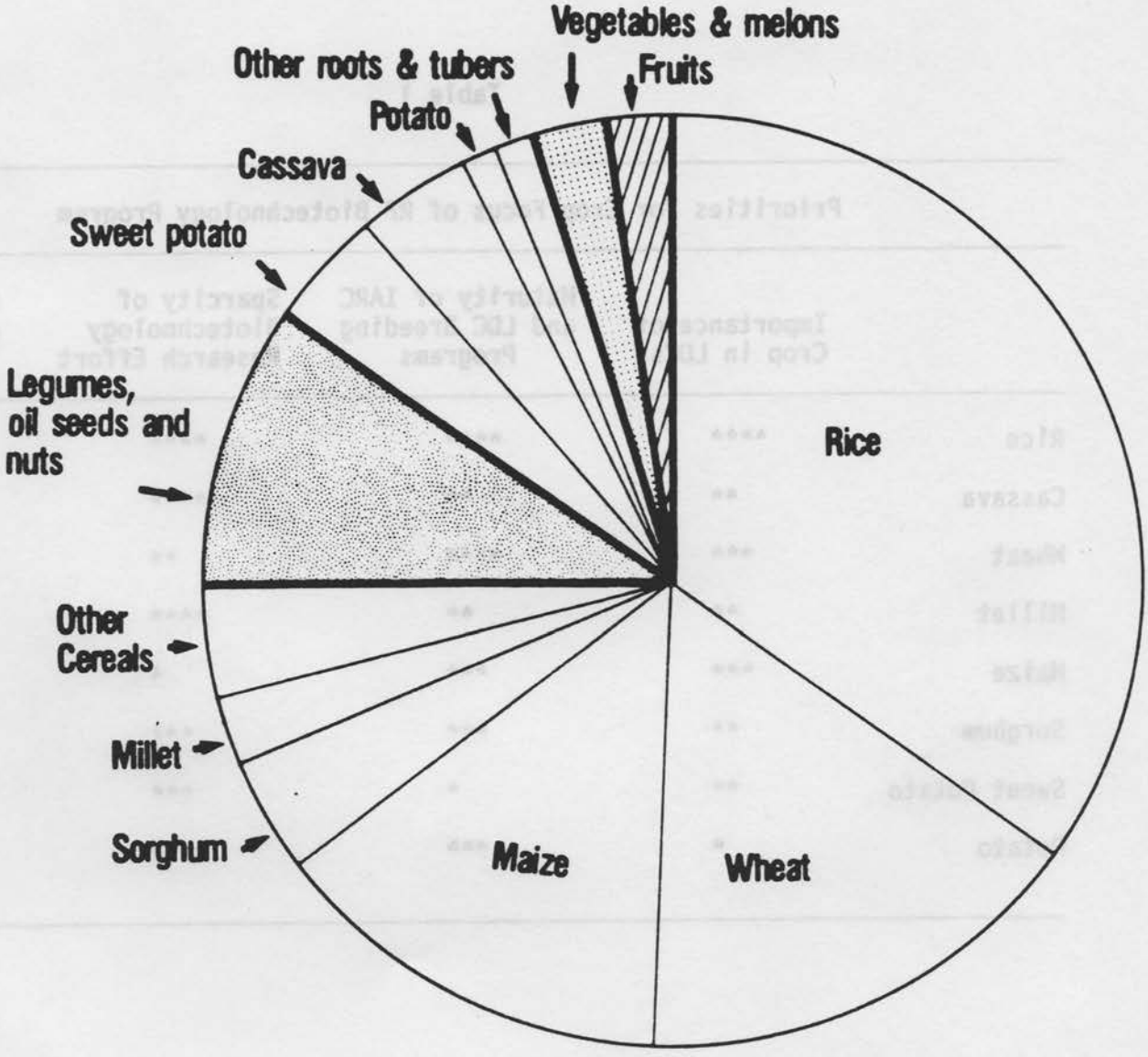
Consultants

Randolph Barker, Cornell University (Impacts and Priorities)
Michael Gale, Cambridge Laboratory, U.K. (Genetic Maps and Markers)
Toshio Murashige, UC Riverside (China and Southeast Asia)

Figure 1

Developing Country Food Crop Production 1982

(edible dry matter)



Sources:
Edible dry matter is calculated from gross production given in the **1982 FAO Production Yearbook** using conversion factors adapted from Wilkes (1982) and Hanson et al (1982). Sugar cane is excluded since it is primarily an export crop.

Table 1

Priorities for Crop Focus of RF Biotechnology Program

	Importance of Crop in LDCs	Maturity of IARC and LDC Breeding Programs	Sparcity of Biotechnology Research Effort	Probability of Near-Term Success
Rice	****	****	****	**
Cassava	**	**	****	***
Wheat	***	****	**	**
Millet	**	**	****	*
Maize	***	***	*	**
Sorghum	**	***	***	*
Sweet Potato	**	*	***	***
Potato	*	***	*	****

**** = relatively high
* = relatively low

Table 2

Agronomically Important Characteristics Identified Among the Wild *Oryza* Species

SPECIES	2n	GENOME	CHARACTERISTICS
O. *nivara*	24	AA	Grassy stunt virus resistance
O. *rufipogon*	24	AA	Source of cytoplasmic male sterility, Tolerance to stagnant flooding
O. *glaberrima*	24	AA	GLH resistance, early vegetative vigour
O. *barthii*	24	AA	Bacterial blight resistance
O. *longistaminata*	24	AA	Floral characteristics for out-crossing
O. *punctata*	24,48	BB,BBCC	BPH, WBPH, GLH resistance
O. *officinalis*	24	CC	BPH, WBPH, GLH resistance
O. *eichingeri*	24	CC	BPH, WBPH, GLH resistance
O. *minuta*	48	BBCC	BPH, WBPH, GLH, blast and bacterial blight resistance
O. *australiensis*	24	EE	BPH resistance, drought tolerance
O. *brachyantha*	24	FF	Rice whorl maggot and stem borer resistance
O. *ridleyi*	48	----	Rice whorl maggot resistance

Source: Progress report prepared by Lesley Sitch and colleagues, IRRI, March 1988.

Table 3

Rice Genetic Maps and Markers	
RFLP Mapping of Rice and Tagging Important Genes	Cornell University, Steven Tanksley IRRI, Gurdev Khush
Analysis of Repeated Sequence DNA	University of Georgia, Gary Kochert
Genome-Specific and Species-Specific Probes	OSTROM Institute, France; Gerard Second University of Perpignan, Michel Delseny
DNA Spacer Sequences as Species Specific Probes	University of Missouri, Lynne McIntyre CSIRO Division of Plant Industry, Australia; Rudi Appels
In situ Hybridization and "DNA Finger Printing"	University of Missouri, Perry Gustafson

Table 4

Research on Development of Rice Protoplast Techniques	
University of Nottingham	E. C. Cocking
Purdue University	Thomas Hodges
Max Planck Institute	Horst Lörz
University of Tsukuba	Hirofumi Uchimiya
IRRI	Javier Zapata

Table 5

Research on Techniques for Genetic Transformation of Rice

Agrobacterium mediated transformation	University of Ghent, Marc Van Montagu
	University of Leiden, Robert Schilperoort
	Washington State University, Gynheung An
Electroporation and other protoplast uptake techniques	Stanford University, Virginia Walbot
	Cornell University, Ray Wu
	Others listed in Table 4.
Electroporation of mitochondria	Stanford University, Virginia Walbot
Particle gun delivery of DNA	Cornell University, Ray Wu
Microinjection of protoplasts, embryoids, and inflorescences	Univ. of California, Davis, Bill Lucas
	Max Planck Institute, Horst Lörz
	University of Leiden, Robert Schilperoort
Liposome fusion	Univ. of California, Davis, Bill Lucas

Table 6

Cloning and Characterizing Rice Genes

ABA-induced genes Rice phytochrome genes Protochlorophyll reductase genes	Rockefeller University, Nam-Hai Chua
Plasmamembrane ATPase genes Protein kinase genes	Salk Institute, Chris Lamb
Genes for carotenoid biosynthesis	Yale University, Alice Cheung
Glutelin genes Prolamine genes ADP glucose pyrophosphorylase genes	Washington State University, Tom Okita
Prolamine genes Glutelin genes	Kyoto Prefectural University, K. Tanaka
Waxy genes	Univ. of Georgia, Susan Wessler
Nitrate reductase genes	Washington State University, Gynheung An
Cold shock genes	Stanford University, Virginia Walbot
Actin genes Alpha-amylase genes	Cornell University, Ray Wu

Table 7

Diagnostic Tools and the Study of Rice-Pathogen Interactions	
Research on *Xanthomonas campestris* pv. *oryzae*, the bacterial blight pathogen	Kansas State University, Jan Leach IRRI, Hei Leung
Research on *Magneportha grisea* (*Pyricularia oryzae*), the blast pathogen	University of Wisconsin, Sally Leong IRRI, Hei Leung

Table 8

Novel Genes for Rice Improvement

Viral genes for resistance to rice tungro virus	John Innes Institute, Roger Hull Washington University, Roger Beachy IRRI, H. Hibino
B.t. toxin genes for resistance to yellow stemborer and other insects	IRRI and collaborators
Maize gene for endosperm carotenoid biosynthesis	Iowa State University, Don Robertson
Wheat genes for inhibitors of rice weevil amylase	Kansas State University, Gerald Reeck
Apomixis in wild Oryza species	Univ. of Calif., Davis Neil Rutger
Pennesitum genes for apomixis	Univ. of Georgia, Wayne Hanna

Table 9
Rank Ordering of Research Problems by Alternative Criteria

Value of Output Foregone (mil $)		Equity Weighted Value of Output Foregone (mil $)		Equity Weighted NPV (mil $)		Equity Weighted NPV BT Potential (mil $)	
Weeds	1699	Upland drought/blast & iron deficiency	8537	Brown planthopper	1944	Tungro virus	6905
Tungro virus	1534	Tungro virus	7907	Tungro virus	1726	Yellow stemborer	3781
Upland drought/blast & iron deficiency	1423	Weeds	7103	Gall midge	1292	Gall midge	2583
Greater lodging res.	1092	Brown planthopper	5361	Greater lodging res.	1228	CMS	2322
Brown planthopper	1059	Gall midge	4216	CMS	1161	Upland drought/blast & iron deficiency	1962
CMS	1032	CMS	3335	Upland drought/blast & iron deficiency	981	Brown planthopper	1944
Submergence	750	Greater lodging res.	3106	Yellow stemborer	945	Submergence	1685
Gall midge	704	Yellow stemborer	2918	Submergence	842	Greater lodging res.	1228
Birds	601	Submergence	2608	Weeds	718	Seedling vigor	1080
Yellow stemborer	516	Drought at anthesis	2156	Seedling vigor	540	Ragged stunt virus	621
Seedling vigor	481	Birds	2050	Birds	412	Drought at anthesis	575
Drought at anthesis	421	Apomixis	1775	Cold at seedling	310	Waterlogging	524
Apomixis	402	Seedling vigor	1753	Drought at anthesis	288	Leaffolder	400
Cold at seedling	278	Bacterial blight	1261	Apomixis	275	Weeds	359
Bacterial blight	246	Cold at seedling	1018	Bacterial blight	274	Sheath blight	336
Waterlogging	235	Rodents	982	Waterlogging	262	Cold at seedling	310
Coastal saline and acid sulphate	230	Waterlogging	885	Coastal saline and acid sulphate	256	Apomixis	275
Rodents	223	Coastal saline and acid sulphate	783	Sheath blight	168	Coastal saline and acid sulphate	256
Crabs	209	Storage insects	770	Storage insects	158	Birds	206
Sheath blight	152	Sheath blight	767	Ragged stunt virus	155	Storage insects	158
Storage insects	143	Ragged stunt virus	703	Rodents	151	Bacterial blight	137
Ragged stunt virus	141	Crabs	682	Crabs	141	Blast	135
Leaffolder	92	Hispa	508	Striped stemborer	132	Striped stemborer	132
Hispa	88	Grain discoloration	495	Whitebacked hopper	121	Whitebacked hopper	121
Grain discoloration	80	Leaffolder	479	Leaffolder	100	Grain discoloration	104
Striped stemborer	73	Striped stemborer	416	Blast	68	Rodents	75
Whitebacked hopper	67	Blast	392	Alkaline soils	63	Drought at seedling	75
Blast	63	Whitebacked hopper	338	Hispa	57	Crabs	71
Drought at seedling	60	Drought at seedling	308	Grain discoloration	52	Alkaline soils	63
Alkaline soils	59	Alkaline soils	221	Drought at seedling	38	Hispa	57
Sheath rot	28	Mealy bug	152	Sheath rot	28	Hoja blanca	29
Mealy bug	26	Sheath rot	138	Grassy stunt virus	26	Sheath rot	28
Grassy stunt virus	26	Grassy stunt virus	129	Leaf scald	21	Grassy stunt virus	26
Leaf scald	21	Grain-sucking bugs	123	Iron deficiency	16	Leaf scald	21
Grain-sucking bugs	21	Leaf scald	112	Mealy bug	15	Grain-sucking bugs	21
Iron deficiency	17	Iron deficiency	83	Iron/mang toxicity	11	Armyworm	17
Iron/mang deficiency	13	Thrips	68	Grain-sucking bugs	10	Iron deficiency	16
Thrips	12	Armyworm	66	Thrips	10	Mealy bug	15
Armyworm	11	Hoja blanca	60	Green leafhopper	9	Iron/mang toxicity	11
Hoja blanca	9	Iron/mang toxicity	51	Armyworm	9	Thrips	10
Green leafhopper	6	Udbatta	34	Hoja blanca	7	Whorl maggot	9
Ufra	6	Ufra	34	Udbatta	3	Green leafhopper	9
Udbatta	6	Green leafhopper	31	Ufra	3	Ufra	3
Ants	4	Ants	27	Whorl maggot	2	Udbatta	3
Aluminum toxicity	3	Diopsis	17	Diopsis	0	Aluminum toxicity	0
Diopsis	3	Aluminum toxicity	12	Aluminum toxicity	0	Diopsis	0
Whorl maggot	2	Whorl maggot	12	Ants	-1	Ants	-1

Table 9 (cont.)
Rank Ordering of Research Problems by Alternative Criteria

Value of Output Foregone (mil $)		Equity Weighted Value of Output Foregone (mil $)		Equity Weighted NPV (mil $)		Equity Weighted NPV BT Potential (mil $)	
Caseworm	1	Root nematode	5	Grain processing	-2	Early maturity	-2
Yellow mottle virus	1	Yellow mottle virus	5	Grain quality	-2	Grain quality	-2
Root nematode	1	Caseworm	5	Caseworm	-2	Grain processing	-2
Black bug	0	Black bug	3	Yellow mottle virus	-2	Black bug	-3
Mole cricket	0	Mole cricket	1	Black bug	-3	Brown spot	-3
High temperature	0	High temperature	0	Seedling maggot	-3	Cold at anthesis	-3
Grain processing	0	Grain processing	0	Peat soils	-3	Vitamin A	-3
Grasshopper	0	Grasshopper	0	Leaf streak	-3	White grubs	-3
Acid sulphate soils	0	Acid soils	0	Cold at anthesis	-3	Leaf streak	-3
White grubs	0	White grubs	0	Vitamin A	-3	Acid soils	-3
Vitamin A	0	Vitamin A	0	Brown spot	-3	Peat soils	-3
Peat soils	0	Peat soils	0	White grubs	-3	Root nematode	-3
Acid soils	0	Seedling maggot	0	Acid soils	-3	Mole cricket	-4
Brown spot	0	Root aphid	0	Early maturity	-3	Root aphid	-4
Naranga	0	Naranga	0	Root nematode	-3	High temperature	-4
Root aphid	0	Acid sulphate soils	0	Mole cricket	-4	Naranga	-4
Seedling maggot	0	Early maturity	0	High temperature	-4	Acid sulphate soils	-4
Cold at anthesis	0	Cold at anthesis	0	Grasshopper	-4	Grasshopper	-4
Grain quality	0	Grain quality	0	Acid sulphate soils	-4	Seedling maggot	-6
Leaf streak	0	Brown spot	0	Naranga	-4	Caseworm	-8
Early maturity	0	Leaf streak	0	Root aphid	-4	Yellow mottle virus	-9

Table 10

Rank Order of Priority Traits for the Rockefeller Foundation's Rice Biotechnology Program

Resistance to tungro virus
Resistance to yellow stemborer
Resistance to gall midge
Cytoplasmic male sterility
Drought tolerance
Resistance to brown planthopper
Submergence tolerance
Greater lodging resistance
Seedling vigor
Resistance to ragged stunt virus
Tolerance to drought at anthesis
Tolerance to waterlogging
Resistance to leaffolder
Resistance to sheath blight
Cold tolerance at seedling
Apomixis
Tolerance of coastal saline/acid sulfate conditions
Resistance to bird damage
Resistance to storage pests
Resistance to bacterial blight
Resistance to blast
Resistance to striped stemborer
Resistance to whitebacked planthopper

Table 11

Setting Priorities and Determining Impact	
Future supply and demand for rice	International Food Policy Research Institute, Howarth Bouis
Priority traits for rice biotechnology	Rockefeller Foundation, Robert W. Herdt
Technological change in Nepal's hill agriculture	Cornell University and IRRI, Krishna Belbase
Differential impact of new rice technology in Thailand	University of Khon Kaen and Kasetsart University, Sarun Wattanutchariya
Differential impact of new rice technology in India	Indian Statistical Institute, Sudhin K. Mukhopadhyay
Differential impact of new rice technology in Bangladesh	Bangladesh Rice Research Institute, Bangladesh Institute of Development Studies; Mahabub Hossain
Differential impact of new rice technology in Indonesia	Center for Agro-Economic Research, Faisal Kasryno Gadjah Mada University, Tumari Jatileksono
Differential impact of new rice technology in China	Rural Development Research Center Justin Yifu Lin
Methodology for the study of the differential impact of new rice technology	IRRI, Cristina David, Keijiro Otsuka and Yujiro Hayami

Table 12

Use of New Techniques for Rice Genetic Improvement

China National Rice Research Institute, Hangzhou
Korean Rural Development Administration, Research Bureau
Shanghai Academy of Agricultural Sciences
International Rice Research Institute, Philippines
International Center for Tropical Agriculture (CIAT), Colombia

Table 13

BIOTECHNOLOGY DEVELOPMENT FOR RICE IMPROVEMENT
A Cooperative Program
of the
China National Center for Biotechnology Development
and the
Rockefeller Foundation

List of Participating Institutions and Scientists

Institute of Genetics, Academia Sinica, Beijing
Zhu Li-huang and Li Liang-cai, Genetic Maps and Markers
Hu Han and Shao Qi-quan, Wide Hybridization
Li Xiang-hui, Protoplasts
Li Liang-cai, Gene Transfer
Bin Wang, Mitochondrial DNA

Institute of Microbiology, Academia Sinica, Beijing
Fong Rong-xiang and Mang Ke-qiang, Yellow Stunt Virus
Tien Po, Probes for Rice Viruses

Shanghai Institute of Plant Physiology, Academia Sinica
Hsia Chen-au and Wang Fu-de, Protoplasts
Hong Meng-min, Waxy Gene

Fudan University, Institute of Genetics, Shanghai
Zhou Gao-zhi, Protoplasts
Tan Jia-zhen and Ge Kou-lin, Gene Transfer

Zhongshan University, Guangzhou
Liu Liong-shi, Wild Compatibility Genes
Li Bao-jian, Gene Transfer

Beijing University, Biology Department, National Open Lab for Plant Genetic Engineering
Chen Zhang-liang, Rice Viruses

Shanghai Academy of Agricultural Sciences, Crop Breeding and Cultivation Institute
Zhang Zhen-hua and others, Rice Anther Culture

Table 13 contd.

China National Rice Research Institute, Hangzhou
Zhao Cheng-zhang, Xiong Zhen-min, Zheng Kang-le, Tissue Culture and Markers

Hunan Academy of Agricultural Sciences, Hybrid Rice Research Institute, Changsa
Yuan Long-ping, Hybrid Rice

Chinese Academy of Agricultural Sciences, Biotechnology Research Center, Beijing
Fan Yun-liu, Nutritional Improvement of Rice

Chinese Academy of Agricultural Sciences, Institute of Crop Breeding and Cultivation, Beijing
Li Mei-fang, Qin Rui-zhen, Tissue Culture Techniques

South China Agricultural University, Guangzhou
Wu Kun-sheng, Genetic Markers

Wuhan University, Department of Biology
Yi Qing-ming, Markers for Photosensitive Male Sterility

Hubei University, Biology Department, Wuhan
Luo Zhong-xan, Characterizing Rice Genes

South China Institute of Botany, Academia Sinica, Guangzhou
Liang Cheng-ye, Ling Ding-hou and others, Hybrid Rice